III. *Microscopic and Systematic Study of Madreporarian Types of Corals.*

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PART I.—MICROSCOPIC STRUCTURE OF THE SKELETAL PARTS.

INTRODUCTORY.

Historical Account of the Literature.

The following account brings forward the most important contributions, zoological and palæontological, to the study of the *origin*, the *microscopic structure*, and *morphology* of the Madreporarian skeleton. The earlier writings in the first half of this century are neglected, since exhaustive accounts of those have been given by Bronn, and by Edwards and Haime.

Dana's* brilliant researches on recent corals and their habits, introduced many

* Dana, "Exploring Expedition of Captain Wilkes." "Zoophytes," 1846, Atlas, 1849, Philadelphia.

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fundamental changes in the systematic arrangement of corals. The large folio atlas published by him in connection with the WILKES' Exploring Expedition in 1849, is in constant use in every large School of Zoology and Palæontology, and has made known the beauty and variety of the existing Madreporarian world to a wide circle of naturalists.

Very soon this work was followed by another, equally great, which embraced fossil as well as recent corals. The publication of the "Natural History of Corals," by EDWARDS and HAIME* in 1857, marks an era in the scientific literature of the Coelenterates. Their work treated Alcyonarians and Zoantharians, the class Zoantharia E.H. including Actinian, Antipatharian, and Madreporarian corals. The classification of the Madreporaria, which EDWARDS and HAIME carried out, still holds its place in all text books. Slight departures from it have been occasionally suggested in special works, but only such as affected a small group of genera. The broad systematic features are still accepted in the sense laid down by EDWARDS and HAIME.

During the latter half of the century, our zoological knowledge of the Madreporaria has made enormous strides of progress, largely as a result of the material brought by the "Challenger" Expedition.

A question which has common interest both for zoologist and palæontologist is the relation of the soft parts of the polyp to the hard calcareous or horny skeleton produced in most corals. It has been found that the mode of development of the skeleton may be very different in the different sub-classes of Coelenterates, and that within each sub-class the greatest variety of form may obtain, both with regard to the elemental parts of the skeleton and their particular manner of combination to build up a connected framework.

The "Sclerite" and the "Spicule" of EDWARDS *and* HAIME.

At the time when EDWARDS and HAIME wrote, comparatively little work had been done in this direction. Those authors were familiar with the spicules of Alcyonarians, and assumed that the compacter Madreporarian skeleton was made up of similar structural elements. They recognized two layers of tissue in the body-wall of the polyp—a "dermic" and an "epidermic"—and said that the "*dermic*" tissue gave rise to "*sclerodermites*" or "*sclerenchymatous nodules*"; that those remained free in Alcyonarians, but united together so as to form cribriform or compact lamellæ and trabeculæ, making up various skeletal parts of Madreporaria (septa, wall, costæ, synapticulæ, columella). The *epidermic* tissue laid down thin, *imperforate laminæ*,

* MILNE EDWARDS and J. HAIME, "Histoire Naturelle des Coralliaires," Paris, 1857. A series of separate publications preceded this work, of which the most generally known are "Recherches sur la Structure et la Classification des Polypiers," Paris, 1848–9, and "A Monograph of the British Fossil Corals," London, 1850–55.

forming the "sclerobasic axis" in Alcyonarians, the basal tabulæ and dissepiments, and the epitheca in Madreporaria. In a few cases individual sclerodermites could also be observed in these epidermic laminæ ex. Melithæa ('Coralliaires,' vol. 1, p. 33).

The sclerenchymatous nodules laid down by the dermic tissue were said to be of two kinds :—

(1) Fusiform-shaped, partly horny, partly calcareous in composition.

(2) Irregular, six-sided bodies, in which the calcareous element dominated.

Both varieties might occur in the skeleton of the same polyp; indeed, the figures illustrative of both are nodules belonging to Alcyonium digitatum (*loc. cit.*, vol. 1, p. 31, Atlas, Plate A1, figs. 1*d*, 3*c*, 3*d*).

In the descriptive text accompanying the figures the term "*spicule*" is used for the fusiform-shaped nodules, and "*sclerite*" for the irregular, more calcareous nodules. We find, however, that the distinction thus made between "spicule" and "sclerite" soon became invalid. KÖLLIKER used both terms synonymously in his 'Icones,' published 1864, applying them exclusively to the skeletal bodies, lying often closely packed, but always individually distinct, in the *dermal tissue of Alcyonarians.*

EDWARDS' *and* HAIME'S *view, as enunciated in* 1857, *that the Madreporarian skeleton was built up of Sclerites, in part or wholly coalesced.*

The "Complete Sclerenchyma" was the term used by EDWARDS and HAIME for the Madreporarian skeleton, and was defined by them as the

"result of the successive and continuous development of the calcareous nodules ("sclerites"), which, instead of being produced in a miliary manner throughout the whole surface of the dermal tissue at once, invade it at one part and another, and unite together as solid lamellæ, the whole of which form the fundamental and essential part of the corallum, properly so-called. . . . In the least perfect form of this sclerodermic tissue each nodule produces small branches, at whose extremity other nodules are developed; this takes place in such a way as to form linear series, which have the appearance of small knotty stems constricted from time to time, and to those we have given the name of "Poutrelles."* In a slightly more perfect form of the scleroderm these nodules produce lateral branches as well, which completely coalesce with those of neighbouring nodular series (poutrelles), and transform a row of trabecula into a kind of cribriform lamella. Usually the sclerodermites approach each other more closely; their branches multiply considerably; soon there remain no more spaces between them, and a continuous and compact lamella results from their union" (*loc. cit.*, vol. 1, p. 32).

The Madreporarian *septum* was said by the same authors (*loc. cit.*, vol. 1, p. 57) to "show all the modifications described above in speaking generally of sclerenchymatous lamellæ." Farther, they said the septum was composed, in the Poritidæ and all trabeculate coral types, of a *single lamella* or leaf ("feuillet"), but when the septum was compact one could often distinguish "*two parallel lamellæ* or leaves, united

* "Poutrelles"="Trabekel" of PRATZ. The nomenclature of EDWARDS and HAIME was retained by PRATZ (see below, 'The Family Fungidæ,' pp. 185–7).

either directly or by an intermediate tissue of a deeper shade," *e.g.*, Desmophyllum. In other cases an empty "space could be seen between the two leaves, *e.g.*, Mussa fistulosa." The "intermediate tissue" in the middle of a compact septum corresponds with what was called the "dark line" of the septum by subsequent authors.

The conception of EDWARDS and HAIME was altogether more a general scheme on which they might base their classification. In histological details it has had to undergo much correction. But it showed a thorough grasp of the leading structural features, and had the great merit of giving prominence to a unit of structure, viz., the sclerenchymatous nodule. To this "unit" they sought to trace back all the varieties and complexities shown by the skeleton in different Madreporarian families. Nothing could be more concise than the description quoted above of the building-up of the Madreporarian sclerenchyma. It is like the bold sketch of a master artist thrown upon the canvas, into which the 'prentice hand might later work the details.

At the same time, criticized scientifically, the whole scheme was ventured upon an assumption, since the individual "sclerenchymatous nodule," to which reference was made, had only been proved to exist in Alcyonarians Its presence in Madreporaria had been argued from analogy.

The surface of the free Alcyonarian spicule may be smooth, granulate, spiny; the same varieties may be observed in the parts of the "complete sclerenchyma" in Madreporaria. Again, the regularity of the rows of granulations on the surfaces of the septa in many Madreporarian genera, as well as the regularity of the "branch-like" union between trabeculæ in other genera, was sufficient to suggest that "nodules" were placed in vertical succession upon one another. The irregular "sclerite" might afford many points of contact with neighbouring sclerites, hence the wholly calcareous "scleritic" form of nodule, instead of the "spicular," was regarded by EDWARDS and HAIME as the unit of structure in Madreporaria. Its origin was also referred to the dermal tissue, in which it was known that the free "spicules" and "sclerites" were developed in Alcyonaria.

Correction of Special Points in EDWARDS *and* HAIME'S *Statement of Coral Structure was made by* LACAZE DUTHIERS *and* KÖLLIKER *in* 1864.

The first correction of the general laws laid down by EDWARDS and HAIME was made by LACAZE DUTHIERS,* when he proved that the hard axis of the red coral originated in the mesoderm (= dermic tissue, E.H), and was not an epidermal structure; farther, the axis originated as free spicules, and not in laminate form. The spicules became subsequently coalescent by means of farther calcareous deposit. It was then thought that the sclerobasic axes of other Alcyonarians were formed in the same way, until, some twenty years later, VON KOCH† proved that EDWARDS and

* LACAZE DUTHIERS, "Histoire Naturelle du Corail," &c., Paris, 1864.

† G. v. KOCH, "Die morphologische Bedeutung des Korallenskelets," 'Biolog. Centralblatt,' Bd. 2, Nr. 19, January, 1883.

HAIME had been partly right. In the Gorgonia polyp, and possibly in certain other Alcyonarians, the sclerobase was of epidermic origin.

In 1864–65 appeared KÖLLIKER's* great work on the fine tissues and skeletal structures of Protozoa and Cœlenterates. The second part was devoted to Hydrozoa and Actinozoa, but, among the latter, chiefly to Alcyonaria. Only one short reference is made to the Madreporarian corals (*loc. cit.*, Part 2, pp. 168, 169, fig. A). The figure is a transverse section through a part of the skeleton of an "Astræa," showing groups of fibres radiating outward from points not exactly central in position. KÖLLIKER writes in the context :—

"These calcareous fibres are grouped in such a way that they produce sometimes star-shaped figures (fig. A), sometimes feather-like forms . . . Farther, one observes in these calcareous fibres lines of layering (Schichtungslinien), which, in individual cases, occur so regularly at intervals of 0·002 to 0·004 millim. that they remind one of the transversely-striped fibres of the enamel of vertebrate teeth. In many species, however, these lines are only very indistinctly marked, or cannot be recognized."

KÖLLIKER was of opinion that the skeleton was formed in the main by a calcification of the "*inner* cœnenchyma" of the polyp, but that *no free calcareous bodies were formed in the process of calcification*;

"for, in the first place, the soft cœnenchyma of the Madreporaria, so far as has been already investigated, possesses no calcareous bodies; and, secondly, even the thinnest lamellæ of a corallum show nowhere a trace of such bodies."

Early Views on Septal Symmetry in Corals.

Meantime several of the first palæontologists of the day were occupied with Palæozoic corals belonging to the subdivisions *Madreporaria rugosa*, E.H., and *M. tabulata*, E.H. The names of LINDSTRÖM, NICHOLSON, KUNTH, suffice to recall the nature of the work which had begun in the decade 1860–70. As I have limited my attention in the present paper to the *M. rugosa* among Palæozoic corals, I shall indicate here only the main contributions which concern that group.

The characteristic feature of Palæozoic, in comparison with Mesozoic and Cainozoic Madreporaria is not the possession of the tabulate base in the central area of most genera, neither is it the thick, rugose epitheca or theca commonly present. It is the pinnate mode of development of the septa in relation to THREE particular septa and the resulting bilateral symmetry of the calyx. KUNTH† first proved the laws which governed the insertion of new septa in most Palæozoic corals, the appearance of main and counter septa in one diameter of the calyx, and of two alar septa in the cross diameter; the appearance of additional "pairs" of septa on either side of the main septum and on the remote side of each of the alar septa. The new septa are

* A. KÖLLIKER, 'Icones Histiologicæ,' Leipzig, 1864–65.

† KUNTH, "Beiträge zur Kenntniss fossiler Korallen," 'Zeitsch. d. D. Geol. Ges.,' 1869–70.

coalescent at their point of origin always with the main septum or with one or other of the alar septa, and this gives externally a characteristic branching appearance of the septa from the epitheca inwards and upwards towards the centre of the calyx.

Although this feature is generally shown throughout all stages of growth in Palæozoic Madreporaria, there are frequent enough examples of Palæozoic species in which the septa appear "pinnately" only in the earlier stages of development, and afterwards are inserted irregularly or with more or less radial symmetry.

KUNTH'S observations had a great influence on the thought of the time, and his results seemed conclusive that tetrameral or bilateral symmetry of the septa characterized the majority of Palæozoic Madreporarian corals, while radial symmetry was accepted as the almost invariable rule in Mesozoic and Cainozoic corals. According to EDWARDS and HAIME, the radial symmetry was founded on a cyclical number of six primary septa, simultaneously developed, and new septa were inserted in definite "orders" of subsequent cycles, the full number of septa being always a multiple of six. HAECKEL proposed the recognition of two main subdivisions of Madreporaria, (i.) *M. tetracoralla*, corresponding to "*M. rugosa*," E.H., Palæozoic corals with tetrameral symmetry; (ii.) *M. hexacoralla*, the Mesozoic and Cainozoic corals with cyclical symmetry of septa, including *M. aporosa* and *M. perforata*, E.H. According to those views, there seemed an immeasurable gap in the evolutionary history of Madreporaria between Palæozoic and Mesozoic corals.

The Publication of LACAZE DUTHIER'S "*Development of Corals*" *in* 1872.

LACAZE DUTHIERS* brought forward in 1872 more exact observations on the developmental stages of corals, and his results deviated in very important features from the laws laid down by EDWARDS and HAIME. His researches included the development both of Actinians and of Madreporaria, and the main results are familiar in every text-book. In the case of Astroides, an Eupsammid common in the Mediterranean, he proved that the septa did not begin to be formed until twelve primary mesenteries had been developed. These mesenteries appeared in pairs, two pairs always following in rapid succession; in other words, developmental pauses took place after the appearance of four mesenteries, then after eight, and after twelve. At the last pause, the twelve mesenteries became equal in growth, and only then the septal invaginations of the basal body-wall took place as a cycle of twelve radial pouches alternating in position with the mesenteries. The insertion of further septa and mesenteries is comparatively of less importance than those of the primary cycles.

From LACAZE DUTHIER'S account of development it was made clear that, at any

* H. de LACAZE DUTHIERS, "Développement du Coralliaire," Prem. Mém., sur les Actiniaires sans polypier. ('Arch. de Zool. Expér.,' 1872, vol. 1, pp. 289–396). Sec. Mém., sur les Actiniaires à polypier. ('Arch. de Zool. Expér.,' vol. 2, pp. 269–348).

rate in *Astroides*, the radial symmetry was not based on the presence of a primary cycle of six radial invaginations, as EDWARDS and HAIME had supposed. On the contrary, the paired insertion of mesenteries followed precisely the same relative order of insertion as that which governed the tetrameral symmetry of the Palæozoic corals.

Nearly ten years later, KOCH* proved, in *Caryophyllia* and other aporose corals, that the increase in the cycles of septa did not take place according to EDWARDS and HAIME'S laws for *Hexacoralla*.

The "Primary" Median Lamella, and "Stereoplasmic" Lateral Layers distinguished in the Septa of Madreporaria.

A nearer relationship of *Tetracoralla* and *Hexacoralla* being little thought of at the time of KUNTH'S work, the interest of palæontologists centred in the working-up of special faunas characteristic of certain geological ages and provinces. About the same time valuable contributions were being made to Palæozoic Madreporarian literature by NICHOLSON, LINDSTRÖM, DYBOWSKI, SCHLÜTER, and attention came to be more and more directed to the preparation of thin microscopic sections.

The broad septum of Zaphrentoids and Cyathophylloids, as well as the free septal spines of Cystiphylloids, were repeatedly figured. (I have here adopted the recent nomenclature of Palæozoic groups given by NICHOLSON, 'Manual of Palæontology,' I.). The "two-leaved" septum described by EDWARDS and HAIME was the general appearance presented by sections of Palæozoic Madreporarian septa, and in nearly all cases a median broader or narrower area represented the "intermediate tissue of a deeper shade" described by the same authors. The origin of the intermediate tissue was not understood; the great variety in its appearance, and its small thickness relatively to the rest of the septum, was perhaps its most striking feature.

LINDSTRÖM regarded it as a *primary* median septal leaf of independent structure, while the lateral layers on both sides of it were called by him "*stereoplasm*," or *secondary* calcareous deposit of lamellar nature.† DYBOWSKI, on the other hand, distinguished only two leaves or laminæ in the septum.

A suggestive paper, written by VON KOCH‡ in 1882, showed a certain return to the fundamental doctrine of EDWARDS and HAIME, that the skeletal structures were composed of a number of individual units. But the nomenclature had altered;

* G. v. KOCH, "Mittheilungen über das Kalkskelet der Madreporaria. I. Das Vermehrungsgesetz der Septen." 'Morph. Jahrb.,' Bd. VIII., 1881.

† LINDSTRÖM, "Contributions to the Actinology of the Atlantic Ocean." 'Kon. Svenska. Vet. Akad. Handl.,' Bd. XIV., No. 6, p. 17, 1877.

‡ v. KOCH, "Mitt. über die Structur von *Pholidophyllum Loveni*, E. H., u. *Cyathophyllum*, sp.? aus Konieprus." 'Palæontogr.,' vol. 28, p. 216, 1882.

instead of "sclerites" and "sclerenchymatous nodules," we hear only of septal "spines," such as existed in numerous Palæozoic corals. And this was only natural, since the septal "spine" had been made familiar in a number of figures, whereas the "nodule" remained unproved as an individual structure. KOCH instituted a direct comparison between the microscopic structure of the septal spines in a Palæozoic genus and that of the "two-leaved" compact septa, both in *Cyathophyllum*, a Palæozoic genus, and in *Caryophyllia*, a recent Turbinolid. He recognized a distinct area of indefinite structure in the middle both of "spine" and of "septum," and outside it a lamellar "stereoplasm" of fibrous *structure*. From that time forward the view of LINDSTRÖM was adopted with more security, and was generalized for the structure of the septa in Madreporaria of all ages.

The brilliancy of the decade 1872–82 *in Zoological Research.*

A strong stimulus had been given to the zoological research of Actinozoa by the embryological works of LACAZE DUTHIERS. We may, in fact, regard the decade 1872–82 as a high tide in the zoological literature of corals. The late Professor MOSELEY* was then producing his brilliant series of papers touching various classes of Cœlenterata. His general reports of "Challenger" material appeared in No. II. of the "Challenger" Expedition volumes, and several papers on special genera appeared in different magazines. Amongst the most interesting of his researches were those on *dimorphism* in the zooids of the Alcyonarian Heliopora cærulæa;† and again the dimorphism in the families Milleporidæ and Stylasteridæ.† He proved that both those groups, which had been formerly classed with Actinozoa, were in reality Hydrozoa.

The researches of the HERTWIGS‡ gave insight into the fine histology of the musculature, the nerve-system, and the generative organs of the Actinians. A couple of years later, in 1882, Professor R. HERTWIG§ published his 'Monograph of the Actinians,' belonging to the "Challenger" Expedition material. The "Report of the Reef Corals" in connection with the same expedition was executed by Mr. QUELCH.||

KLUNZINGER'S¶ three volumes of the 'Corals of the Red Sea,' appeared in the years 1877–80, accompanied by a series of photographic plates. This author suggested

* MOSELEY, "The Structure and Relations of the Alcyonarian Heliopora Cærulæa," &c., 'Phil. Trans. Roy. Soc.,' 1876.

† "Structure of a Species of Millepora occurring at Tahiti," 'Ann. Nat. Hist.,' 1876. "Preliminary Note on the Structure of the Stylasteridæ," 'Ann. Nat. Hist.,' 1877.

‡ HERTWIG, O. & R., "Die Actinien anat.-histol. untersucht," 'Jen. Zeits.,' vol. 14.

§ HERTWIG, R., "Die Actinien der 'Challenger' Expedition." Jena, 1882.

|| QUELCH, "Challengei Reports," vol. xvi., 1886. This report is notable for the description of the curious Recent coral, *Moseleya*, as well as for the reasons given by Mr. QUELCH in favour of the abandonment of the *Rugosa* (*Tetracoralla*) as a separate sub-order of Madreporaria.

¶ C. B. KLUNZINGER, "Die Korallthiere des Rothen Meeres." Berlin, 1877–80. "Wachsthum der Korallen," 'Würtemb. Jahreshefte,' 1880; Jahrg. 36, p. 62.

many changes in the systematic arrangement of Madreporarian families and sub-families made by EDWARDS and HAIME; in many cases agreeing with VERRILL in preference. A separate paper, written by KLUNZINGER, in 1880, gathered together the special data concerning modes of budding and the increase of Madreporarian polyps.

1881–82.—*The Discovery of the* Calicoblastic, *or Lime-forming Cells, and of the* Ectodermal *origin of the Madreporarian Skeleton.*

Two authors, v. HEIDER* and v. KOCH† may be said to have almost simultaneously discovered the existence of a skeletal-forming layer of cells in the Madreporarian polyp. The same year saw also a purely palæontological work devoted entirely to the discussion of microscopic details of the skeleton and applying those with success to the systematic grouping of genera. The series of microscopic researches published by PRATZ‡ are unique in their kind (*vide* p. 20). Careful study of this palæontological work indicates a certain connection between the observations made by PRATZ on Jurassic and Cretaceous genera and those made on recent corals by v. KOCH and v. HEIDER. But, from the fact that each author had already concluded his own work before seeing the other's, written contemporaneously, the zoological and the palæontological interests have remained, so to speak, estranged and have mutually missed all the significance which they might have had. Moreover, v. KOCH and v. HEIDER did not agree in the details they gave of the skeletal-forming cell, and the matter has been somewhat in abeyance. The zoologists who have since published papers support v. KOCH; hitherto no palæontologist has taken up the question. As I find it to be one of considerable importance, I shall enter fully into the points of agreement and difference between KOCH and HEIDER.

HEIDER proved in the paper quoted, the general identity in the anatomy and histology of Cladocora with facts previously determined for Actinians. He writes, "The brothers HERTWIG came to a conclusion (based on their investigations of the mesenteries in Actinians) with which, so far as my research has gone, I can only agree. It is, in the main, that Actinians and Corals (Madreporarian) are still more closely allied with one another than they have as yet been regarded" (*loc. cit.*, p. 28). He then describes for the first time the lime-forming cells, to which he gave the name "*calicoblast.*" He found that the cell-nucleus was active during the earlier changes of the cell-contents from organic into inorganic conditions, but gradually shrank as the cell became filled with the granular or fibrous deposit. From that he concluded that the *cell ceased its organic life when the change had completed and became*

* A. v. HEIDER, "Die Gattung Cladocora, Ehrenb.," 'Sitzungsber. der K. Akad. der Wiss. Wien,' December, 1881.

† G. v. KOCH, "Über die Entwicklung des Kalkskeletes von Asteroides calycularis u. dessen Morphologische Bedeutung," 'Mitth. Zool. St. Neapel.,' 1882, p. 284.

‡ E. PRATZ, 'Ueber die verwandtschaftlichen Beziehungen einiger Korallengattungen mit hauptsächlicher Berücksichtigung ihrer Septalstructur,' "Palæontographica," vol. 29.

practically a small body of calcareous fibres. These calicoblast cells, were in HEIDER'S opinion, of *mesodermal* origin ; he thought that the ectoderm apparent on the basal embryonic disc disappeared before maturity.

HEIDER'S paper was published in December, 1881, and in the same month KOCH had finished his manuscript, "On the Development of *Astroides calycularis*," quoted above. Therein he describes how the *ectodermal* layer of cells on the basal embryonic disc of *Astroides* continues in the mature polyp and separates out the calcareous deposit of the various skeletal parts. Unlike HEIDER, KOCH had observed no calcareous particles or fibres within the cells of this ectodermal layer, and he therefore looked upon them as secreting cells, *actively separating out calcareous matter, and at the same time continuing their own organic existence.*

HEIDER had not pursued his research to the skeleton, in order to see what became of the calcified cells which he had seen. KOCH, on the other hand, had in previous papers already given special attention to the mature skeleton. He now showed, by means of transverse sections, that the embryonic skeletal deposit was laid down in the form of individual calcareous "spheroids" or "ellipsoids, built up of concentrically-layered, always rhombic crystals." These grouped together here and there, and gave rise to an embryonic skeletal disc. Then the polypal wall pouched itself upwards in a ring of radial folds, and the ectoderm on both sides of the pouches deposited similar "spheroids" or "ellipsoids." In this way a calcareous, radially-placed structure took origin within each of the invaginated pouches, and these radial structures were the septa of the young *Astroides* polyp. KOCH, however, did not follow out the mode of combination of these "spheroids" or "ellipsoids" to form the fully-developed septum. Yet the transverse sections of the septum of *Caryophyllia* which he published in the same year (*vide ante*, p. 89), give no sign whatever of being composed of individual spheroids or ellipsoids, but show fibres arranged parallel with one another and radiating outwards on both sides of a median darker plane in the septum. These embryonic "spheroids" of *Astroides* gave therefore no basis for general statements with regard to the Madreporarian skeleton.

An important feature of the embryonic spheroid may be at once noted. KOCH writes that near the periphery and towards the centre of the basal disc, the spheroids were more or less free from one another, and seemed then to attain what might be regarded as their normal development. "At such places," he says, "the most of them showed very plainly a dark streak dividing them into two halves."

HEIDER took the opportunity, in a later paper,* of comparing KOCH'S description of the lime-secreting cell with his own. After an examination of *Astroides* and *Dendrophyllia*, HEIDER so far modified his earlier opinion as to say that the calicoblast cells might be ectodermal in origin, and wander towards the edge of the mesoderm, forming there one or more cell-layers. He still maintained the complete

* A. R. v. HEIDER, 'Arbeiten aus dem Zoolog. Ins. zu Graz,' vol. 1, No. 3, "*Korallenstudien.*" Leipzig, 1886.

conversion of the calicoblast cell into inorganic deposit, and gave figures with fibre and granule-containing cells. The crystalline "spheroids" and "ellipsoids" of KOCH might possibly, he suggested, be formed by the combination of a number of the changed calicoblasts.

Although HEIDER had made thin transverse microscopic sections of *Cladoeora*, he did not advance our knowledge of the fine structure of the mature skeleton beyond the stage which KÖLLIKER had reached. In fact, HEIDER frankly admits in his paper, in 1886, that he is at a loss to account for the difference between the simple deposit observed in the embryonic skeletal disc, and the various complex structures of the mature skeleton. He surmises "that the individual skeletal parts in the Madreporaria are formed in a manner analogous with the skeleton of Alcyonarians," but that in the former the calicoblasts produce a connected calcareous layer at the outer limit of the mesoderm, "whereas the analogous cells in the Alcyonarian polyp form, as is well known, calcareous spicules, which remain isolated throughout the whole life of the polyp" (*loc. cit.*, p. 180).

This surmise of HEIDER'S shows that he stood much in the same position with regard to the skeleton of Alcyonarians and Madreporarians, as EDWARDS and HAIME had done thirty years before. Instead of the "sclerenchymatous nodule" (equiv. sclerodermite, sclerite, spicule) which the authors of "Coralliaires" had pronounced to be common to both groups, the term "spicule" was now limited in its application to the Alcyonaria, while the "spheroid" or "ellipsoid" of KÖLLIKER and KOCH depicted the unit-form in certain Madreporaria, and the "septal spine" in others. Too little was known of the "spheroid" to venture upon either its closer identification with, or differentiation from, the "spicule," yet there was always an inclination towards identifying.

Short Review of KOCH'S *Works on the Madreporarian Skeleton.*

VON KOCH has done more than any other author in investigating the details of microscopic structure in different groups of Madreporaria.

In 1877 he published a short account of *Stylophora digitata*, PALLAS.* The habit of the coral is branching; the calices are very small, about 1 millim. diameter, canaliculate coenenchyma extending between the calices and supporting the coenosarcal continuations of the polypal body wall on slight echinulations.

I may state here that the echinulations on the coenenchyme are, according to my results on microscopic structure, the exact homologue of "granulations" on the surfaces of septa, &c.

KOCH described the skeleton in its minute structure as "built up of more or less regular ellipsoids, often extended to a considerable length," and agreeing with that

* G. v. KOCH, "Mittheiln. über Cœlenteraten, Anatomie von *Stylophora digitata*, PALLAS," 'Jenaische Zeitschr.,' vol. 11, pp. 375–81, Plate 22, 1877.

previously figured by KÖLLIKER. Of the echinulations, he writes: "The small irregularly outlined prominences on the surface appear to be the ends of the incompletely developed crystals which make up the individual ellipsoids." The illustrative sections are both transverse and longitudinal. The transverse sections show the zig-zag outlines round the radiating groups of fibres called spheroids and ellipsoids;* but the longitudinal section (Plate 22, fig. 6) does not carry out the idea of either a spheroid or ellipsoid of fibres. Instead of individual symmetrical groups of fibres, there is a continuous long axis, which corresponds to the centre of radiation in the transverse section, and from which the fibres diverge in a uniformly upward and outward direction. Such a longitudinal section gives indisputable proof that the *skeleton of Stylophora is* NOT *built up of individual ellipsoids.* The terms "spheroid" and "ellipsoid," as applied at any rate to *Stylophora*, are merely descriptive of an appearance seen in transverse section. Nevertheless KOCH constantly stated in subsequent works that the Madreporarian skeleton was in most cases made up of calcareous spheroids and ellipsoids.

In 1879 a short paper was published by KOCH,† in which we learn that he had tried in vain to isolate the "crystallographische einheitliche Elemente" in the skeletons of different sub-classes of *Anthozoa.* He found that in all the types examined, small rhombic crystals were the ultimate structures, but he could not discover how these crystals arranged themselves into the larger crystal-groups, nor could he demonstrate that any such groups (ellipsoidal or spheroidal) were separable. So far as Alcyonarians came in question, he could state that the crystals were arranged concentrically and regularly in the spicule, yet in such a way that their axes more or less crossed each other. "In all other forms of calcification," KOCH concludes, "I have not got much beyond what is already known" (*loc. cit.*, p. 322).

His next important paper is that in 1882, which I have already referred to on p. 89. He makes there a minute examination of two Palæozoic and one recent species, and has nowhere occasion to mention "ellipsoidal" or "spheroidal" groups of crystals. He compares the solid septum of *Cyathophyllum* sp.? with the septal spines of *Pholidophyllum Loveni*, and finds their nearest structural analogue in the Alcyonarian spicule. As this paper of VON KOCH'S has largely influenced palæontological literature, I shall give a sketch of its contents.

Pholidophyllum Loveni‡ possesses no leaf-like septa; but longitudinal series of

* *Stylophora*: a transverse section may be seen in NICHOLSON'S 'Manual of Palæontology,' vol. 1, p. 245, fig. 125A.

† G. v. KOCH, "Bemerkungen über das Skelet der Korallen," 'Morph. Jahrb.,' Bd. 5, 1879, pp. 316–22, Plate 22.

‡ *Pholidophyllum Loveni*, a Silurian species, had been described under various generic names. EDWARDS and HAIME described it as *Cyathophyllum* (?) *Loveni* ('Brit. Foss. Corals,' p. 280, Plate 66, figs. 2, 2A). LINDSTRÖM removed the species from the genus *Cyathophyllum*, and erected for it a new genus *Pholidophyllum* ('On some Operculated Corals, Silurian and Recent,' by G. LINDSTRÖM. Wisby, 1870). He called attention to a "covering of small, ($\frac{1}{2}$ millim.), very thin scales, tightly clustered

septal spines project from the wall into the lumen of the calyx. The spines may vary in length and thickness, their microscopic structure is, however, always the same. An internal mass, according to KOCH, of small crystals, indifferently arranged, occupies the central part of the spine, which appears clearer in the centre and darker at its peripheral area, by transmitted light. The peripheral area is then surrounded by a zone of radiating calcareous fibres, which always is transparent and clear. Lamellar lines of thickening are shown passing from spine to spine, and giving rise to a thecal thickening composed of their compacted basal portions. This lamellar thickening is the equivalent of LINDSTRÖM'S stereoplasm.

Transverse sections are then given by KOCH of the broad leaf-like septa and theca in *Cyathophyllum* sp. and *Caryophyllia cyathus* (recent). He writes: "A dark streak runs along the middle of the septum more or less regularly, it appears to be sometimes made up of several individual parts, and possesses a radiating structure. At the sides of this dark streak, which I shall name the '*primary streak*' ('Primärstreif'), a clearer, likewise crystalline, and usually finely striped mass lies, which is limited by a darker edge, but is not very sharply defined from the perfectly transparent mass of thickening (Ausfüllungsmasse)."

Sometimes LINDSTRÖM'S term "stereoplasm" has been applied by other authors only to the outer "Ausfüllungsmasse," or "secondary thickening" of KOCH in leaf-like septa; sometimes it has been used to include both the outermost thickening and the finely-striped crystalline fibres as described by KOCH. When used in this latter sense, it has then been directly brought into contradistinction with the dark "Primärstreif" of KOCH. This want of uniformity in the use of the term "stereoplasm" arises mostly from the vagueness of ideas with regard to the *essential* structure, as well as an uncertainty how much of the septum is really "*primary*" and how much "*secondary*." And it is hopeless to attempt carrying out a strict terminology, when authors are in doubt about the principles which are meant to be conveyed by the terms.

KOCH does not enter into the question of the difference between the "Primärstreif" in its microscopic character and the radiating fibres. He simply makes a general comparison of the darker central mass in the septal spine of *Pholidophyllum* with the primary streak of the septa in many Madreporaria, or with the darker, inner part of the large spicules of many Alcyonarians, while the clear, radially-built

together in longitudinal rows along the costæ;" these he thought to be "secretions of an *exothecal* nature" homologous with the opercula of certain Rugose corals, with the epithecal valves of *Cystiphyllum prismaticum*, and possibly also with the scales and opercular valves of recent *Primnoa*,—Alcyonarians belonging to the Gorgonidæ. This homology, indicated by LINDSTRÖM in 1870, derives new significance, since we now know that the whole skeleton of Madreporaria is of ectodermal origin (*cf.* LINDSTRÖM, 'Geol. Mag.,' 1866, Plate 14, fig. 40, and 'Öfvers. Vet. Ak. Forh.,' 1868, Plate 6, fig. 4). Similar scales are present on the epitheca of *Rhizophyllum Gotlandicum Roem.*, from the Silurian beds of Gothland.

outer part would answer to the corresponding parts in the corals named. The lamellar deposit, which represents the wall in *Pholidophyllum*, he regards as identical with the "secondary layers of thickening" in *Madrepora* and other recent corals.

In the same year, 1882, KOCH'S embryological paper on *Astroides calycularis* was published (*ante*, p. 91), and the primary skeletal deposit was described by him as entirely composed of calcareous spheroids and ellipsoids.

In the following year a paper* appeared which may be regarded as a *résumé* of this author's results on the structure and morphology of the Madreporarian skeleton. He distinguishes three main types of structure among corals:—

(1.) "*The simplest forms of calcareous skeletal structures are the so-called spicules* observed in Alcyonarians" . . . . "further, in a number of fossil corals, one is led to think of the possibility of the skeleton being composed of coalesced spicules, as, *e.g.*, with some probability in *Pholidophyllum*, then, perhaps, also in *Syringophyllum* and similar genera."

(2.) "*The connected calcareous skeleton of the Madreporaria.*" . . . . "The fine structure of the Madreporarian skeleton is fairly simple. It is always composed of crystalline spheroids." . . . .

(3.) The skeletal structures of the fossil Rugosa appear to be closely associated with those of recent Madreporaria, since considerable identity may be recognized in the fine structure of both.†

These results are far from presenting any general truth with regard to the skeletal structure, and its mode of deposition. Neither do they yield any sound basis for morphological comparison. For example, the type of structure which KOCH NICHOLSON,‡ and others had observed in transverse sections of the recent genus *Caryophyllia* is that indicated in Group (3) above as typical of Rugose corals of Palæozoic age. On the other hand, close analogy had been demonstrated by KOCH in 1882 between this type of structure in Group (3) and that demonstrated for *Pholidophyllum*. A year later, the latter was brought into affinity with the Alcyonarians in Group (1) above, and separated from any connection with its Rugose and recent neighbours of the previous year. The septal spine of *Pholidophyllum* is, in short, looked upon as a kind of spicule, and if we were to follow KOCH'S papers

* KOCH, "Morphologische Bedeutung des Korallenskelets," 'Biolog. Centralblatt,' vol. 2, No. 19, pp. 586, 587, January, 1883.

† This refers to the septa of *Caryophyllia* and *Cyathophyllum*, as well as to a number of examples given by KOCH, and other authors. In 'Palæontographica,' 1882–3, Bd. 29, KOCH contributed an article on budding, "*Die Ungeschlechtliche Vermehrung* (Theilung und Knospung) *einiger Palæozoischen Korallen*," in which occasional reference is also made to septal structure (*loc. cit.* p. 347), "Stauria and Fascicularia show, in their general form, as well as in the fine structure, great identity with the recent genera, *Mussa*, *Caryophyllia*, *Galaxea* (the coenenchyme excepted in the last). Everywhere distinction can be plainly made between the primary layer of the septum and the stereoplasm."

‡ NICHOLSON gives an instructive figure on septal structure in 'Manual of Palæontology,' vol. 1, p. 247, figs. 127, A, B, C, where *Caryophyllia* is compared with "Rugose" types.

of 1882 and 1883, the inevitable conclusion to be drawn would be, either that the compact septum of *Cyathophyllum*, *Caryophyllia*, &c., was composed of individual spicules, or that the whole septum had a structure entirely analogous with a single spicule.

The type of structure in Group (2) of KOCH is based upon the spheroid and ellipsoid seen in *transverse* sections of certain Madreporarians, and in embryonic stages of Astroides calycularis. This type is characteristic, it is assumed, of recent corals (Madreporarian); at the same time the Rugose corals seem closely allied.

After all, therefore, a review of KOCH's work leaves us with a number of facts and several important figures, but in as great confusion as ever regarding the ultimate structural unit in Madreporaria. It is almost a relief to return to the sclerenchymatous nodule of EDWARDS and HAIME. For what is this spheroid? Is it a spicule? We can see and separate the spicule, then why not the spheroid? It is noteworthy that the spheroid has *been presented from first to last by one or two transverse sections*, no longitudinal section has demonstrated it. The "septal spine" of *Pholidophyllum* might be compared with a spicule, it certainly never could be called a spheroid. Neither had the primary streak and stereoplasm of *Caryophyllia*, &c., ever betrayed, in figures given, any individual structure akin either to a septal spine, a spicule, a spheroid, or sclerenchymatous nodule.

Progress of Work on the Septa of Palæozoic Corals.

As I have already said, several palæontologists engaged in the study of Palæozoic corals prepared their sections for microscopic work, but the state of preservation was seldom sufficiently good to permit of all the details being seen. NICHOLSON* accomplished much in the field of *Madreporaria tabulata* E. and H., and for the Monticuliporoids. He has also published a number of sections illustrating special work on the *M. rugosa*.

In 1879, SCHLÜTER† published thin sections accompanying his work on Devonian corals, and the same author continued his special study of the corals of the Eifel and Rhine districts in 1880–1–2 in a series of papers.‡ The thin sections show the general relations of the different skeletal parts, but lead us no further with regard to fine structure. FRECH'S§ papers, also on Devonian corals, give several sections in which more detail may be seen. A longitudinal section made through a septum of

* NICHOLSON, "On the Structure and Affinities of the Palæozoic Corals," 1879; "Monograph of the Girvan Silurian Fossils," NICHOLSON and ETHERIDGE, 1878–80.

† SCHLÜTER, "Devonische Korallen und Dünnschliffe v. Spongophyllum Kunthi u. Calophyllum paucitabulatum," 'Sitzungsber. d. Vert. de Naturh. ver. d. Pr. Rh. in Westphalen,' 1879, p. 402.

‡ Later papers appeared in 1880–81 of the same journal; "*Zoantharia rugosa* aus d. Rheinisch. Devon. Mittel und Ober," 'Sitzungsbericht, No. 3, Ges. Naturf. Fr. zu Berlin,' 1880; "Ueber Neue Korallen d. Mitteldevon d. Eifel," December, 1882, 'Sitzungsber. d. Niederrh. Ges. f. Natur. und Heilkunde, p. 203.

§ FRECH, "Die Korallenfauna des Oberdevons in Deutschland," 'Zeitschr. D. Geol. Ges.,' 1885, p. 21.

Cyathophyllum minus Roem. sp. (*loc. cit.*, 'Zeitschrift,' 1885, p. 31, Plate 1, fig. 2*c*), shows several rows of dark points, each row forming a central zone surrounded by light-coloured "stereoplasm." In the latter, no structure of any kind is presented. The author describes this septum as consisting of coalesced spines directed upwards and inwards. The rows of dark points in longitudinal section correspond to the primary streak (Primärstreif, KOCH) in the middle plane of the septum. FRECH'S sections, therefore, corroborated KOCH'S comparison of the structures of the *Pholidophyllum* spine and *Cyathophyllum* septum (*cf.* pp. 253, 254).

In the same year FRECH published a sequel to his paper on Devonian corals, entitled "Ueber das Kalkgerüst der Tetrakorallen" ('Zeitschrift,' 1885). As I shall have occasion to refer to this in Part II. of the present paper, I shall merely remark here that it gives a short account of the main structural types recognized in the septa of *Tetracoralla* up to that date. A good longitudinal section is given of *Endophyllum*, showing dark axes of the septal spines surrounded by "structureless stereoplasm" (Taf. 41, fig. 6).

No further work with regard to septal structure is given by FRECH in his next paper,* published 1886.

WAAGEN'S† description of the permo-carboniferous fossils of the Salt Range includes a number of specially interesting Coelenterate types. The *Rugosa* are represented by *Lonsdaleia* and *Amplexus*. A figure of a transverse section of *Lonsdaleia Indica* shows septa "distinctly composed of two parts, a central one, which is of dark colour, and a peripheral or coating one, which is light coloured and finely fibrous." The dark-coloured part, which can, however, when differently preserved, appear as a distinct white line, represents what has been called by KOCH the "primordial stripe" or "primordial septum" (*loc. cit.*, p. 899, Plate 101, fig. 3*b*).

The fibrous structure of the "peripheral" part of the septum is shown very clearly in transverse and longitudinal sections given by SCHÄFER‡ in the course of a paper on *Phillipsastræa*. "The septa," he writes, "are formed of bundles of calcite fibres which lie on either side of the median plane of the septum. From this starting point on this plane each fibre passes upwards and outwards in the direction of the proximal end of the septum." He compares the "feather-like structure thus produced" with that described by PRATZ for *Thamnastræa* (see below, pp. 187, 188). In these "fibrous bundles," proved by PRATZ for the first time in certain Mesozoic and younger genera, and by SCHÄFER for the first time in a Palæozoic genus, we have a correct rendering of microscopic *longitudinal* sections which showed fine details of structure. No use is made by either of those authors of the terms primordial septum, stereoplasm,

* FRECH, "Die Cyathophylliden und Zaphrentiden des Deutschen Mitteldevons," 'Pal. Abh.,' vol. 3, Part III., Berlin, 1886.

† WAAGEN, "Salt Range Fossils," 'Palæontologia Indica,' ser. 13, vol. 1, 1887, Calcutta.

‡ R. SCHÄFER, "On *Phillipsastræa* D'ORB," 'Geol. Magazine,' London, September, 1889, vol. 6, p. 398, Plate 12.

secondary thickening, outfilling mass, ellipsoids, spheroids, spicules, &c.! SCHÄFER demonstrated farther that each calcite fibre was a crystallographic individual, as KOCH had shown in certain recent Madreporaria. And he pointed out that the vesicles and tabulæ agreed with each other in their histological structure, but differed from the septum in so far as the position of the deposit was concerned. "In the tabulæ and vesicles the calcification could only take place from below upwards; the septa, on the contrary, were arched over by the ectoderm, and the calcification could continue *both upwards and on either side.*"

Progress of Work on the Septa of Mesozoic and Cainozoic Corals.

One of an important series of systematic papers was published in 1887 by ORTMANN (see foot note, p. 185), in which this author, like QUELCH, abandoned the suborder Madreporaria Rugosa. He then laid down a new system of classification (see pp. 312–314).

In 1888, a paper appeared by HINDE* on the typical species of the genus *Septastræa*, *S. Forbesi*, E.H., from the Miocene Formation of Virginia and Maryland. He said that the "primary streak" of the septum in this genus was really double. The septa could readily be split in the middle plane, and the inner face on both halves differed from the outer. Each of the inner layers had a lattice-like appearance, being composed of well-marked linear ridges, parallel with each other, and either vertically or obliquely placed, while transverse growth-lines crossed the ridges at intervals. HINDE pointed out that the powdery calcareous deposit present in those inner layers might possibly be the result of subsequent change and disintegration in the course of fossilization, and need not necessarily be looked upon as the original form of the skeletal deposit in the "primary streak." The peripheral parts of the septum were composed of radiating fibres.

In 1890, a "Monograph of the Coral Fauna of the Triassic Strata" in different parts of the Eastern Alps was published by FRECH.† The systematic aspect of this Monograph is treated below (Part II., Chapter X.); little special work was done on the microscopic structure of skeletal parts. The only thin section is one made transversely through a calyx of *Isastræa profunda*, REUSS, *var. nov. Major* (*loc. cit.*, p. 22, Plate 5, fig. 4c). I shall quote the author's description, as it best shows the standpoint at present taken by FRECH:—

"The microscopic structure of the septa agrees with that observed in the case of Devonian Cyathophyllids. The wall (theca) and the septa originally consist of light-coloured spines (trabeculæ) and are later thickened by a darker-coloured skeletal mass (stereoplasm). The primary spines are, in cases of good preservation, plainly visible as isolated pillars in the middle of the septa, and their diameter is

* G. J. HINDE, "On the History and Characters of the genus *Septastræa* D'ORB.," 'Q. J. Geol. Soc.,' 1888, pp. 200–226, Plate 9.

† F. FRECH, "Die Korallenfauna der Trias," 'Palæontographica,' vol. 37, 1890–91.

no longer added to, even in the most strongly-developed septa. The strengthening of the septa and wall takes place wholly by deposited stereoplasm, which shows clearly the structure frequently described by PRATZ, VON KOCH, and myself. The "primary streak," composed of primary spines, is placed, as a rule, somewhat excentrically within the septum. Numerous spinate continuations ("Seitendornen" *nov. nom.*) stand out from the sides of the septa; in their arrangement they follow the course of the original primary spines, notwithstanding that they consist, like the sides of the septa, of stereoplasm. . . ."

We may conclude, from the analogy drawn with Cyathophyllum that FRECH believes a single granulate ridge in an Astræid septum extending from the wall inwards is the equivalent of the septal spine in Pholidophyllum, Cystiphyllum, and other Palæozoic genera. But he gives to the term "spine" a quite special application. By it he means only the central part, that part which KOCH had described in Pholidophyllum as clearer centrally, and darker peripherally, when seen by transmitted light; that part which FRECH himself had shown to be composed of a series of dark points connected or disconnected in certain species of Cyathophyllum, and which, in other cases, he describes as "isolated rods" or "pillars" in the midst of a *structureless* stereoplasm; that part which WAAGEN and FRECH himself found very variable according to fossilization, and which HINDE surmised had been probably entirely disintegrated in Septastræa, and whose ultimate appearance could not be looked upon as true indication of its original condition. Yet the "primary streak," or "primordial septum," is said to be composed of those questionable "primary spines." And all the rest of the septum, including the "radiating fibres," as well as the "Ausfüllungsmasse" of KOCH, is looked upon as "stereoplasm," or secondary thickening. I shall have occasion to show, in the course of my paper, how entirely untenable those ideas of FRECH are with regard to primary spines and septum.

Since FRECH refers to PRATZ, in the matter of this stereoplasm, I may remark that PRATZ never for a moment confounds with stereoplasm the radiating fibres which *wholly* composed the individual *trabeculæ* of the septum in the genera he examined. He used the term "trabecula" in quite a different sense from FRECH—in the sense of "poutrelle," E.H.—and never had occasion to differentiate any central "spine" or "trabecula" from an outer stereoplasm or secondary thickening.

I do not quite see why FRECH introduces the new name of "*Seitendornen*," since the septal eminences, to which the name is applied, have always been known satisfactorily enough as "*granulations*." I may so far anticipate the results of my own work as to say that these granulations have, in the Triassic Astræids examined by FRECH, a very distinct structural bearing. *Not the whole of a septal ridge*, in Montlivaltia, Thecosmilia, &c., is the equivalent of the primitive "septal spine," seen in *Cystiphyllum* and other Palæozoic genera, but *only so much of it as corresponds on the surface of the septum to one of these granulations.*

An important contribution to our knowledge of the septal types among Jurassic corals was made by KOBY (see foot note, p. 275) in a series of figures with descriptive notes.

Progress of Zoological Work on Recent Madreporaria.

Several papers by BOURNE and by FOWLER, published in the 'Quart. Journ. of Microscopic Science,' may be said to have continued the anatomical work which had been done in England by MOSELEY, in Germany by KOCH and HEIDER. In referring to the papers of BOURNE and FOWLER, I direct my attention here to points which concern the Madreporarian skeleton. Morphological and anatomical features will be referred to in the course of this paper.

The excellent microscopic transverse sections of wall and septa deserve to be noted, they are among the best which have been given. Also the various terms for the median area of the septum—primary streak, primary septum, primary spines—are scarcely used by those authors. The particular areas in question are fitly called in general "centres of calcification," whether the area be seen as a "line" or a "point" in transverse section. The "centre of calcification" was, with those authors, a neutral term, taking nothing for granted about the dark line (ex. *Euphyllia Flabellum*) or the dark points (ex. *Mussa*) themselves, but indicating merely the fact observed that the calcareous fibres, in all cases, diverged outwards from those areas.

Both BOURNE and FOWLER had abundant opportunity of confirming KOCH's statement that the skeleton was entirely of ectodermal origin. At the same time, they accepted HEIDER'S term of calicoblast for the lime-forming cells of the ectodermal layer. They farther agreed with KOCH in regarding the calicoblast as a secreting cell, separating out the calcareous material which gave rise to the skeleton, while itself remaining intact as an organic cell of the polypal ectoderm. The observations made and figured by HEIDER of calicoblasts containing fully-developed fibrous deposit, and the nucleus shrunken or vanished, were entirely discredited both by BOURNE and FOWLER. Another explanation was given by FOWLER of the curious, elongated cells with fibre-bundles, observed by HEIDER; while the roundish cells with calcareous, granular, and fibrous contents were little regarded. BOURNE* said HEIDER might have inferred the rod-like (fibrous) appearance within the cells could not be calcareous in structure, otherwise the rods would have been dissolved by the action of the acids used in decalcifying the specimens. In defence of HEIDER I would draw attention to the fact that the latter saw those fibres in cells, many of which *were still highly protoplasmic*, and that my experience has been a very slow action of decalcifying acids on the contents of such cells. The skeleton proper dissolves rapidly, but the superficial layers next the body-wall of the polyp dissolve slowly and incompletely, leaving protoplasmic remnants.

On the other hand, both FOWLER and BOURNE recognized two main varieties of calicoblasts in the ectoderm, "rounded or polygonal, soft-looking, granular cells," and "long, narrow, columnar cells." The same varieties had been described by HEIDER,

* BOURNE, "On the Anatomy of *Mussa* and *Euphyllia*, and on the Morphology of the Madreporarian Skeleton," 'Q. J. M. S.,' No. CIX., p. 25, Aug., 1887.

in the soft condition, and also in a more calcified state containing the "Stäbchen," or small rods.

To FOWLER* first, and then to BOURNE, we owe an important observation with regard to the position occupied by the long columnar cells. Those clothe, in *Lophohelia* and in *Mussa*, the uppermost, most actively-growing parts of the septa at and near the periphery of the calyx, whereas the ectodermal cells elsewhere are smaller in these two genera.

In the genus *Fungia* no long columnar cells were observed by BOURNE, the whole ectoderm being composed of smallish cells.

FOWLER and BOURNE have accomplished much for palæontology by confirming, without doubt, the presence of a continuous ectoderm as the external layer of the body-wall in Madreporaria. This layer produces no skeleton on the oral surfaces of the polyp, but it is the active skeleton-former throughout its whole aboral surface, whether smooth or crumpled, single or invaginated. Those authors thus refuted, conclusively, the idea from which HEIDER has never freed his mind, that the mesoderm lay next the skeleton, for nothing else can be supposed to be meant when HEIDER writes that the "calicoblasts wander in from the ectoderm to the edge of the mesoderm." At the same time there was an end made to any direct comparison between the origin of the Alcyonarian spicule and that of the various skeletal parts of Madreporaria (*antea* p. 93).

I find, however, that KOCH, FOWLER, and BOURNE are wrong in their conception of the calicoblast. My investigation of superficial layers of the skeleton have given fullest confirmation of HEIDER'S idea, that the calicoblasts were actually converted into calcareous groups of fibres. I hope to show, in the course of this paper, that the *fibre-containing calicoblasts which lie next the skeleton are shed off, so to speak, from the polyp*, new cells constantly *taking* their place in the ectoderm by cell-division. *The shed calicoblasts build up successive layers of calcified cells, which hang together at first by their cell-walls, and ultimately, as crystalline changes continue, form the individual laminæ of the skeletal structures. The whole Madreporarian skeleton is composed of such laminæ, any apparent variation in microscopic structure is accounted for by some difference in the particular shape and position*, locally, *of the ectoderm.*

The Microscopic Researches of PRATZ.

I briefly referred to the work of PRATZ in connection with the publications which marked the year 1882 (*antea* p. 91). His research deals chiefly with a number of fossil genera which had been referred to Fungidæ and to Poritidæ by EDWARDS and HAIME. Some of those are *Cyclolites* (Cret.), *Leptophyllia* (Cret.), *Thamnastræa* (Tri.-Tert.), *Trocharæa* (Up. Jur.), *Microsolena* (Up. Jur.), *Astræomorpha* (Tr.).

* FOWLER, "The Anatomy of the Madreporaria," III., 'Q. J. M. S.,' Aug., 1887, "*Lophohelia prolifera*," p. 9.

Of recent genera, *Coscinaræa* and *Siderastræa* are included, but those were not examined in the same detail as the fossil genera. PRATZ was enabled, by means of careful selection of well-preserved material, and the preparation of very thin sections cut in all directions, to attain a clearness of conception with regard to the essential structure of the skeleton in those genera. He held himself wholly within the limits of the types examined, building up for them an analytic table of their classificatory features, as complete in its way as it also was original. I shall defer the consideration of this table to later parts of the present paper (Part I., chaps. iv. and v., Part II., chap. x.).

It is not too much to say that no other author shows in the same high degree as PRATZ a thorough acquaintance with and mastery of the past and current literature of Madreporaria, and has held himself at the same time so free from mental bias, and so much aloof from the changing opinions and the controversial interests of contemporaries. The result is, that his work is one of the few which is from beginning to end alive with scientific instinct. It is a work whose high value can only be slowly recognized, since few are sufficiently versed in the study to realize what PRATZ accomplished at a time when nothing but confused terminology and hazy ideas of skeletal structure were finding expression in the rapidly written papers of some of his fellow-workers.

I have never made the personal acquaintance of this author, yet his original microscopic sections, now in the possession of the Munich Museum, have largely influenced my work. The terminology which PRATZ uses is EDWARDS' and HAIME'S. He shows that in the fenestrated septa of *Microsolena*, *Thamnastræa*, &c., the trabeculæ (poutrelles, E. H.) are composed of a series of nodules, and the nodules are themselves made up of smaller symmetrically-arranged prominences. The structure of the trabeculæ is wholly fibrous, radiating fibres passing upwards and outwards in bushlike or pinnate fashion from an ideal axis in the centre of the trabecula. PRATZ writes in one place that he "thought he could distinguish smaller fibre-bundles passing to each of the smaller prominences of a nodule;" of this he was, however, uncertain. What he proved was the complete bush-like group of fibres corresponding to each nodule of the series, in *Cyclolites* for example (*cf.* fig. 38*c*, below).

My work will show that these smaller fibrous bundles to which he referred are universally present in Madreporaria wherever the skeletal surface is finely granulate.

Although microscopic sections of Madreporaria had been frequently made and described before PRATZ published his work in 1882, he was the first to apply such work systematically. The genera examined were mostly grouped by PRATZ in a sub-family Pseudoastræinæ, which he referred to the family Fungidæ, at the same time pointing out a certain similarity in their habits of growth with Astræinæ. A few genera were formed by PRATZ into a sub-family Pseudoagaricinæ; this sub-family will be shown below to be unnecessary.

I have purposely removed the work of PRATZ out of its due succession in the

historical review of the literature, because my own paper may be looked upon as the direct continuation of the methods which PRATZ used.

Purpose of the Present Paper.

My interest in Madreporaria began while I was still a student in Professor RAY LANKESTER'S Class of Zoology and Comparative Anatomy, at University College, 1889–90. I then determined to make the group a subject of special research, and to study its palæontological aspect. With this in view I came to Munich in spring, 1891. There, by the permission of Professor VON ZITTEL, I had all the advantages offered by the large coral collection in the Palæontological Museum of Munich University. Dr. RUDOLF SCHAEFER, Custos of the Museum, who had already published special work on Palæozoic corals, kindly helped me in my early studies. To him I owe much. Amongst other things, he pointed out to me the interest attached to microscopic investigation of fossil corals, taught me various methods of making sections, and has throughout my farther work guided me in my selection and use of literature. In this way he directed me towards the line of study which I have mainly followed, and whose results are embodied in this paper.

At the same time the necessity for such work was being borne in upon me by my own experience in preparing a monograph of the Upper Jurassic coral fauna from Stramberg. The longer I worked with the identification of genera and species, the more dissatisfied I became with the conventional methods of work.

The synonymy of Jurassic corals is wont to be fairly extensive, and it soon becomes clear that the individuality of the author has much to answer for in the erection of genus, species, or variety. No fixed standard of research can be traced in the various monographs of the special faunas, and the general results obtained by different authors may be highly satisfactory from a particular palæontological or geological point of view, but cannot be said to have an absolute value for the science of Madreporarian evolution.

When my descriptive work for the Stramberg monograph was completed, and I tabulated the list of species in order to compare them with the fossil faunas next in age, I felt that the apparently exquisite *Upper Jurassic* age of my fauna had been very largely a foregone conclusion! While the list gave no indication of the close relationship which existed, on the one hand, between the fauna I had examined and any typical Palæozoic fauna, and on the other, between it and any typical recent fauna. The arbitrary line cutting off the Tetracoralla or Madreporaria Rugosa (Palæozoic) from all later Madreporaria had been disproved by a goodly number of the Stramberg corals. Neither was the radial arrangement of septa in cycles by any means very definite or very general in the Jurassic types. There was, therefore, a certain protest against the first basis of sub-division in Madreporaria, viz., the tetrameral or hexameral symmetry of the septa.

Again, a certain sameness runs through the external macroscopic features of most of the Madreporarian genera, which happen to be well represented in Jurassic strata. *The genus can, as a rule, only be identified with certainty after a careful microscopic investigation.* Many genera erected by FROMENTEL cannot be criticised or made use of because of the want of such data. Again, one finds in some authors the *habit* of the corallum outweighing any considerations of fine *structure.* Under the genus "*Latimæandra,*" as many varieties of Madreporarian types are hidden at the present day as could ever have been attributed to the name of "*Madrepora*" in the earliest works on corals.

In short I found myself face to face with the fact that the genera and families of EDWARDS and HAIME were no longer quite in touch with more recent work, and yet no recent work gave any general standard of research. The literature seemed split up into ever so many factions. The only hopeful prospect seemed to be in microscopic work, and that I determined to do before publishing my monograph of the Stramberg fauna.

The collection of St. Cassian corals which I had myself made offered a number of specimens in admirable state of preservation. Besides, these corals being of Triassic age had a particular phylogenetic interest attached to them.

Dr. HOFER, Custos of the Zoological Collection in Munich, kindly handed over to me several recent corals which he had collected from the Red Sea. These were then specially prepared for the examination of the relation between the polypal and skeletal parts. Dr. SCHAEFER placed at my disposal his own collection of recent Madreporaria, which has greatly facilitated my studies.

I selected carefully the recent corals, with which I went to work, as far as possible making an examination of the skeleton of corals whose internal anatomy had already formed the subject of special zoological study. I chose also leading types from the Astræidæ, Fungidæ and Perforata; good microscopic sections had already been published of *Caryophyllia* and *Flabellum*, two well-known types of Turbinolidæ. Thus I hoped to arrive at some fairly embracive series of different structural types —*if such existed in Madreporaria.* The result has proved that different structural types do exist, and form a surer method of determining Madreporarian genera and groups than any other method known to me.

While engaged in the work of this paper, I learnt that Dr. VOLZ,* Assistant to Professor FRECH in the Breslau Museum, had commenced a monograph of the St. Cassian corals, which should form the second part of "Triassic Corals." The first part of this publication by Professor FRECH had appeared in 'Palæontographica,' 1890.

* Since this paper was entered at the Royal Society, I have received the Introduction to the paper on St. Cassian Corals by Dr. VOLZ, and it deals with microscopic features observed in these Triassic corals. "Die Korallenfauna der Schichten von St. Cassian in Süd-Tirol." (Inaugural Dissertation by WILHELM VOLZ; Stuttgart, Schweizerbart'sche Verlag, 1895.)

I therefore abandoned my original intention of including St. Cassian types in the present paper, and have limited my treatment of Triassic corals to the already published Zlambach fauna (*vide* chapter x. below). As there is a representative collection of this fauna in the Munich Museum, I have been in a position to examine original specimens and make microscopic investigations when necessary.

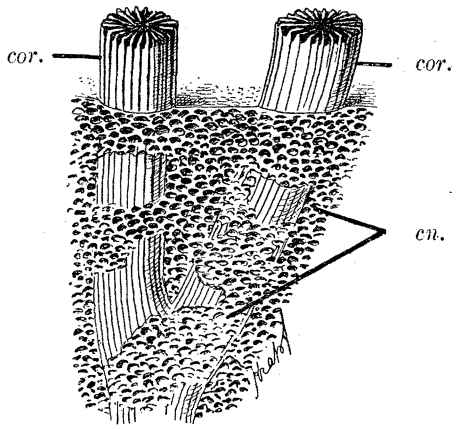
I am glad to have this opportunity of thanking GEHEIMRATH VON ZITTEL for his kind permission to work in the museum and library of the Palæontological Institute —a permission to which has been added much personal encouragement throughout these years. GEHEIMRATH VON ZITTEL has, moreover, kindly revised for me the system of Madreporarian families which I propose in the concluding chapter of this paper.

CHAPTER I.—MICROSCOPIC INVESTIGATION OF THE RECENT GENUS *GALAXEA*.

THE SKELETAL PARTS.

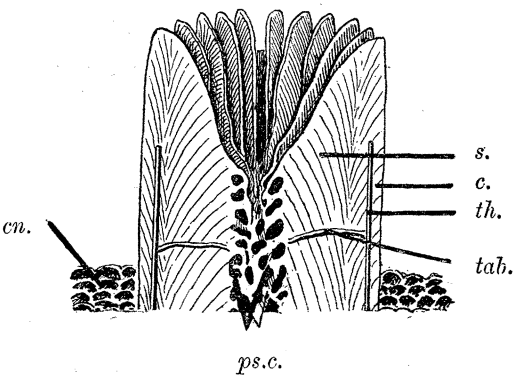
The genus *Galaxea* is a colony-building form in which the polypal tubes are surrounded by a delicately-formed cœnenchyme, only the actually inhabited calicinal

Fig. 1A.



Branching *corallite* of *Galaxea* with surrounding *cœnenchyme* (twice natural size).

Fig. 1B.



Enlarged drawing (diagrammatic) of half of the calyx, showing the skeletal parts: *s* = septum, *c* = costa, *th* = theca, *tab* = tabula, *ps.c.* = pseudocolumella, *cn* = cœnenchyme.

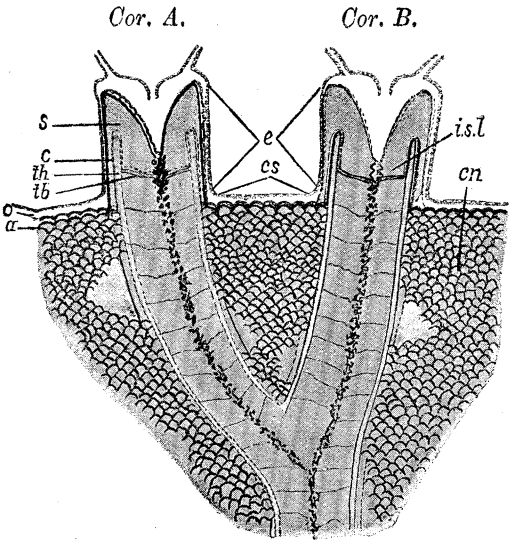
portion of the tubes rising freely above the cœnenchyme. Two corallites are shown in fig. 1A, twice their natural size. The upper parts of the calyces have been cut across. The upper surface of the cœnenchyme is about half an inch below that of the corallites. Part of the cœnenchyme has been removed in order to show the branching of the corallites. Fig. 1B shows the lanceolate, exsert septa, and their relations to wall and basal structures.

During the life of the colony, the cœnenchyme is covered by living tissue, the

"cœnosarc." The cœnosarcal tissues are the continuation of the body-wall of the corallites, and enclose canalicular extensions of the visceral cavities of the polyps.

It is convenient to distinguish an "*oral*" and an "*aboral*" body-wall in the sense in which FOWLER applied those terms, viz., the "oral" body-wall for the upper and outer surface of polyp and of cœnosarc, the "aboral" body-wall for the lower and inner surface. The latter lays down the various skeletal parts of the corallum, external to its ectodermal layer of calicoblast cells. The *oral* body-wall takes no part in forming the skeleton, although the ectodermal layer is continuous with the lime-secreting ectoderm of the aboral wall. These relations are diagrammatically represented in fig. 2.

Fig. 2.



GALAXEA—cœnenchymatous type. *o.* = oral body-wall; *a.* = aboral body-wall; *cs.* = cœnosarc; *cn.* = cœnenchyme; *e.* = edge-zone; *s.* = septum; *c.* = costa; *th.* = theca; *tb.* = tabula; *is.l.* = interseptal loculus. (Compare the similarly treated figures, 22, 35, 36, 56.)

The figure is a longitudinal section through two corallites of *Galaxea* and the cœnenchyme surrounding them. In Corallite A the aboral body-wall is shown at that part where it clothes one of the principal septa. A dotted line indicates the position of the same body-wall at the part adjacent to the septum, where it clothes the theca and the basal tabulæ within the theca. In Corallite B the aboral body-wall is supposed to be cut through at the part resting on theca and tabulæ, while the dotted line indicates its position on a principal septum.

It will be seen from the figure that the septum projects some distance above the theca, *i.e.*, is "exsert," and also projects outwards beyond it, giving rise to a costate portion "*c.*" The aboral wall clothing the margin of the septum is therefore carried out much nearer the oral wall, and the visceral cavity or its continuation over the lip of the corallite is there necessarily narrower than in the adjacent thecal portions.

The "intrathecal" visceral spaces in the interseptal loculi of the calyx are represented outside the calyx by "extrathecal" spaces between the aboral body-wall on the theca and the oral body-wall. The term "Randplatte" has been given by HEIDER and KOCH, and has been generally accepted for these extrathecal portions of the visceral cavity. I propose to translate this useful term into English as the *edge-zone*. It is understood in the term that the mesenteries of the interseptal loculi are continued into the intercostal loculi. "Cœnosarc," on the other hand, signifies an extrathecal part into which the mesenteries do not continue; a canalicular system may be developed in it, but has not any immediate connection with the mesenterial loculi of the calyx.

In *Galaxea* a well-developed edge-zone extends over the lip of each corallite, and its body-wall, oral and aboral, is continuous with that of the cœnosarc. The mesenteries are, however, not continued into the cœnosarcal parts of the colony (*vide* FOWLER, "Madreporaria," 'Q. J. M. S.,' February, 1890, "*Galaxea esperi*").

The under surface of the whole colony is covered by an epitheca with concentric furrows. It takes its origin from the same part of the aboral body-wall which deposits the cœnenchyme throughout the colony. The edge-zones of the peripheral polyps are not continued into cœnosarc, but are closed at their lowest portions, and the epithecal deposit is laid down by the angle between aboral and oral body-wall.*

In the same paper some suggestions are made with regard to the absence of the "Randplatte" in various colonies, a subject frequently referred to in the papers of FOWLER.

EDWARDS and HAIME gave to the cœnenchyme of *Galaxea* the special term of peritheca, as its appearance differed on the one hand from the costal parts between the corallites of many Astræids, *e.g.*, Heliastræa, and on the other hand from the ribbed or echinulate cœnenchyme in the Oculinids and the "Perforate" types. Without entering at present into the question of the morphology of parts, it will be seen from fig. 2, above, that the "peritheca" in *Galaxea* is the deposit made by a common cœnosarc, and as such may be included with the cœnosarcal deposit in Pocilloporidæ, Madreporidæ, and others, under the general term "*Cœnenchyme*." One can distinguish various structural types of cœnenchyme, porous or compact, granulate, costate, smooth, &c., but these distinctions are not such as to necessitate special names.

We have then the following structural parts composing the skeleton of *Galaxea* (*cf.* figs. 1 and 4).

(1) *Radial structures*, the septa and their extrathecal costal continuations. These have in *Galaxea* striated surfaces and serrated edges.

(2) *Tangential structures*, the parts of the wall present between neighbouring

* The best general discussion of the relations obtaining between the "Randplatte" of the polyps and the cœnenchyme in cœnenchymatous colonies has been given by BOURNE, in his "Anatomy of *Mussa* and *Euphyllia*" ('Q. J. M. S.,' No. 109, pp. 41–43).

septa. These are in *Galaxea* smooth on their inner surface, striated on their outer.

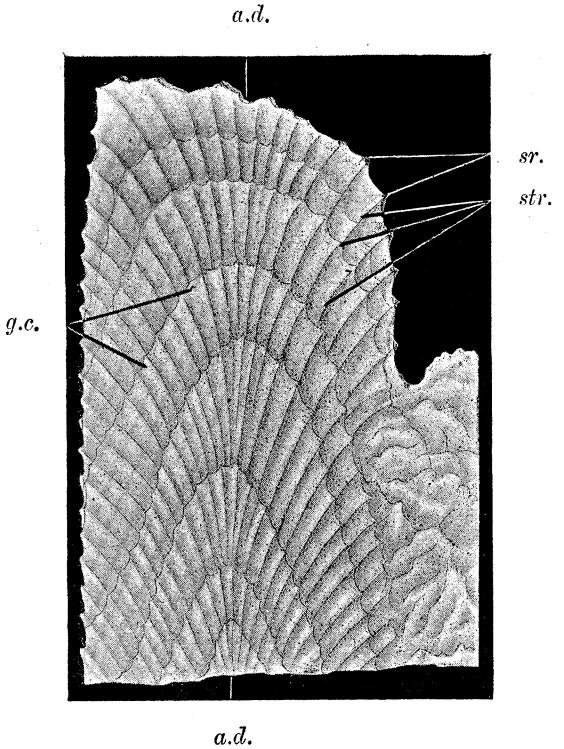
(3) *Basal structures*, the *columella* in *Galaxea* at the central part of the calyx represents irregular prolongations of the septa; the calicinal *tabulæ* are smooth basal deposits from the aboral wall; the *cœnenchymal* tissue is in *Galaxea* fine and vesicular, composed of small "*dissepiments*," and is the basal deposit of the cœnosarcal part of the aboral wall.

(4) *Epitheca*, a concentrically-furrowed basal plate formed as the edge-zones of the peripheral polyps are withdrawn.

Lateral Surface of a Radial Structure.

On examining a "radial structure" closely with hand lens, the serræ at the edges are seen to be the pointed tips of a pair of striæ on the opposite surfaces. The striæ

Fig. 3.



Lateral surface of a radial structure: *str.* = striæ; *sr.* = serræ; *a.d.* = area of divergence of striæ; *g.c.* = growth-curve.

are dotted along their course with minute granulations. Fig. 3 is an enlarged drawing made from a slightly-polished septum, the actual width of the septum from the columellar to the costal portion is not more than 2 millims. The striæ are

disposed fan-shaped upon the surface, diverging from a line about half-way between wall and columella. The lighter curves running transversely across the striæ mark successive septal edges, corresponding to distinct periods of growth in the life of the polyp. The part between two successive curves represents the addition made to the septum (incl. costa) during a single period of polypal growth, and I shall, in future, call such a part the *growth-segment of the septum*, or a *septal segment*.

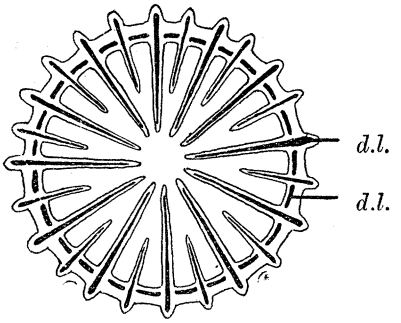
Microscopic Sections through Septa of *Galaxea*.

Location of the "Dark Line" in Transverse Sections of the Calyx.

A polished microscopic section cut transversely through a septum of *Galaxea* shows the appearance, already described in the introductory chapter, of a "dark line" in the median plane, and on both sides of it lighter-looking "stereoplasm" composed of radiating calcareous fibres. *Galaxea* is one of the forms in which the "dark line" is plainly seen to be broken up into a number of "dark points," and sometimes short, dark lines. These component parts of the "dark lines" have been in recent coral literature variously named *spines*, *septal spines*, *primary spines*, *trabeculæ*, *longitudinal ridges*, while the dark line itself has been called "*primary streak*," "*primary septum*," "*Urseptum*."

The "dark line" in the wall of *Galaxea* is similarly constituted of separate "points" and "short lines." Its position in the wall is, however, much nearer the inner than the outer surface, a fact indicating that the deposition of calcareous substance takes place chiefly on the extra-thecal part of the thecal fold. A diagrammatic representation of the position of the "dark line" in the septa and wall of *Galaxea* is given in fig. 4.

Fig. 4.



Diagrammatic section, showing the position of the "dark line" in the radial and tangential skeletal elements of *Galaxea*.

Throughout Madreporaria we find that the "dark line" is extremely variable in its position in the *wall*, but in the septa of all types, the "dark line" is *always in the median plane*.

Each of the radial and tangential structures of the skeleton has two lateral surfaces culminating in a serrated edge, and in the living state the polypal flesh folds over the edge and clothes both surfaces. In the tangential structures, *i.e.*, wall, of *Galaxea* the fold of the aboral body-wall descends much farther over the outer surface than on the inner or calicinal surface. In the radial structures, *i.e.*, septa and costal, both the lateral surfaces are clothed by the polypal flesh to equal distances below the serrated edges. Comparison of the actual structures in the skeleton with the transverse sections made of them, displays at once that the "dark line" in the section corresponds with the sharp edges of wall and septa in the skeleton. Further, that the symmetry of the calcareous deposit in the septa, and its asymmetry in the wall is correlated with equality or inequality respectively in the length of the flaps of the polypal folds.

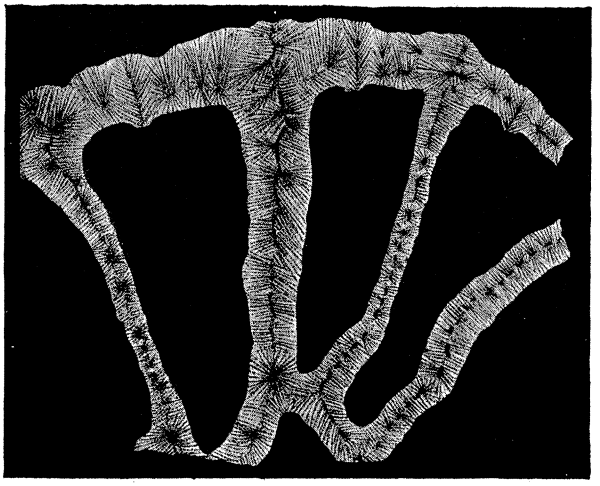
The consideration of these fundamental relations between the polyp and the skeleton is necessary before we can understand the microscopic sections of the dry skeleton. For the present the "dark line" is to be thought of as a structural appearance in the sections corresponding to the sharp angle made by the polypal folds where they bend over septa and wall. And I shall make no use of the terms "primary septum" = dark line, and "stereoplasm" or "secondary thickening" = the fibrous deposit on both sides of it. The distinction which those terms virtually express is not valid according to the results of my work.

The Growth-lines of the Septum.

Fig. 5 is a drawing of a typical transverse section of *Galaxea*, showing in its median plane *dark points*, and *short, zig-zag, dark lines*, around which fibres are placed, and radiate outwards to the surfaces. In a fairly thick section that is all that can be said of the fine structure. But in thinner sections (fig. 6) an examination with high-power lens shows exceedingly fine wavy lines crossing the calcareous fibres at right angles. As the fibres are arranged in groups around the "points" and "zig-zag lines" of the median plane, the wavy cross-lines fall into corresponding curves around those "points" and "lines." The same curves are followed by all the cross-lines in one half of the septum, from median plane to surface. The margin of the transverse section is, in consequence, notched in appearance (*cf.* fig. 6). The curves between the notches in the section correspond to granulations of the surface striæ. The width from any one of the wavy cross-lines to the next is about ·0036 millim., or, roughly calculated, about twenty-seven of them are present in one-tenth of a millimetre. KÖLLIKER described, in 1864, the striped appearance of the fibres in the transverse section of an *Astræa*, which he figured (*vide antea*, Introd., p. 87), and since that time most authors have referred to a "lamellar" appearance of the so-called "Ausfüllungsmasse" or stereoplasm, without making a closer investigation of the subject.

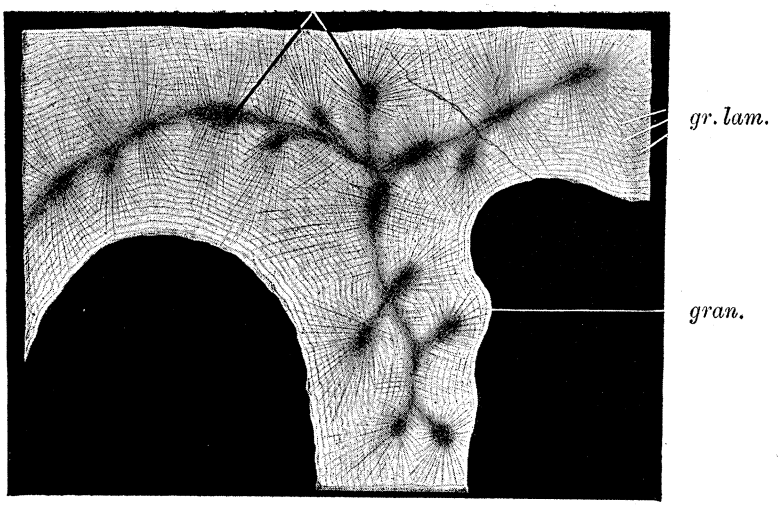
The "cross-lines" seen in transverse section represent actual lamellæ. This is proved by the fact that the fibres are crossed by similar wavy lines in sections cut longitudinally. Tangential longitudinal sections show them best, in radial longitudinal

Fig. 5.



Transverse section of a few septa and part of the wall (low power).

Fig. 6.



Transverse section of part of septum and wall showing the radiating lines of structure passing out from the "dark points," and also the wavy cross-lines corresponding to successive "growth-lamellæ" (high power); *d.p.* = dark points; *gr. lam.* = growth-lamellæ; *gran.* = granulation.

sections they are naturally very obliquely cut, and appear with zig-zagged edges irregularly outlined against one another. The lines may be compared with the growth-lines ("Anwachsstreifen") of other animal groups, and each individual

lamella is simply a *calcareous-growth-lamella.* In *Galaxea* we have seen that these lamellæ are not smooth plane surfaces, but are thrown, as it were, into a series of gentle pleats around definite axes in the median plane of the septum. The axes are represented in transverse section by the darker "points" and "short lines" in the centre of each series of curves.

Structural Relation of Septal Granulations to the "Centres of Calcification" in the Median Plane.

Finding that no matter what family of Madreporaria I selected from, the skeleton always showed these wavy growth-lines, I felt it absolutely necessary to examine them in detail.

Within each tiny wave a minute group of crystalline fibres lies. Sometimes the fibres are almost parallel with one another, sometimes more decidedly divergent. The inner part of the wave towards the median plane looks darker by transmitted light than the outer curve of the wave. And since each wave of the wavy line shows the same structure and appearance, the whole succession of lamellæ presents in sections a striped or banded appearance. If a section happens to cut the lamellæ very obliquely, the ends of the fibres are exposed in successive lamellæ. This gives a bright beaded appearance to the wave edges of the lamellæ, and considerably heightens the effect of alternating dark and light bands.

The fibres of the individual lamellæ are laid down always in the same direction, and with the same crystallographical orientation, so that, viewed with weaker magnifying power, the short fibres of successive lamellæ seem to merge with one another. The original disposition of the fibres, end to end, in successive lamellæ, is therefore one cause of the apparent radiation of fibres around the dark points in the median plane. By reason of continued crystalline change, the individual lamellæ may become ill-defined, and the fibrous structure arranges itself in definite bundles according to the primary curves of the growth-lamellæ.

In other words, a transverse section made through a granulation on one of the side surfaces of the *Galaxea* septum proves that a radiating bunch of fibres extends into it from a dark point in or very near to the median plane of the septum. And a transverse section of a septum passing through two opposite or nearly opposite granulations on the two surfaces of the septum shows two radiating bunches streaming outwards, apparently from a common centre, of opaque, structureless aspect, in the median plane of the septum.

Probably it is owing to this very frequent *appearance in transverse section* that the "spheroid" and "ellipsoid" came to be used in speaking of the Madreporarian skeleton (Introd., pp. 93–97). For sometimes the "centre" is really circular in section, sometimes it is elliptical.

I may state at once that, among the numerous corals I examined, the individual

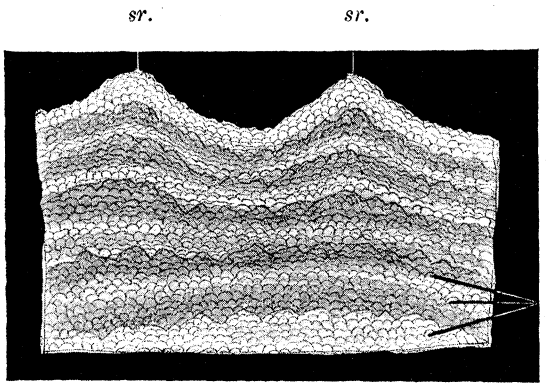
growth-lamellæ were best seen in such specimens as had been not very long removed from the sea-water. In them the fibres, even viewed with low magnifying power, were plainly seen to be interrupted by lines corresponding to growth-lamellæ. In oldish recent specimens, the radiating groups of long fibres struck the eye at once, while the original lamellar structure was less marked. In poorly-preserved fossil material the lamellæ could usually be traced, but only as mottled markings across a pronounced fibrous structure. At the same time one cannot generalize altogether, as I have seen almost all stages in a single specimen.

The Superficial Growth-Lamella Examined.

The Skeletal Elements Composing it.

The natural question suggests itself—what are the microscopic characters of the outermost growth-lamella upon the surfaces of the septum? On examining, I found that not only the surface of the septum, but also the surface of *all the skeletal parts* of *Galaxea*, showed a continuous stratum of minute calcareous elements, laid down like roofing-slates, or like epidermal scales upon one another. Similar minute

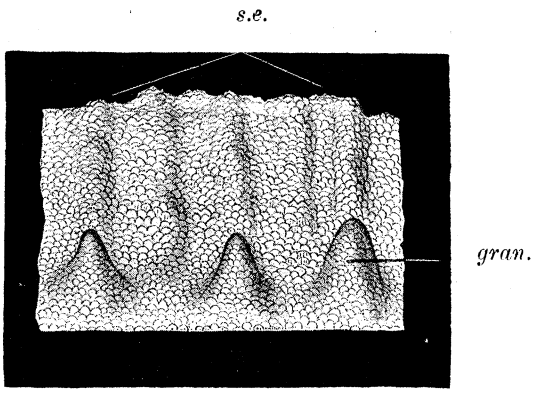
Fig. 7A.



sr. = serræ; *sc.* = scales.

The irregular lines running roughly parallel with the serrated septal edge indicate growth-lamellæ which have been cut during the polishing of the section.

Fig. 7B.

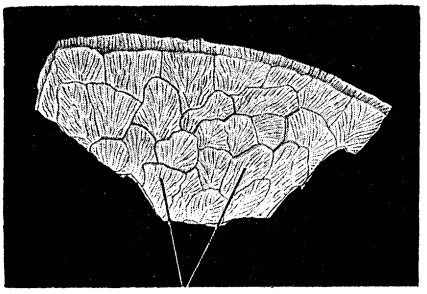


s.e. = septal edge; *gran.* = granulation covered with the calcareous scales.

elements were present in all other genera which I examined. To give an idea of their appearance and size, I have shown them in fig. 7A as they are arranged on two neighbouring teeth or "serræ" at the edge of a septum. The relative size of serra to septum will appear by comparison with fig. 3, where a whole septum is uniformly enlarged to about sixteen times its real size. Fig. 7B is another drawing of the scale-like elements showing them on part of a thicker, more striated and granulate septum.

In each of the skeletal elements a number of fibres is present, as shown in fig. 8A, drawn under high-power lens. The fibres are not always in the form of divergent groups, but appear often to lie more loosely side by side. The thick fringe of fibres at the edge is produced by the similar skeletal elements of subjacent layers. The

Fig. 8A.



sc.

Calcareous scales on the surface of a dissepiment (from the cœnenchyme of *Galaxea*—highly magnified).

breadth of these fibre-containing elements varies on an average from ·01 millim. to ·015 millim., the height is much less, about ·003 millim. Their natural position on the surface is with the broad edge directed obliquely upwards and outwards relatively to the septal plane, and the fibres arrange themselves in the same direction.

The Isolated Skeletal Element.

I made many attempts before I succeeded in isolating the individual pieces. They came apart with least trouble from the almost transparent dissepiments of the *Galaxea* cœnenchyme. A few lamellæ as seen on the surface are represented in fig. 8B; these broke down fairly readily into their constituent cells. When thus separated, most were seen to be entirely filled with a bush of minute fibres, others had granular contents, or partly fibrous, partly granular (fig. 8C). Their resemblance to the calicoblast or lime-forming cell, which HEIDER* first discovered and described, was so striking that I at once sought for farther proof of the identity of the two.

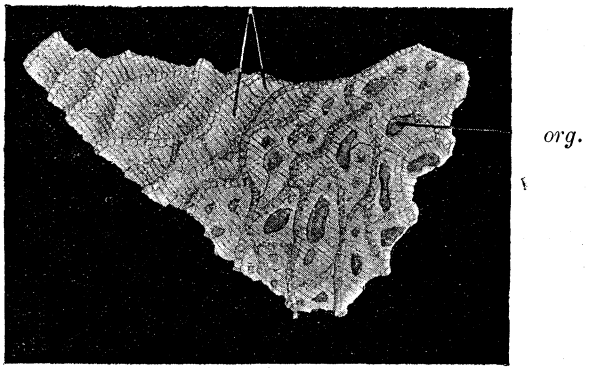
It has been frequently mentioned by writers on corals that organic remnants, after removal of the polyp, may be found on the skeleton. Wherever on the surface I found such remnants, they consisted of calicoblasts which showed in shape, size, and contents, the varieties already drawn by VON HEIDER. The cells were round, or obovate. The contents varied from yellowish organic cell-material to the inorganic fibrous condition. Comparison of my own observations on several corals with the

* A. R. VON HEIDER, *vide* Introd., p. 91, "Die Gattung *Cladocora*" and "Korallenstudien."

figures given by VON HEIDER left no doubt that the *isolated skeletal element was a calcified calicoblast cell.*

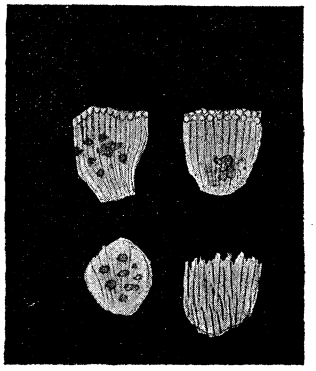
The scale-like arrangement on the surface presents irregularities—sometimes like thicker zones, sometimes thicker patches (*cf.* fig. 7A). Those are doubtless due to irregular disposition of the calicoblasts as they originally separate from the ectodermal polypal layer. We may look upon the superficial layers of the skeletal elements and of incompletely calcified calicoblasts as the outer layers of a many-layered ectoderm. The ectoderm of the Madreporarian polyp is figured by KOCH, FOWLER, BOURNE as a simple layer of cells. I have observed, on the contrary, that a section through soft and hard parts shows an ectoderm, sometimes composed of a simple cell-layer, sometimes several cells deep. HEIDER's figures indicate a similar observation.

Fig. 8B.



Galaxea dissepiment, showing several growth-lamellæ; those at or near the surface show organic remnants (*org.*) while those below have passed almost wholly into the fibro-crystalline (*f.c.*) condition.

Fig. 8C.



Individual scales separated from dissepiment = calicoblasts in various stages of calcification.

The calicoblasts remain adherent to one another in dense groups or may be more uniformly distributed. And in this manner they are gradually left behind on the skeleton, and completely calcify, while active cell-division develops constantly new ectodermal cells. The calicoblasts adherent to the skeleton represent such as were already in course of losing living continuity with the polyp at the time when the polyp was removed from the skeleton.

The above observations made on the skeletal surfaces will be seen to carry out fully the opinion of HEIDER, that the skeletal deposit forms, in the first place, *within* the calicoblast (*cf.* Introd., pp. 91–93 and 101, 102). I pointed out in the preceding chapter that KOCH's view of the extra-cellular deposition of the skeleton had been accepted by FOWLER and BOURNE. The figures given by the two last-named authorities are confined entirely to preparations made from completely decalcified

specimens. My observations have been made partly on dry skeletons, partly on skeletons from which the soft parts have been freshly removed, organic tissues remaining here and there adherent, and partly on preparations showing the body-wall in position.

Coalescence of Calicoblasts to Form a Growth-lamella.

Having thus succeeded in isolating the structural unit of the Madreporarian skeleton, it was easy to trace the connection between it and the growth-lamellæ. Actual measurement proved that the distance between lamellar bands was the same as the height of a single calicoblast—in *Galaxea*, from ·0025 millim. to ·0035 millim. And the minute groups of fibres in the individual waves of the "wavy" outline of the lamellæ agreed in their appearance and dimensions with those of the calicoblasts, and of the isolated skeletal elements of the superficial layers. Moreover, in studying the surface of the skeletal parts, I had frequent opportunity of observing that the outlines of the cells became vaguer in proportion as the calcification was more complete. The growth-lamellæ, immediately below the surface, still showed, in sections, indications of the individuality of the fibrous groups, but no actual limit. *I concluded therefore that the growth-lamellæ were originally layers of calicoblasts, and that their wavy outlines corresponded to the originally independent cells.*

The Fascicle of Fibres.

Longitudinal Tangential Septal Section. (Fig. 9.)

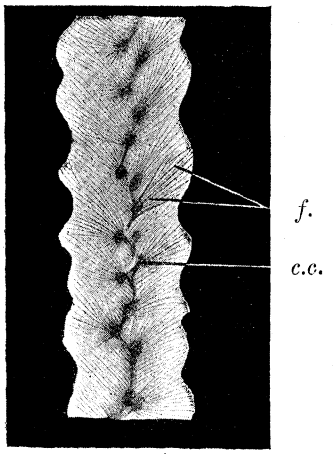
Comparison with fig. 3 will show that a tangential section of a septum will meet the surface striæ obliquely to their axis of length. I tried, with little success, to make slant sections which would meet a single stria parallel with its axis.

Fig. 9 is a small part of a slant section, showing in the axial part of the striæ "short dark lines" and knob-like ends, which are, in a general way, directed alternately upwards and outwards towards surface granulations. The study of a series of sections showed that it was a definite plan of growth which gave rise to this alternation in direction. At the beginning of any particular period of growth, the calicoblasts are grouped at first around a common centre of calcification at the upper edge of a stria, but, ultimately, two centres are developed on either side of the median plane. In this way, a pair of granulations are marked out on opposite surfaces of the stria, usually slightly alternate with one another in position.

It will now be clear why in a transverse section of the *Galaxea* septum there should be sometimes a single centre in the middle of a group of fibres, sometimes two centres, and why a centre may be seen either in the median plane or out of it. At the same time this is by no means to be looked upon as a general feature of septal structure. The "double centre" is, indeed, frequently met with, but it seldom

happens that the two centres diverge so far from one another out of the median plane as is the case in *Galaxea*. It is this which produces, in thick transverse sections of *Galaxea*, the effect of a zig-zagged dark line in the "middle" of the septum, instead of the appearance common in Astræids of a *straight* "dark line."

Fig. 9.



f. = fascicle of fibres emerging in a surface granulation.
c.c. = centre of calcification.

The tangential longitudinal section demonstrates farther that the calcareous fibres are directed upwards and outwards from the centres, or short axes, of calcification to the lateral surfaces of the septum. Thus the bundle of fibres is formed emergent at a granulation (*cf. antea*, p. 113). To this bundle I shall apply the name of a "*fascicle*" of fibres.

It will be found that when the granulations are small, as in *Galaxea*, they represent usually the emergent ends of individual fascicles. On the other hand, large granulations usually represent a number of fascicle-ends which have become coalescent.

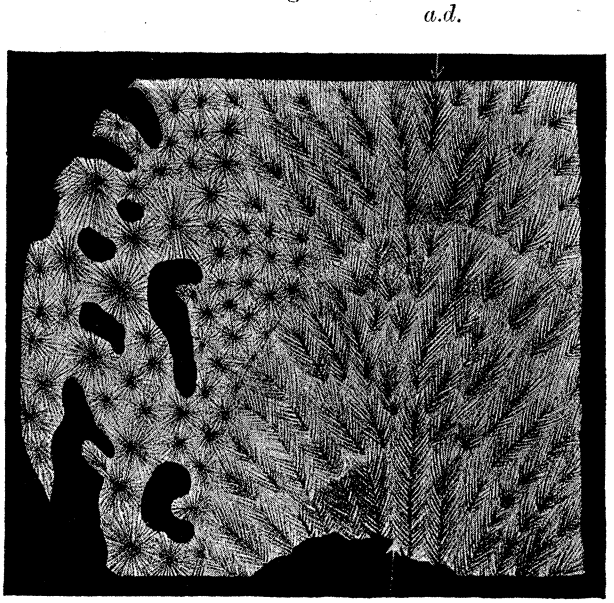
Every fascicle of fibres may be said to have an axis or ideal line of direction. The dark lines in the septum are nothing but the ideal axes of calcification around which the active deposition at the edge of the septum took place. Each uprightly-standing "axis" in longitudinal sections represents the height added at that part of the septal segment during a single growth-period, the actual deposit being the fibres of opposite fascicles. The latter are then lengthened during the next growth-period, while a new axis forms directly above the preceding, and a new pair of fascicles takes origin.

Radial Longitudinal Sections.

Full confirmation of what I have said with regard to successive axes of calcification and successive fascicles is given by radial longitudinal sections of the septum.

Fig. 10 is a longitudinal section passing through the septum and columella, the thecal part of the septum being left out. The correspondence of the vertical *series of fascicles* seen in this section, with the *striæ* on the septal surface (*cf.* fig. 3), may be very easily demonstrated practically, by watching the various stages during polishing and preparation of a thin section. It may also be deduced from measurements. The complete width of this septum is about 2 millims., and by using the hand lens one can count 15 or 16 striæ on the surface. On the other hand, the width of a series of fibres measured with the micrometer is on an average ·12 millim.

Fig. 10.



The striæ branch out to right and left from an area of divergence (*a.d.*) in the plane of the septum.

The individual fascicles are met in the section, fig. 10, sometimes transversely to their axes (*e.g.*, near the columella), sometimes more obliquely. In the latter case the distance from one fascicle in a series to the next above and below it is so slight that the individuality of separate fascicular groups is lost, and the fibres *appear* to be arranged continuously.

I made also a few microscopic preparations of the thinnest septa with mere indications of granulate eminences upon their surfaces. These showed conclusively that each granulate eminence, however small, surmounted a "dark point" in or near the median plane. The usual figure presented was that of a stellate group of fibres; where the surface had been obliquely cut in polishing, the figure became distorted and elliptical. In all cases the limiting lines between adjacent fascicles were irregular, and corresponded to the superficial furrows around granulations.

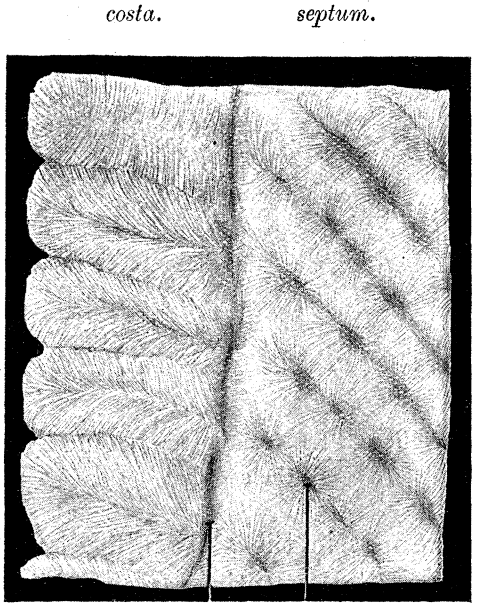
The general bearing of these observations will be better understood in the course

of the paper. Already, however, I have verified the statement which I made in Introd., p. 93, with regard to the homology of the cœnenchymal eminences in *Stylophora*, and the granulations present on the septa and costæ of many Madreporaria. Both the "cœnenchymal eminence" of *Stylophora*, and the "septal granulation" of *Galaxea* are the external expression of form produced by the growth of the fibres of the fascicle in a definite direction.

Radial Longitudinal Section through Wall and Septum.

I have given in fig. 11 a drawing of a longitudinal section which passes very obliquely out of the plane of the septum into that of the wall between two septa. Only a small part of the septum is introduced, that part in which the series of fascicles are all directed towards the costal continuation of the septum.

Fig. 11.



Radial longitudinal section through wall and septum of *Galaxea*.
c.th. = centre of calcification in the theca.
c.tr. = centre of calcification in the septal stria or trabecula.

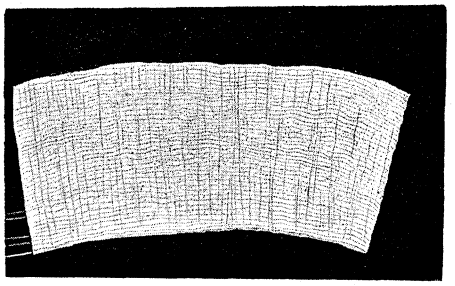
Little fibrous deposit is seen on the inner side of the dark line in the wall, whereas on the outer side, long fascicular groups extend to the serrate costal ridge, which is present on the outer surface of the wall between two septa-costal ridges. The shadowy line in the drawing giving apparent continuity to the dark centres and axes in the median plane is an attempt to reproduce the effects got by changing the focus of the microscope.

The transverse sections, fig. 5 and fig. 6, show apparently contradictory facts regarding the relations of the "dark lines" in wall and septum. In fig. 5 they are drawn separated from one another, in fig. 6 they appear continuous. The same corallite varies in this respect in *Galaxea* at different parts, according to the relative rapidity of growth between septum and wall. When the "dark line" of the septum passes continuously through the wall, more rapid growth of the septum is indicated.

Structure of Tabulæ, Dissepiments, and Columella.

The complications in the skeletal structure of the septa and wall arise as the direct result of the wrinkled and pitted character of the ectoderm which envelops those parts of the calyx (*cf.* "*Mussa*," p. 136). If we examine the structure of a dissepiment we find it much simpler. The surface of either tabula or dissepiment in *Galaxea* is *smooth*, no serræ, no striæ, no granules, and consequently its finer structure betrays no "dark points" and no radiating "fascicles" of fibres. We have in the dissepiment

Fig. 12.



Galaxea dissepiment: *g.l.* = growth-lamellæ.

a smooth structure composed of successive growth-lamellæ, laid down on one surface only, and either horizontally or slightly arched. The fibres of the lamella are seen in sections to be grouped in tiny "waves" just like those of the septal lamellæ. Fig. 12 shows the regularity of the banded lamellæ and the fibres placed perpendicular to their surfaces.

The columella is not laid down as a flat basal structure in *Galaxea*, but as occasional continuations of the septal edges. In any single calcareous piece of the irregular columellar framework, the same structure may be observed as in a marginal serra of the septum. Reference to fig. 10 will illustrate the structure.

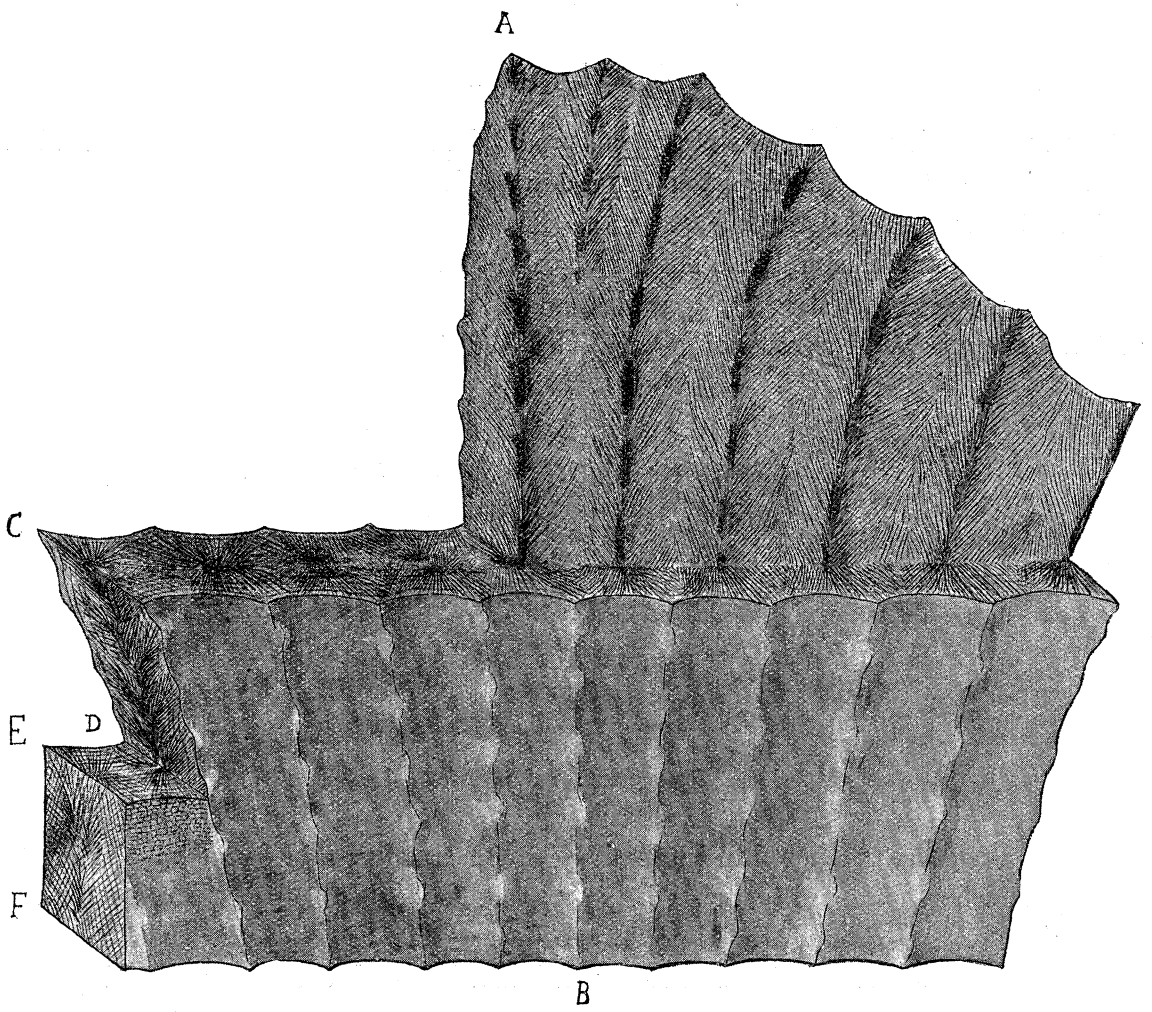
Brief description of the illustration of a typical Galaxea *septum.*

Fig. 13 gives a diagrammatic representation of a *Galaxea* septum. It will be seen that the striæ diverge towards both sides from a line AB on the surface of the

septum. At the same time these striæ are set with granulations. In order, now, to show the arrangement of the "axes" of the fascicles and that of the growth-lines, the septum is represented as if cut in different directions.

Fig. 14 shows a septum of *Mussa* cut similarly, and given here for the sake of comparison with *Galaxea*.

Fig. 13.



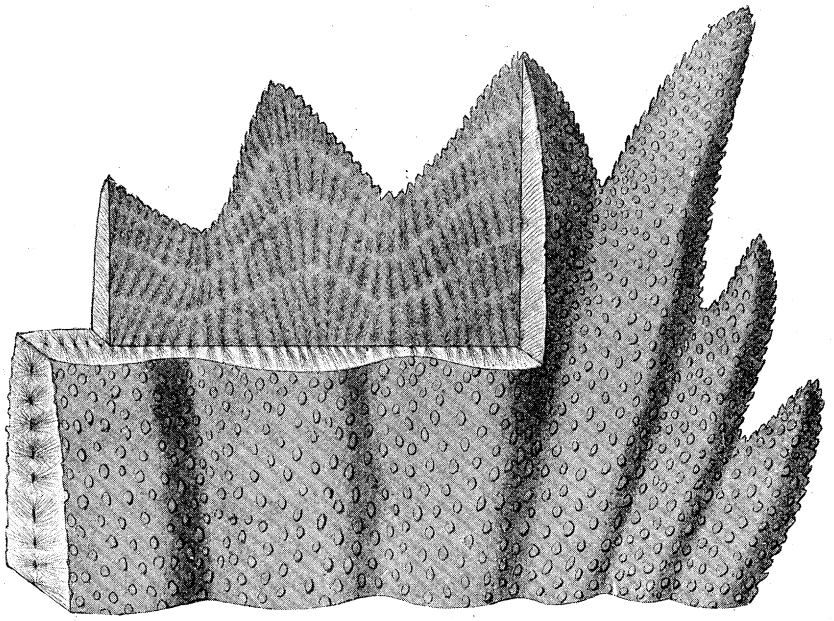
Diagrammatic view of the structure of a *Galaxea* septum.
AB direction of the "area of divergence" of septal striæ.
CD tangential section through a pair of striæ on the opposite surfaces of the septum.
EF tangential section cut obliquely to the direction of striæ.

In the upper part of the figure one must imagine the one half of the septum removed and the median plane exposed; in the lower part of the figure the septum is complete and the striated surface seen. Corresponding to the striæ in the lower part, vertical series of fascicles are present in the upper part, and from the axis of each fascicle the calcareous fibres diverge in an upwardly radiating direction. At the upper edge of the septum the fascicles give rise to fine serræ.

A horizontally-cut surface is shown by the septum at the middle of the figure. In such a section the calcareous fibres radiate outwards from the axes of the fascicles towards the surface of the septum.

At the left side of the figure a section, CD, has been cut exactly through two oppositely placed striæ. It will be seen here how the axes of the fascicles at first rise upwards, and then bend alternately towards the one surface or the other. At the same time the arrangement of the fibres is shown round the axes, and their relations to the surface; these are such that the axis of each fascicle ends in a granulation at the surface.

Fig. 14.



Similarly cut septa of *Mussa*, showing its more complex structure (ref., pp. 136–139). Four successive growth-segments are shown in longitudinal section. Distinct "fans" of diverging trabeculæ are present in each septal ridge. In *Galaxea* (fig. 13) the whole septum is composed of one such "fan" of diverging trabeculæ.

The growth-lamellæ are also indicated in the figure. Viewed in a horizontal section, they follow the direction of the surface in a general way, enclosing the axes of the fascicles like a hemispherical series of concentric laminæ on either side. But in tangential section CD, the lamellæ are no longer parallel with the surface. They still surround the fascicles concentrically; at the same time, since new lamellæ are constantly laid down around the upwardly-growing apex, each individual lamina makes an angle with the surface ultimately presented. This is the necessary result of the growth in height of the septum. A tangential longitudinal section, EF, cut anyhow through the septum, passes obliquely through striæ, and gives a more complicated figure.

Each lamina (average width ·003 to ·005 millim.) is a deposit of calicoblasts, the

wavy outline corresponding to originally *separate* cells. I have indicated to the left the scale-like arrangement of such a series of calcifying calicoblasts at the surface. Naturally, any individual series is not completely calcified before the next is laid down, but calcification is incomplete to some depth below the surface, and the regular fibrous laminæ are the result of slow crystallization (*cf.* fig. 8B).

One of the most important features in the figure is the relation of individual fascicles to the successive septal segments. It will be remembered (p. 110) that I defined the *growth-segment of a septum as the part between two growth-curves,* representing the additions made to the height of a septum during a single growth-period. The figure shows that each growth-segment is composed of a horizontal row of individual centres (axes) of calcification. The fibrous deposit around each axis is coalescent with that of neighbouring axes, and the growth-segment is therefore compact.

But each of the individual fibrous groups of the septal segment is only one in a vertical series. It is necessary to have a name for the vertical series, and no better name can be chosen than trabecula (= "poutrelle," E.H.; *cf.* Introd., p. 85), so long as it is clearly understood to refer to the fibrous deposit itself, and not to the "dark" centres of calcification. *The trabecula of* Galaxea *is composed of a vertical series of fibrous groups, each of which is deposited around a distinct axis of calcification within a single growth-period.* The axis of calcification bends out of the median plane, usually forking to opposite sides. The fibrous deposit around the divergent forks of the original axis bulges out on the lateral surface of the septum, and gives rise to a granulation.

Superficially, the trabecula of *Galaxea* is made apparent in the form of a pair of *striæ on the opposite lateral surfaces of the septum.* The "serra" in which an opposite pair of striæ culminate at the edge of the septum, is the tooth or growing apex of the trabecula. The average distance from apex to apex is ·1 to ·12 millim. in *Galaxea.* The axes of the fibrous groups are lens-shaped, and uniformly disposed in the median plane; in other words, calcification in *Galaxea* goes on rather bilaterally than radially.

I shall give the name of *trabecular part* to the individual fibrous group formed by the fascicles at one centre of calcification. The fibres of a trabecular part may be differently arranged in different genera, and even in one septum there are sometimes differences. Galaxea *affords an example of perfect uniformity in the structure of its trabecular parts, and, therefore, also in the structure of its septal-segment.*

Thus one might any day erect an exact model of the delicate calcareous framework of *Galaxea,* using, as the fundamental unit of structure, a minute bush of fibres representing the last most highly calcified stage of the calicoblast. The calicoblasts would have to be cemented together to form a lamella, but while building up the model in purely lamellar stages, in which the polyp built up the original, care would have to be taken to mould each new lamella into the form of ridge and furrow, granulation and

groove, which give to the septa and wall of the corallite its beauty of design, and which express outwardly the limits of the fibres belonging to the individual fascicles. And by the time we had built such a model of *Galaxea*, and another of *Mussa*, of *Heliastræa*, and of the largest possible number of Madreporaria, we would know something of the classificatory value of their skeletal features.

That the skeleton of the coral, when thoroughly examined, is by no means a small aid towards the establishment of a natural system of classification, has been testified by M. EDWARDS and HAIME'S treatment of the Madreporaria. Certain *external* appearances have been found to be characteristic of the various Madreporarian families and to be correlated with features of difference in the polyp itself. The main families recognized by EDWARDS and HAIME half a century ago, are recognized to-day after much searching study of the soft parts of the typical genera.

The close and critical examination of external features to which those authors submitted the corals, practically exhausted the subject from a macroscopic aspect. Still, the microscope could put many points in a clearer light, as PRATZ has already shown.

And now the identification, proved above, of HEIDER'S calicoblast or lime-forming cell with the ultimate skeletal unit on the surface of all skeletal structures, the demonstration of the part which the fibrous cell-unit plays in building up a definite skeletal lamella, makes that lamella the cell-for-cell equivalent of the ectoderm itself. Is the ectoderm smooth—so is the skeletal lamella. Is the ectoderm wrinkled, pitted, grooved—the skeletal lamella is then ridged, granulate, fluted, and the fibres of the whole series of skeletal lamellæ, instead of being arranged parallel to one another, are grouped into fascicles. The fascicles may vary in shape, and may be gathered together in different ways, their arrangement being necessarily illustrative of the original irregularities of the component lamellæ, and at the same time therefore illustrative of the form of the body-wall of the living polyp where it is applied to the supporting skeleton.

Bearing this in mind as the fundamental law of Madreporarian skeletal structure, it is clear that the starting-point of any examination of the coral skeleton with a view to its classificatory value, is,—firstly, the variation of the calcified calicoblastic growth-lamella from a smooth plane surface to the most complicated furrowed patterns; secondly, its shape at all growing edges where the primary double layer of deposit forms either in laminate shape or around separate centres in the hollows of the ectodermal fold.

THE SO-CALLED "PRIMARY STREAK."

Appearance of the "dark points" and "dark line."

In the course of the historical account of the literature I showed that recent speculation was inclined to regard the "dark line" of septum and wall as structurally

independent of the lighter-looking "stereoplasm" or fibrous tissue. The dark line in the septum has attained in fact the name of primary septum, and where it has a disconnected character, the individual points have been regarded as sections of "primary spines." This view has lately found expression more especially in the works of FRECH (Introd., pp. 99, 100), FOWLER and BOURNE have spoken of the "dark line," whether seen as a continuous line (ex. *Euphyllia*, *Flabellum*) or as disconnected points, in sections (ex. *Mussa*), as a "centre of calcification," using "centre" in a general sense. My results fully justify the term "centre of calcification."

The appearance of the "dark line" with transmitted light, although generally opaque, is not always so. It varies very considerably even in perfectly fresh skeletons. The "points" in a transverse section of *Galaxea*, for example, appear at one place homogeneous, and yellowish or dingy-brown in colour, in another place the "point" seems a fairly large, circular area filled with granular, powdery material, and then it is usually dark.

Regarding the "line," it may be said that very often the mere fissure between the two halves of a septum, which forms readily in all sections, often gives the appearance of a median "line"; but such a fissure usually ends irregularly in smaller cracks, or bends suddenly out of the median plane across one of the halves. It is, therefore, easy to distinguish it from a "dark line," which breaks up into a series of "dark points." Several authors have observed that the "dark line" in certain genera is so constituted, but it was long looked upon as a fairly accepted fact that the median "dark line" in other genera, *e.g.*, *Euphyllia*, *Flabellum*, was a really continuous line representing a special median lamina. HINDE (Introd., p. 99), in examining *Septastræa*, a genus structurally resembling *Flabellum*, found, instead of a distinct lamina in the median plane of the septum, a separable fenestrated tissue on the inner or median surfaces of both halves of the septum.

Those are the already observed facts on which the theory rests of a "primary septum" composed of "primary spines." No one has sought to explain the origin of the said "spines," or how it came about that they are so remarkably varied in size, colour, composition, whereas the rest of the septum, throughout the whole group of Madreporaria, has a perfectly definite fibrous calcareous structure.

Similar Dark Bands of the Growth-lamellæ.

In studying the "dark line" of the median plane of the septum, an important consideration appeared to me to be the exact similarity in appearance presented by the dark bands at the inner surface of each of the growth-lamellæ composing the fibrous portions of the septum (*cf.* below, figs. 30A and B). It was not difficult to recognize the cause of the latter appearance. For each calicoblast which I had observed at the superficial parts of the skeleton showed *an unchanged cell-remnant at its proximal skeletal end.* This fact can be confirmed by the use of stains.

When, now, the small size of the individual calicoblasts is remembered, it will be readily seen that adjacent proximal ends would give the appearance of a continuous band. These bands, like the "points" in the median plane, sometimes appear brownish. The highest magnifying power never displays any structure in the case of points or bands that appear dark, but only shows a *general black amorphous substance, which I can only regard as the carbonized residue of the originally unchanged organic parts of the calicoblasts.* The ultimate appearance of these portions would naturally vary according to the rapidity or slowness of subsequent changes. And infiltration of water might entirely remove the residual products and introduce foreign material; very often small crystals of salt are present.

Not infrequently the hyphæ of fungi and algæ penetrating the skeleton spread more especially in these lamellar bands, the mere fact that the growth-lamellæ are there apposed to their neighbours affording an easier ingress for the hyphæ. Decalcification proved, however, that the hyphæ ramified anywhere and everywhere, as well as in the lamellar planes. Further, decalcification brought out very clearly the identity of the *median* dark bands or points with those of the fibrous *lamellæ*. Usually, as decalcification proceeded, small tears appeared where the dark points of the median plane had been, and also in the lamellar bands; at the end of the process, the same places showed occasionally undeterminable fragments, organic and inorganic, or were entirely empty.

Thinking the "axes" of the fascicles appeared sometimes virtually solid, I thought of possible chitinous intermixture, and tested them alongside of spicules of Alcyonarians and sclerobases, partly calcareous, partly horny. The results for the "fascicle axes" of *Galaxea* were, however, always negative.

I shall frequently have to refer to the so-called "dark line" and "primary septum" in the course of the succeeding chapters.

Meantime, from examination of *Galaxea*, it may be taken that at the growing edge of the septum, the invaginated septal folds are pushed up into a series of small conical pouches, to which in the skeleton the serrated tips of the surface striæ correspond. The calicoblasts apposed to the free serrated tip arrange themselves with their proximal ends practically coalescent, and thus give rise to a *ring or circular mass of organic points*; by continued growth, the successive rings of points become the apparently homogeneous, yellowish or yellowish-brown axis in the median plane. It may also be noted that the fibres immediately surrounding the axis are diffused with finely intermixed yellowish substance,* indicating probably that the calicoblastic cells at the growing margin of the septum are at the time of deposition less completely converted into calcareous fibres than those at some distance below the margin.

* The colour was sometimes so intense as to suggest that it was inherent in the skeletal tissue in these parts. Brown-coloured barklike "epitheca" has been described for certain Turbinolids. The question deserves farther investigation.

FOWLER and BOURNE have observed the specialized character and large size of the calicoblastic cells at the growing points of the skeleton in several corals, among others *Galaxea*. Both these authors regard the calicoblasts as ectodermal cells, which merely secrete calcareous substance without being themselves calcified. They correlate the large size of these cells at the growing-points with more active deposition of the calcareous substance on the skeleton. This view is thoroughly confirmed by my observations; but since I find that the cells themselves become incorporated in the skeleton, it becomes readily understandable that those large, actively secreting cells should be incompletely calcified and retain an organic residue of some significance. This organic residue is at the actual growing apex. Whether it becomes afterwards carbonized and dark-looking, or may be otherwise chemically acted upon, even be entirely hollowed out in some cases, is a secondary matter. The term "*spine*" *is, according to my results, entirely inappropriate,* and is given in ignorance of the cause of the appearance in question; on the other hand, the term of "centre" (resp. "axis") of calcification is thoroughly fitting and may be retained.

It is of interest to compare the figures given by VON KOCH of the *embryonic skeletal deposit* (KOCH, *loc. cit.*, "Development of Astroides," 'Mitth. Neapel Stat.,' 1882, Plate 20, fig. 7). The transverse sections of "spheroids" and "ellipsoids" show calcareous fibres radiating around a central point where no fibres are present. The centre of the "sphæroid" or "ellipsoid" is the same as the "dark point" in the so-called "primary streak" (Primärstreif) of the septum. This is rendered clear by comparing the figures given by VON KOCH, in the same plate, of the growth of the septum vertically upward from the basal disc. At the same time no one thinks of calling the centre of the embryonic sphæroid a *primary sphæroid*! Why then the centres of the mature fibrous groups "primary spines," and the median area in which they happen to be most marked (because the deposit from opposite flaps there coalesces) a "*primary septum*"? *In all cases we have simply to do with centres and axes (ideal) of calcification, around which the calicoblasts are grouped in the living polyp, and from which therefore similarly oriented fibres ultimately radiate when complete calcification has taken place.*

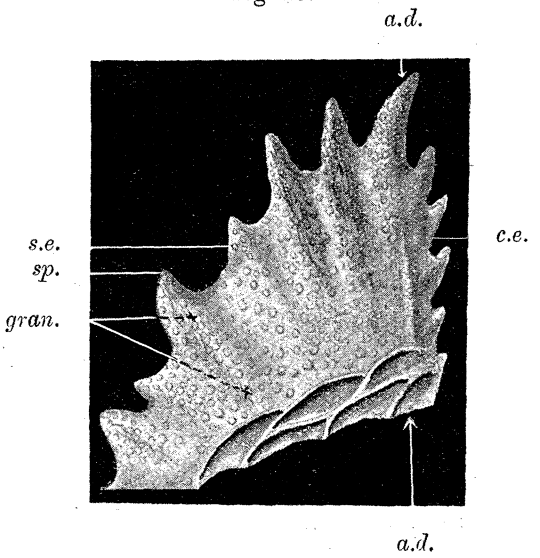
CHAPTER II.—MICROSCOPIC INVESTIGATION OF RECENT AND FOSSIL ASTRÆID TYPES.—*MUSSA*.

THE SKELETAL PARTS.

The genus *Mussa* is a well-known living representative of the sub-family Astræinæ, fam. Astræidæ, E.H., in which the septa have toothed or spined upper and inner edges, and have usually strongly-ridged lateral surfaces. *Galaxea* has previously ranked as an Eusmilinid genus, *i.e.*, with *smooth* septate edges, although the closer study followed out above has shown it to have serrated septa. It was desirable to compare the fine structure of the *Galaxea* calycinal parts, more especially the septa,

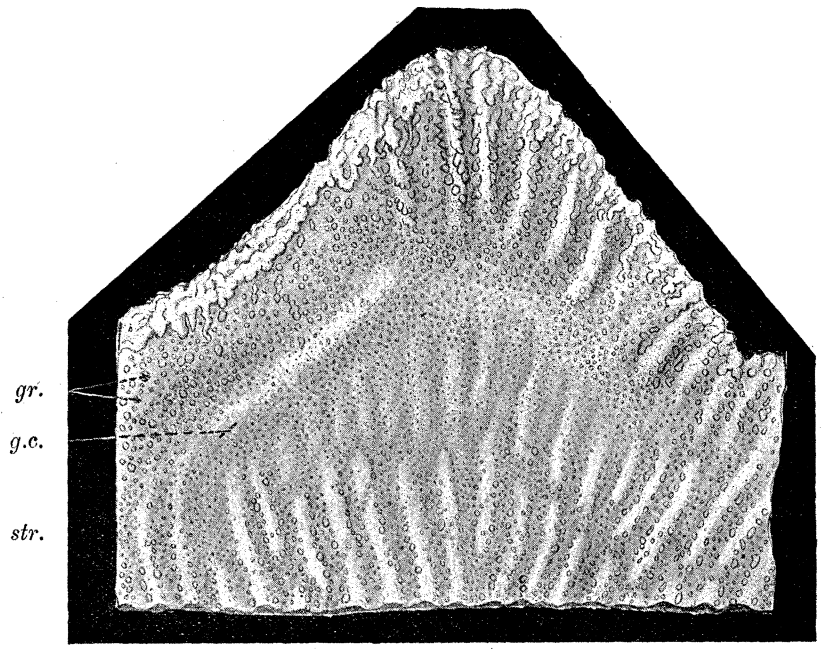
with those of Astræinæ genera. And first I selected *Mussa*, since the anatomy of the polyp had been thoroughly investigated by BOURNE (Introd., p. 101).

Fig. 15.



Upper or growing part of a *Mussa* septum; *s.e.* septal edge; *c.e.* costal edge; *sp.* spiniform teeth. *gran.* granulations coalescing on a septal ridge; *a.d.* area of divergence of septal and costal ridges.

Fig. 16.



A single spiniform tooth (40 times magnified) of one of the small, fine septa in *Mussa*, showing upwardly diverging striæ (*str.*) growth-curves (*g.c.*) and variously sized granulations (*gr.*).

The septum of *Mussa* runs out into spines of unequal length and size; these are the

"dents spiniformes" of EDWARDS and HAIME. In transverse section a single spiniform tooth is elliptical in outline, the middle part being distinctly thicker, and forming on the septal surface the most prominent part of a ridge. The surface ridges are profusely covered with granulations, of irregular size and distribution (fig. 15). Frequently the granulations on the middle of a ridge are larger, and coalesce with one another in any direction.

The shorter thinner septa of the higher cycles in *Mussa* have less prominent marginal spines and surface ridges. On each spine granulations are profusely distributed, but are of smaller size, and fine striæ may be distinguished on the lateral surfaces of a spine, resembling the striæ on the *Galaxea* septum (fig. 16). That these cannot be observed superficially on the thicker septa is due to the richer deposit of lime which obscures the original lines of structure.

The wall in *Mussa* is entirely formed by lateral thickening of the septa at the peripheral part of the calyx. A certain part is also taken by the dissepiments which are placed here at a high angle. Sections transversely cut through the wall show, however, no independent tangentially-placed ring of calcification in the intervening dissepimental deposit. This type of wall is characterized as a *pseudotheca*, in contradistinction to a *theca*, with distinct thecal centres of calcification, such as has been described for *Galaxea*.

MICROSCOPIC STRUCTURE.

Identity in the Fine Structure of the Mussa *"Spine" and the* Galaxea *Septum.*

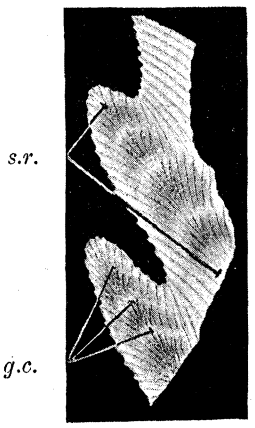
A drawing is given in fig. 17A of two adjacent spiniform teeth of a thick septum of *Mussa*, after slight polishing of the surface. Then the essential lines of structure corresponding to the striæ of *Galaxea* are easily demonstrated. And again the same evidence is afforded of the *periodic* growth upwards of the colony. Successive growth-segments, defined by distinct curves of growth between them, may be seen in each spine. Each segment is composed of a curving row of segment-parts parallel with the septal edge. The latter diverge from one another at a greater angle than in the septum of *Galaxea*, and vary more in their respective sizes and height, but the structure of each individual segment-part is the same in all, namely, a diverging group of fibrous fascicles.

Fig. 17B represents the lower of the two spines in fig. 17A, sufficiently magnified to show the fibrous fascicles. Both figures may be compared with similar preparations of the *Galaxea* septum (figs. 3 and 10). The individual parts of the successive segments are attached directly end to end, so as to form continuous trabeculæ, diverging from one another in fan-shaped form. As, moreover, the individual parts of the same growth-segment are rigidly attached side by side, the whole structure is necessarily compact.

The compactness is here associated with very close setting of the original centres

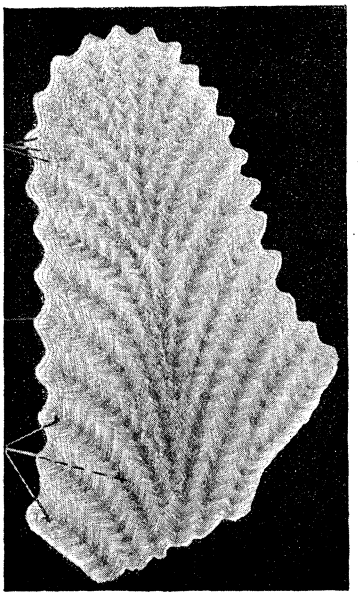
from which during any given period calcification proceeds. At the beginning of any particular growth-period the calcification goes on only *locally* at certain points of the calicoblastic layer of the colony. It then spreads outwards from those original *centres* as growth continues, and forms, before the close of the said growth-period, one continuous compact septal segment. In *Galaxea* the septal segment is in the form of one simple curve; in *Mussa* it embraces several curves according to the number of septal teeth, *each of which repeats the structure of the single curve of* Galaxea.

Fig. 17A.



Two spiniform teeth in a thick *Mussa* septum (low power). *s.r.* septal ridge; *g.c.* growth-curves marking three successive growth-segments in that septal tooth.

Fig. 17B.



One tooth (high power). *tr.* trabeculæ; *sr.* serra; *g.l.* growth-lines. The "area of divergence" of the trabeculæ runs along the middle.

The edge of a spiniform tooth in *Mussa* gives clear indication of this structure; it is finely serrated, each serra being the growing apex of a trabecula, just as in *Galaxea*.

The microscopic structure gives, therefore, conclusive evidence that *each individual spiniform tooth and corresponding ridge in the* Mussa *septum is homologous with the complete* Galaxea *septum*.

The terms "Stria," "Ridge," "Spine."

Hitherto the term "stria" might mean, according to EDWARDS' and HAIME'S precedent, either the faint ridges on a *Galaxea* septal surface, or the broad, strongly-developed ridges on the septum of types like *Mussa*. Yet a very perceptible difference may be seen by looking merely at the lateral surfaces of the septum in

both cases. In *Galaxea*, each "stria" is really linear, being almost knife-edged, and having a single granulation now and then upon it. In *Mussa*, the ridge has no sharp edge, but is a broad swelling, on which numerous granulations are scattered, apparently irregularly.

The "stria" in *Galaxea* is the surface appearance presented by a single vertical series of trabecular parts—is, in fact, uni-trabeculate; while the "ridge" of *Mussa* is an appearance produced by a diverging group of trabeculæ—is, in contradistinction, multi-trabeculate.

I shall in future give more than a descriptive value to the terms "stria" and "ridge." *The term "stria" may be limited to the superficial aspect on one side of a bilaterally symmetrical trabecula; the term "ridge" to the superficial aspect on one side of a group of trabeculæ.* In *Mussa*, the component trabeculæ of a ridge are all bilaterally symmetrical. The fibres aggregate either on both sides of one centre, or of two centres not diverging far from the median plane of the septum.

It is necessary to define those terms clearly, as I wish to avoid the use of the word "spine," which has been applied by FRECH (*cf.* Introd., p. 100) to ridges on the surface of Astræinæ septa. This same word "spine" has been used in several different senses:—

(1.) *For the surface ridge.* The appearance in question is not a spine at all.

(2.) *For the dark points seen in transverse section* in the median plane of the Astræid septum. Latterly the term "spine" has been qualified by "primary" when used in this sense, but has been invariably applied to the axis of a complete vertical series. Again, this "primary spine" was regarded as the equivalent of "trabecula," *i.e.*, both were entirely limited to the dark central area around which fibrous deposit aggregated. EDWARDS' and HAIME'S use of "poutrelle" and PRATZ' use of "Trabekel" referred to the actual calcareous structures, and that is the sense in which I use trabecula. The "primary spine" is a term which must inevitably be given up, since its existence as an "isolated pillar" (FRECH) has never been proved.

(3.) *For the spiniform tooth at the edge* of septa in *Mussa*, *Isophyllia*, &c.

(4.) *For the short, spinate, calcareous growths* (septal spines) projecting horizontally into the calyx in the place of septa in *Madrepora*, as well as for similar growths in Palæozoic genera, whatever their position in the calyx. These are the structures for which originally the term "spine" was used, and for which it must be retained.

I shall throughout the present paper limit the application of the term "septal spine" to this original use of it. It will be found to be the morphological equivalent of a *single trabecular part* in *Mussa*, *Galaxea*, &c.

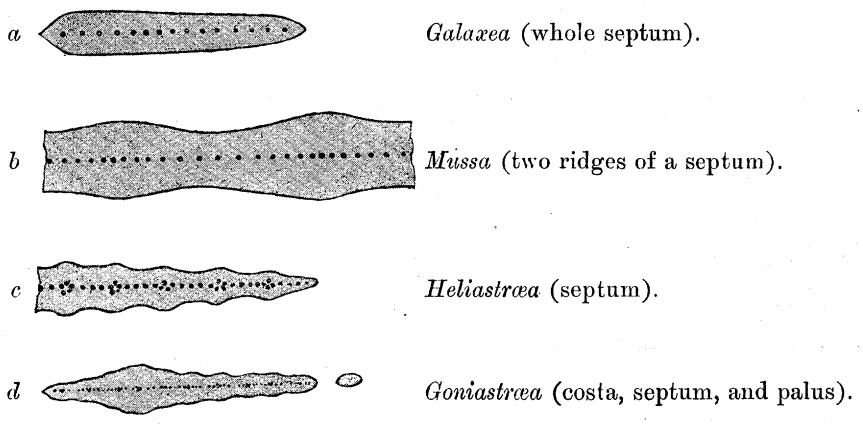
(5.) *For spinate outgrowths from the theca of Turbinolidæ.* The ornamentations on the Turbinoloid theca take sometimes one form, sometimes another;

when they are spinate, the term "spine" is justly given. At the same time, the context makes it usually clear that these are thecal outgrowths and have no connection with septal spines.

Projection Figure, representing the Distribution of Trabeculæ in various Septa.

In order to bring out clearly the homology between the septum of *Galaxea* and the ridges of the *Mussa* septum, I give a comparative diagram of their component

Fig. 18.



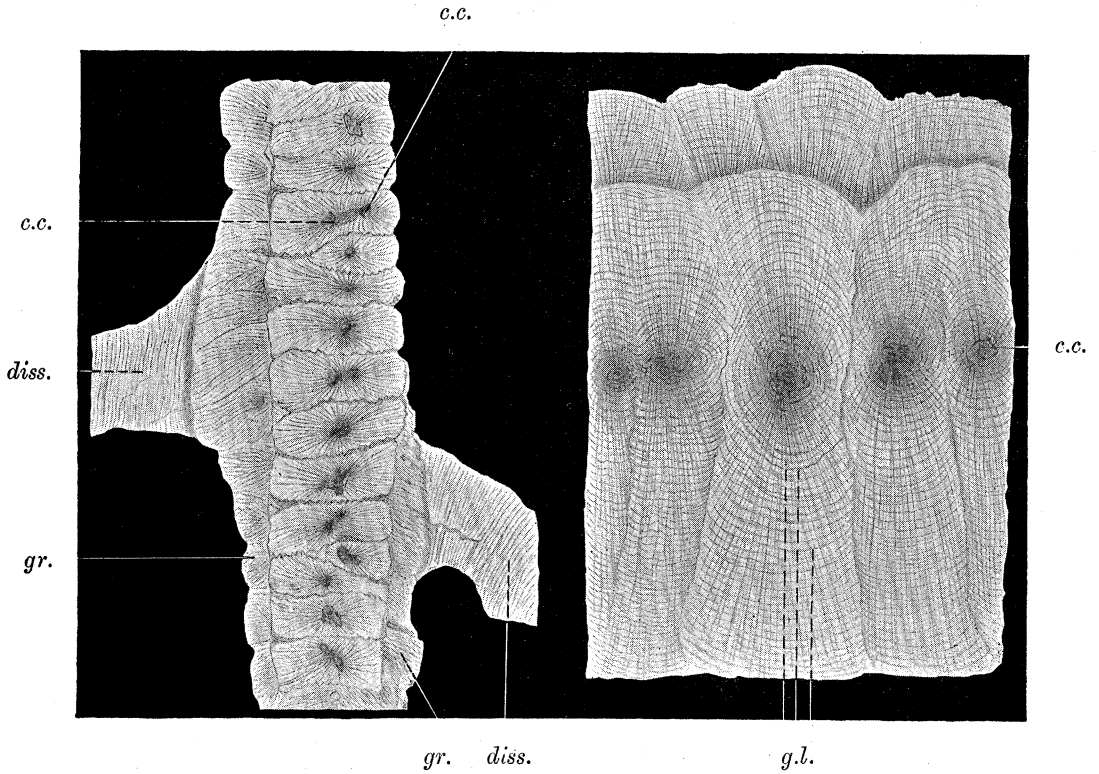
Scale diagram, showing the distribution of "centres of calcification" seen in transverse sections of various septal types.

trabeculæ (fig. 18), as represented by the distribution of the centres of calcification in a transverse section of the septum. The dimensions of the figures are drawn to true scale. Owing to their large size, only two of the ridges of *Mussa* are introduced; some six or seven ridges are present in the complete septum. Each point in the figures represents the ideal axis of a trabecula.

The projection figure of the *Galaxea* septum (fig. 18A) may be described as one symmetrical series of points, representing the symmetrically diverging group of trabeculæ. That of the *Mussa* septum (fig. 18B), if completely given, would be a symmetrical series of points, as many times repeated as there are ridges on the septal surfaces. And as the trabeculæ in the middle of a group are more closely packed together than those on either side, the whole projection figure reminds one of a graphic representation of sound waves.

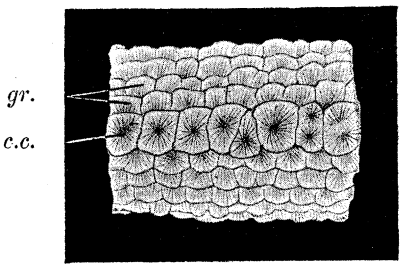
After realizing the projection figure of *Mussa*, we may transfer it with but little variation to many other genera belonging to the group of Astræinæ. In *Heliastræa* (fig. 18C), instead of uniform bilaterality in the fine structure of the trabeculæ, those in the thickest part are especially marked out from the others, inasmuch as several centres of calcification are arranged round an ideal axis, radially and at the same time

Fig. 19.



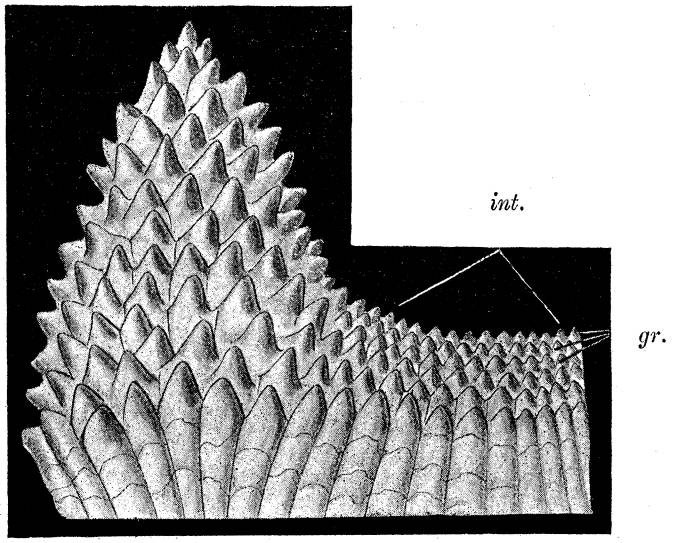
Transverse section through a thick spiniform tooth of the *Mussa* septum (low and high power); *c.c.* centre of calcification; *gr.* granulation; *g.l.* growth-lines, signifying successive growth-lamellæ (p. 125); *diss.* dissepiment.

Fig. 20A.



Transverse section through the *thin intermediate part* of a *Mussa* septum between two spiniform teeth. Several tiers of granulations are met on either side of the median plane.

Fig. 20B.



Diagrammatic drawing of a thick spiniform-toothed ridge and of the *thin intermediate part* (*int.*) with closely placed, small granulations.

to some extent spirally. The same is true, in a less degree, of the closely packed centres of calcification in the *Goniastræa* septum.

Transverse Sections through the Septal Spiniform Teeth.

As a glance at the septum of *Mussa* (fig. 15) shows, it is impossible to make a transverse section through a complete septum, cutting all the spiniform teeth perpendicularly to their axes of length, since such a section would represent a curve nearly parallel to the margin of the septum. This fact must be remembered in the consideration of the accompanying transverse sections. The thick part of one spiniform tooth of a septum has been selected for fig. 19, as the axes of the fascicle pairs in the median plane are there met almost perpendicularly, and thus show the regularity of their distance from one another—the cross-diameter of a fascicle is about ·08 millim. The continuation of this transverse section to the interdental part on both sides is not included in the figure; it naturally shows the fascicles more and more obliquely cut. The lateral parts in fig. 19, marked "gr" represent the emergent ends of fibres belonging to surface granulations. The granulations are particularly large on the thickest part of the ridge; the section has cut obliquely across the septum.

On the other hand the granulations are much smaller at the thin ends of the individual teeth or ridges, and a section which is fairly thick may cut through several upgrowing rows of granulations towards the septal edge. Such a section is given in fig. 20A, and to elucidate it, a drawing is made (slightly diagrammatic) of the surface of the ridge at both its thickest and thinnest parts (fig. 20B).

Fascicles of fibres must be imagined within each granulation shown in the surface drawing, their axes necessarily placed obliquely upwards in the direction of growth. The thin part with crowded small granulations is that which is represented in section in fig. 20.

The surface relations are very easy of demonstration by studying the fine edge of a septum with strong lens and then gradually polishing it and watching the stages. My chief reason for insisting upon the relation of the granulations is because the appearances in fig. 19 might seem at first sight to suggest a lateral deposit of "stereoplasmic" nature differing from a median "primary" deposit.

Such sections are highly characteristic of the granulate septa in Astræinæ, and more especially for thick septa of calyces belonging to a full-grown corallum. The greater lengthening and thickening of the granulations in the latter case is undoubtedly the result of the continued growth in thickness of the skeletal parts after their full growth in height has been attained. Microscopically examined, the extra thickness is produced by continued lengthening of fibres round fascicular axes. If this increase goes on long enough, the granulations next one another may often coalesce.

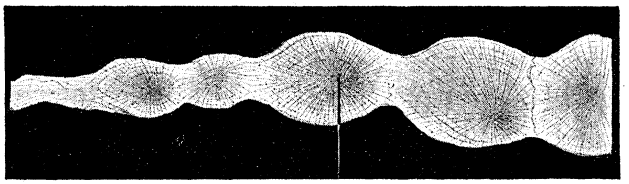
When the orientation of the fibres is the same throughout growth, from the

laying down of the first laminæ at the edge of the septal invagination to the laying down of the last layers some distance below the edge of the septum, it will be seen that (in the *Mussa* septum at least) the terms of "primary septum" and "stereoplasm" cannot well be applied in the sense of two distinct structures.

"Secondary thickening" is, on the other hand, suitable as a general term implying the continued growth in thickness characteristic of the first and second cycles of septa,* and in respectively less degree of other cycles. But it may not be taken as meaning any difference in the microscopic calcareous laminæ of the septum.

Fig. 21 is a transverse section through the thinnest septum present in a complete

Fig. 21.



c.c.

Transverse section of a very fine septum ·05 millim. thick (*cf.* fig. 19).

calycinal section. Its interest is in the fact that, although its thickness is only ·05 millim., the distance from one centre of calcification (*c.c.*) to the next is ·08 millim., exactly the same as we have already observed in the thickest septa. We may deduce, therefore, that in *Mussa* there is a minimum distance of ·08 millim. between one trabecular axis and the next, *irrespective of the particular "order" to which a septum belongs.*

Comparative Results derived from the Minute Structure of Skeletal Parts in Galaxea *or* Mussa.

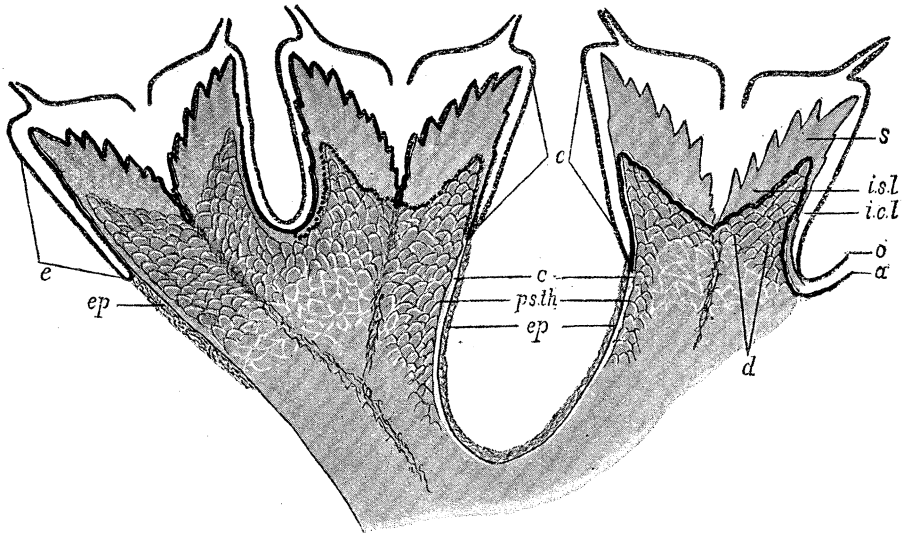
I have not thought it necessary to repeat the details of microscopic structure in *Mussa*, in so far as they coincide with those of *Galaxea* (*cf.* fig. 14). In both, the growth-lamella is formed by the coalescence of calcified calicoblasts, about ·003 millim. in height. The lamella is composed, therefore, of fine calcareous fibres set at right angles to its waved surface. Successive lamellæ are smoothly extended at the base of the polyp and form there the smooth dissepiments. In considering the septum, which differs in the two genera, it will be well to bring it into relation with the ectodermal layer of the polyp (ref. figs. 2 and 22).

The basal body-wall of the Astræid coral polyp, which rests on the dissepiments, is pocketed or invaginated upwards into the visceral cavity; and the invaginations take place all round the polyp, so as to form a complete ring of radial folds. Each

* The septa of these cycles are usually called primary and secondary septa. This use of the term "primary septum" refers to its better development and its early appearance in the embryo.

flap of the fold is drawn at a number of places inwards to the visceral cavity of the polyp. Corresponding to the irregularities on the endodermal or visceral surface of the body-wall, small pits are present on the ectodermal, skeletal-producing surface. Subsequently, *the skeletal layer of the septum is an exact cast of the form of the ectodermal flap*; that is, the original form of every pit (of various shapes and sizes at different parts of the flap) is represented by that of the corresponding eminence on the skeletal layer. The component calcified calicoblasts of the layer have their fibres set at right angles to the sides of the pit, and the eminence of the growth-lamella assumes a hemispherical, conical, or any other form, according to the shape of the ectodermal pit; in *Mussa*, the pits are mostly cylindro-conical. In all cases the fibres radiate around what was formerly the axis of the pit. By continued deposition of lamellæ a fascicle of fibres is determined, whose axis coincides with this axis.

Fig. 22.



MUSSA.—Non-cœnenchymatous type; *o.* = oral body-wall; *a.* = aboral body-wall.
e. = edge-zone; *s.* = septum; *c.* = costa.
is.l. = interseptal loculus; *ic.l.* = intercostal loculus.
ps.th. = pseudotheca; *ep.* = epitheca; *d.* = dissepiments.
(*cf.* also p. 156, and figs. 2, 35, 36, 56).

The ectodermal pits at any one growth-period are arranged in rows in *Galaxea* and in *Mussa*, and as the polyp grows upward, the new pits are exactly above the foregoing. Hence, in the skeletal surfaces of the septum, we find a continuous corrugation or "stria," on which the granulations are placed. The structure on any one stria is the same in *Mussa* and *Galaxea*. But there is an important difference in the distribution of striæ on the septa of the two genera, a difference which results from the particular form of invagination of the body-wall into radial folds. This difference will be made clear by a comparison of fig. 13 with fig. 14. The latter shows the

septum of *Mussa* cut in various directions, transversely and longitudinally, and shows the relation of the surface sculpturing to the internal microscopic structure.

In *Galaxea* one long radial fold is formed, each flap of which is pleated, and the edge delicately crimped out; in each crimp of the edge a serra of a septal stria develops. In *Mussa*, the radial fold is notched out into a series of pockets; within each pocket a "*spiniform* tooth" develops, and the flaps on either side of the pocket are goffered and crimped in a system exactly corresponding to that marking the single long pocket of the *Galaxea septum*. The notching out of the septal fold of *Mussa* allows it to have a greater areal extension, the pockets of the body-wall springing away from one another all along the low curve of the broad oval disc. This gives rise to a certain divergent arrangement of the pockets on one side and the other of the peripheral area of the calyx, the apices of the pockets being directed at right angles to the curve of the oral disc. At the same time, calcification goes on independently within each pocket, and produces there a fan-shaped group of fascicles in each growth-period. The "pockets" of the septal fold of *Mussa* are sufficiently deep to allow at least some three or four successive growth-segments to be within them.

During each growth-period a varying number of growth-lamellæ are deposited, more in thick septa than in the higher septal cycles; and, since further deposition goes on during several successive periods in *Mussa*, the septa of the main cycles attain in this genus unusual strength and thickness.

A very important point in *Mussa* is the effect produced by the stretching away of neighbouring pockets from one another. The ridges corresponding to the pockets appear afterwards definitely arranged on the radial structure. They pass inwards and upwards from the periphery towards the centre of the calyx, and outwards and upwards from the periphery towards the costal edge. The periphery of the calyx is indeed marked out as an "*area of divergence*" for the surface ridges of septum and costa. It is at this area of divergence that new pockets are invaginated, and therefore new ridges intercepted, during the course of upward growth; and the ridged radial structure is always highest at that part, *i.e.*, most exsert (*antea*, fig. 15).

So far as I have yet gone, I may distinguish two types of the Madreporarian septum:—

(1.) *Galaxea*. The radial invaginations of the aboral body-wall, in which radial skeletal structures are formed, have fluted flaps, and lay down a septum with striated, granulate surfaces and a serrated margin.

(2.) *Mussa*. The radial invaginations of the basal body-wall are drawn out into long free pockets, broad at the base and narrowing towards the apex. *Each pocket* has fluted flaps, and lays down a corrugated, granulate *ridge*, with finely-serrated margin. The whole radial structure is composed of a greater or less number of such ridges, which form adjacent ridges directed upwards and inwards in the "septal" portion of a radial structure, and

upwards and outwards in the "costal" portion. Between septal and costal portions there is, therefore, in *Mussa* an "area of divergence" of *ridges* not represented in *Galaxea*. This *complexity of structure* is characteristic of "*Astræinæ*" genera, as distinguished from a large number of the genera hitherto classified under the "*Eusmilinæ*," E.H.

The structure of both these septal types is shown in various sections, diagrammatically treated, in figs. 13 and 14, above.

In both *Mussa* and *Galaxea* I have been able to prove that there is no reality in the terms *primary spines, primary trabeculæ, primary septum.*

The anatomical researches of FOWLER and BOURNE have proved that the ectodermal calicoblasts are larger and often differently shaped above the apical *growing-parts* of the skeleton. FOWLER has proved this in *Lophohelia* and *Galaxea*, BOURNE in *Mussa* and *Euphyllia*. At the same time, no such observation was made by BOURNE on *Fungia*, and it cannot by any means be generalized.

I have indicated above the influence which the size of the cells and activity of the deposit may have in producing the appearance of the "dark line" = "primary septum" or "dark points" = "primary trabeculæ" at the median area of the septum (*antea*, p. 126). According to the amount of unchanged organic cell material, we may expect a more marked difference in the appearance of the individual growth-lamellæ. The growth-lamellæ deposited at the growing-edge of the septum are those which are afterwards observed in the median plane. They are at the same time those which have usually more unchanged organic material and a less clear crystalline deposit; those which in fossil material are found in the most highly disintegrated condition and have the most varied appearances, called forth by secondary change. No definite limit can be drawn between growth-lamellæ nearer the centre and nearer the periphery. Secondary change begins apparently at the centre and extends outwards, sometimes affecting the whole series of fibrous growth-lamellæ, which originally composed the septum.

HELIASTRÆA.

The Corallum.

The corallum of *Mussa* is usually described as branching, that of *Heliastræa* as massive. And the difference in the form of corallum is regarded as correlated with a difference in the mode of polypal increase—fissiparity in the case of *Mussa*, gemmation in *Heliastræa*. The opinions with regard to the budding of coral polyps are still divided; up to the present it has not been possible to distinguish in all cases satisfactorily between so-called budding, bud-fission and fission.

The diagrammatic figures (2, 22, 35, 36, 56) are given to illustrate various methods of calycinal union in cœnenchymatous and in non-cœnenchymatous colonies. In *Galaxea*, the calyces are said to be "surrounded" by cœnenchyme (ref. *antea*, p. 107), in *Heliastræa* they are said to be "united by costæ," in *Mussa* they are usually described as "free."

Yet, in all three genera, the soft parts of adjacent polyps are continuous. In *Mussa*, it is true, *groups* of adjacent polyps become independent of one another in the corallum correlated with the branching growth.

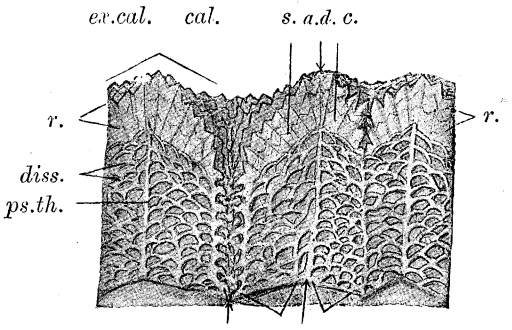
The facts show three different forms of the extracalycinal skeletal parts. In *Galaxea*, the costæ are narrow, and the intermediate space between calyces is entirely occupied by dissepiments. In *Heliastræa*, the costæ are so wide as to come usually into contact, dissepiments being developed between them. In *Mussa*, there are no dissepiments between the costæ.

The mode of increase is essentially the same in all three genera, so far as the skeletal structures afford evidence. Side branches are in all cases in open communication at their origin with the oral surface of a main branch.

General Similarity of the External Skeletal Features in Mussa *and* Heliastræa.

A hand-lens examination of the radial and basal skeletal structures of *Heliastræa* (*cf.* fig. 23) is sufficient to demonstrate that they are built up on the same general plan as those of *Mussa*.

Fig. 23.



Skeletal parts of *Heliastræa*. *cal.*, calycinal parts; *ex.cal.*, extra calycinal parts; *s.*, septum; *a.d.* area of divergence of septal and costal ridges; *c.*, costa; *r.*, ridge; *d.*, dissepiment; *ps.th.*, pseudotheca; *ps.col.*, pseudocolumella.

The radial structures, comprising septum and costa, show in *Heliastræa* as in *Mussa*, prominent teeth at their edges, and ridges on their lateral surfaces. The ridges diverge from a peripheral "area of divergence," passing in the same radial plane inwards and outwards. This "area of divergence" is the thickest part of the radial structure. At some distance below the uppermost edge of septum and costa, the tangential thickening at this area is almost sufficient to bring the neighbouring radial structures into contact. The dissepiments at the same area are strongly developed and placed more or less vertically, affording a means of coalescence of the expanded "areas of divergence." Sometimes independent "centres of calcification" are present like those in the wall of *Galaxea*, but less regular in position. Inasmuch as the wall is not composed of clearly-defined tangential structures, but may be

variously developed, it approaches the "pseudothecal" type of *Mussa*. There are, however, all transitional stages in different genera between a "pseudotheca" arising from lateral septal thickening and a "eutheca," such as that observed in *Galaxea*.

In *Heliastræa*, as in *Mussa*, growth-curves may be distinguished on the septal surfaces, marking the limits between successive septal growth-segments. A "diagonal" pattern is traceable on the lateral surfaces of the septum in *Heliastræa*, owing to uniformity in the breadth of the septal ridges and the height of the septal segments. In other words, the additional height attained by the ridge during a single growth-period is from ·35 millim. to ·45 millim., and that is also its average breadth.

Only one large granulation is marked out on the ridge during a growth-period; hence each vertical series of large granulations on the surface corresponds to successive stages of growth of the ridge.

These stages are again indicated by the successive platforms of dissepiments in the interseptal loculi, many of the dissepiments resting on the granulations of adjacent septal surfaces.

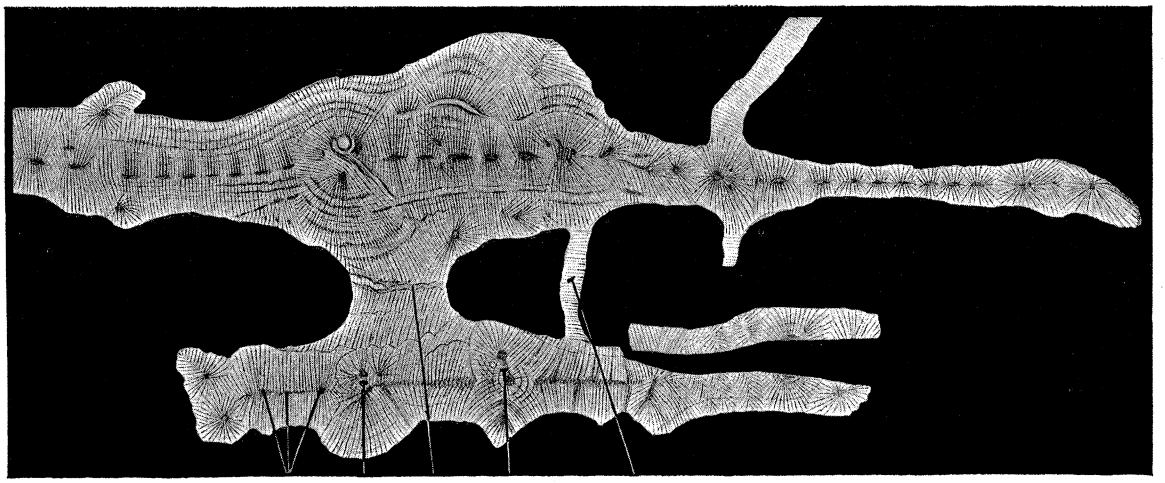
Although the external appearance of the individual ridges in *Heliastræa* and *Mussa* differs considerably, their essential microscopic structure is very similar. In both a number of trabeculæ are present. But the fibres are arranged according to two different systems in *Heliastræa* (*cf.* fig. 18c). First, there are small-sized trabeculæ, "*tr.*," in which the fibres practically arrange themselves in two oppositely-placed fascicles during a single growth-period. This is the system already observed in *Mussa*. Second, there are larger-sized trabeculæ, "*Tr.*," in the middle of each ridge, corresponding in position to the larger granulations. In these trabeculæ the "centre of deposit" is in reality a *group of centres*, very closely placed. Fibrous fascicles proceed from two, three, or more centres, and pass outward to the opposite lateral surfaces. Each large granulation represents, as a rule, coalescent fascicles belonging to this group. The appearance in transverse section of one of these larger trabeculæ, is that of radially-arranged fibres instead of the almost wholly two-sided arrangement of the fibres in the smaller trabeculæ. I propose to call the large-sized trabeculæ, with a group of centres, *compound trabeculæ*, and the smaller-sized trabeculæ *simple trabeculæ*.

Transverse Sections.

The microscopic structure of the trabeculæ composing the septum in *Heliastræa*, is represented in the sections. Figs. 24A and 24B are horizontal transverse sections of the septum. In fig. 24A it will be seen that in some parts the dark-looking centres of calcification are closely placed in rows; occasionally a pair of axes are cut corresponding to the portions of fascicles bending outwards to the surface. At intervals in the section thicker trabeculæ are present, in which the growth-lamellæ become strongly concentric and bend in out-springing curves around a common centre. In the centre there is not one dark point nor two, as we have observed

in sections of *Galaxea* and *Mussa*, but three or four distinct centres of calcification are present. The concentric growth-lamellæ curve in and out around them in the middle part, although the later curves no longer follow the individual centres but enclose all. The diameter of the smaller, "simple" trabeculæ, is from ·04 to ·05 millim.,

Fig. 24A.



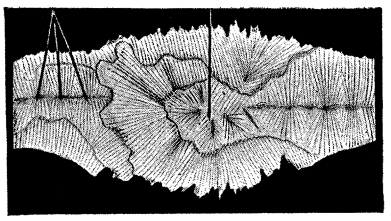
Transverse section of two adjoining septa of *Heliastræa*, one of the septa having split along the median plane (containing the so-called "dark line") of the septum.

c.Tr. Centres of calcification in *compound* trabeculæ.

c.tr. „ „ „ *simple* trabeculæ.

ps.th. Pseudothecal, and *d.*, dissepimental deposit is shown to be *without* individual centres of calcification.

Fig. 24B.



Thick central portion of a septal ridge formed by a "compound" trabecula (*Tr.*); and the thinner lateral wings of the same ridge passing into corresponding furrows—only "simple" trabeculæ (*tr.*) are present in these. (Magnified 70 times.)

that of the larger trabeculæ varies according to their position, those at the peripheral part of the septum being largest. Their average diameter is from ·09 to ·12 millim.

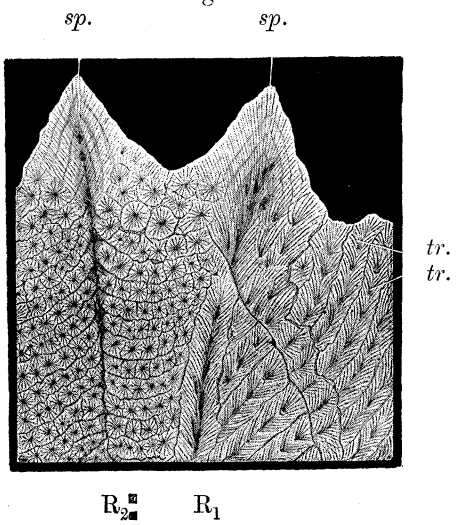
Fig. 24B shows four small fascicles in the centre of a large trabecula, and the fibres radiate upwards and outwards. It may be said that radial symmetry marks

the system of fascicles in the thick, central portion of any septal ridge, while bilateral symmetry marks the thinner, lateral wings.

Longitudinal Section (Radial).

Fig. 25 shows a longitudinal section parallel with the surface and passing through

Fig. 25.



Longitudinal section parallel with the septal plane; R_1 septal ridge met along the median plane; R_2 septal ridge met very obliquely; *tr.* trabeculæ; *sp.* spiniform teeth.

two septal ridges. The thick part of one ridge, "R_1," and the thinner lateral area next it are met by the section nearly in the median plane; in the other ridge, "R_2," the section passes obliquely through the septum towards the outer surface.

The arrangement of the fibres in the different parts comes better out in longitudinal than in radial sections. The highly oblique position of the fibres in the central "primary" deposit of the compound trabecula, and their less oblique position in the subsequent thickening of the same trabecula is readily perceived. In the other trabeculæ of "R_1" the fibres are also seen to be directed obliquely upwards, but in R_2 the figure shows only dark points from which fibres radiate. As R_2 is cut near the surface, and this appearance of the fibres proves that they are cut almost transversely to the (ideal) axis of the fascicle, it may be deduced that the fascicles bend sharply from an upward direction perpendicularly outwards to the surface.

The general conclusions for the *Heliastræa* septum which may be drawn from these sections are:—

(1.) The primary deposit laid down at the edge, at the beginning of an active period of growth, is limited to certain areas at some distance from one another; this primary deposit is represented by the central part of the main trabeculæ.

(2.) As the growth proceeds, deposit takes place more uniformly and fills up the intervening spaces.

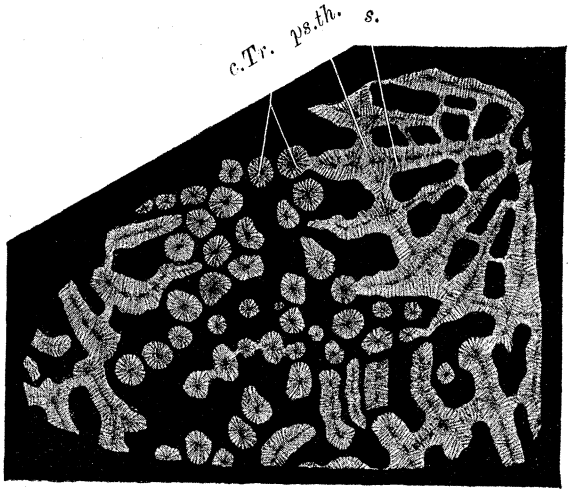
(3.) The fibres of the primary deposit are laid down within small conical pouches of the body-wall, and are obliquely and radially placed with regard to the centre of calcification; those which are afterwards deposited are laid down from the side-flaps of the septal invagination, and have, in consequence, a tendency to be less and less oblique. The fibrous deposit in the small trabeculæ is uniformly oriented throughout; in the larger trabeculæ, however, the first-formed fibres are fairly distinct from the fibrous deposit made towards the close of the same growth-period and during succeeding periods.

In the sections* of *Heliastræa* yellowish matter was often seen penetrating the fibres, and especially in the laminæ near the median plane of the septum. It often made the fibres seem brown, instead of clear and crystalline as they appeared in other parts. The organic nature of this yellowish matter was capable of chemical proof by the action of re-agents. I regarded it as a less altered condition of organic cell-material than that which gave rise to the dark "axes" in the *Galaxea* fascicles.

The Costæ.

An interesting feature is frequently noticeable in the costate portion of the *Heliastræa* septum; viz., the entire absence of small trabeculæ. The ridges often run out

Fig. 26.



Transverse section showing the radial trabeculæ (comp.) in the intercalycinal portions of the *Heliastræa* skeleton; *c.Tr.* costal trabeculæ radial in structure; *ps.th.* pseudotheca; *s.* septum.

nto longish trabeculæ, in no way connected with one another. The transverse section (fig. 26) shows how these individual trabeculate ends produce a figure of radial sym-

* Special care was taken in mounting, neither canada balsam nor shellac being used. Sections were viewed under water or pure glycerine.

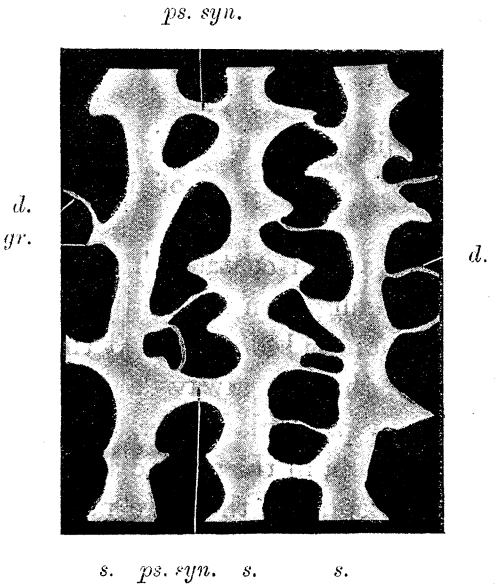
metry corresponding to that which I have described above for the larger trabeculæ in the calycinal part of the septo-costa. But I could not observe any difference in the orientation of the fibres, apparently the costal deposit begins to be laid down somewhat later than that in the exsert septal part, and there is not a primary as distinct from a secondary direction of the fibrous deposit.

Longitudinal Section (Tangential).

Generally speaking, the diameter of a fascicle in a large trabecula of *Heliastræa* is about the same size as that of *Mussa*. The fascicles emerge rapidly on the thick part of the ridge, and it is their coalescence which gives rise to the large granulation corresponding to an individual growth-segment in the ridge.

Secondary thickening may continue to accumulate on the granulation until the latter comes into contact, in the interseptal loculus, with a similarly thickened granulation projecting from the adjacent face of the next septum. By this contact a "*pseudosynapticula*" is formed such as PRATZ has described in the group of Pseudoastræinæ. It has been thought that "pseudosynapticulæ" were not present in Astræids, but my observations show them to be fairly common.

Fig. 27.



Longitudinal section (low power) through three adjacent septa, showing "pseudosynapticular" union between them, by means of the continued growth of granulations; *d.*, dissepiment; *gr.*, granulations; *ps. syn.*, pseudosynapticula; *s.*, septum.

A tangential section is given which has passed through three neighbouring septa (fig. 27), and shows how the dissepiments often weld granulations together. The same section shows occasional pseudosynapticular union. The figure may be directly

compared with similarly-cut sections figured by PRATZ in illustration of *Cyclolites* ('Palæontographica,' *loc. cit.*, 1882, Plate 14, fig. 7), and of *Thamnastræa* (*loc. cit.*, Plate 14, fig. 12).

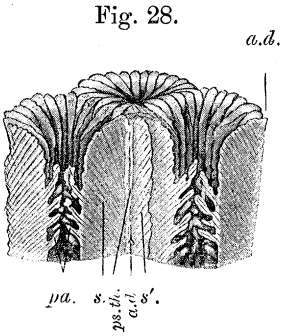
GONIASTRÆA.

The Chief Structural Difference from Mussa *and* Heliastræa *is the almost complete absence of an Edge-Zone* (*Randplatte*).

I selected *Goniastræa* in order to study more especially the relations of the pali to the septa.

The external features of the calyces are exhibited in fig. 28. *Goniastræa* has

Fig. 28.



Skeletal parts of *Goniastræa*. *s.*, large septum in one calyx; *s'.*, small septum in the adjoining calyx; *pa.*, pali; *ps.th.*, pseudotheca; *a.d.*, area of divergence.

faint ridges on the septa resembling those of *Heliastræa*, but so small and flat as to be scarcely visible were it not for the presence of distinct pointed granulations upon them.

The walls of adjoining calyces are in contact throughout their entire length, the *ridges* of the radial structures passing from the peripheral "area of divergence" into two *septal* wings instead of a septal and a costal. At the same time, it is noteworthy that in any one radial structure there is always a longer and a shorter wing. In other words, the long septa in any particular calyx correspond to the short septa in adjoining calyces, and the short septa in the same calyx correspond to the long septa in adjoining calyces. The short septa are therefore practically homologous with the costal wings of septa in genera like *Mussa* and *Heliastræa*.

This is of interest in the study of the edge-zone (Randplatte) in Astræids. The costæ are formed by the polypal edge-zone in *Mussa* and *Heliastræa*, and it would seem at first sight that genera like *Goniastræa* and *Prionastræa* were devoid of edge-zones. KLUNZINGER however notes that very often in these and allied genera an irregular appearance of intermediate tissue occurs in slight furrows between the walls. In transverse sections of the skeleton also, angular spaces occur between the walls of calyces more or less filled by calcareous deposits. The latter is laid down

around several centres of calcification without any definite position relative to calycinal parts.

The edge-zone may at the same time be regarded as much curtailed. In correlation with this fact we find that increase of the colony is said to take place by means of "*central*" *and* "*parietal*" *intracalycinal* budding. As KLUNZINGER says, central intracalycinal budding is not distinguishable from the fission ("Theilung") in *Favia*.

A study of various skeletons shows that all these forms of increase are identical with what has been called "septal budding" in fossil Palæozoic forms. In *Goniastræa*, "budding" is indicated in a calyx in two ways :—(1) Two pali in front of septa extending from opposite walls grow more rapidly upwards than the rest of the pali and are thickened so as to coalesce with the septa and form a diametric line of fission across the calyx—this corresponds to "central" intracalycinal budding; (2) Two pali in front of septa extending from adjacent walls of the calyx form with their septa a curving line of fission (sometimes the septa themselves coalesce without the aid of pali)—this corresponds to "parietal" intracalycinal budding. Both are merely varieties of "endothecal budding." The extreme form of intracalycinal budding is shown by meandroid colonies.

On the other hand polyps with a well-developed edge-zone send out their buds in the edge-zone, the buds being then said to be "extracalycinal." An extracalycinal bud may, on developing, remain in communication with the mother-polyp by means of its edge-zone (ex. *Heliastræa*); or the mother-polyp and the bud may gradually become disconnected and the bud grow up as an independent branch (ex. *Calamophyllia*). *Mussa* is a genus which produces intracalycinal and extracalycinal buds almost with equal facility, the extracalycinal buds developing as branches, the intracalycinal buds remaining as a "fissiparous" series at the head of each branch. Both modes of budding may lay the same claim to ancientness, since both occur in Palæozoic colonies, but the intracalycinal buds became in primitive forms always distinct from the mother-polyp. The earliest cases of fissiparous, meandroid colonies are, so far as I know, of Triassic age, being the "Latimæandroid" variety of the genus *Isastræa*.

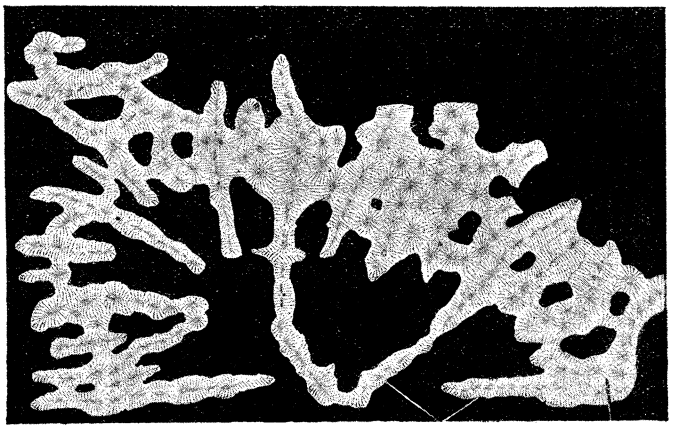
MICROSCOPIC STRUCTURE.

Transverse Sections of Septa.

Fig. 29A is a transverse section made through one-half of a calyx. The septa are seen to pass through the thickened *septal* wall into the adjacent calyces. In this figure elliptical centres of calcification are seen in the median plane of the septa at regular distances, and corresponding in position to the ridges on the opposite septal surfaces. Although this is a correct conception of the structural form in the *Goniastræa* septum, it has been rendered rather diagrammatic in the drawing, which also omits to introduce the fine growth-lamellæ.

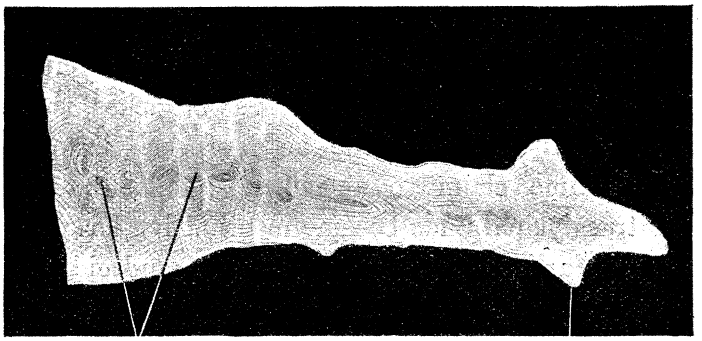
The transverse sections seldom show such a definite and regular septal structure; I have drawn in fig. 29B a transverse septal section with fairly typical structural features. The actual number of growth-lamellæ present in one-half of a primary septum is as much as from 40 to 50; in the drawing far fewer are given, for the sake of clearness.

Fig. 29A.



Transverse section (20 times magnified). *s.*, septa; *ps.th.*, pseudotheca.

Fig. 29B.



Transverse section (70 times magnified) of a septum of *Goniastræa*, showing the curving lines of the growth-lamellæ crossed by the calcareous fibres. *c.c.*, centres of calcification; *gr.*, granulation.

The centres of calcification are placed very closely, and in the thin part of the septum always singly. Where the septum thickens in the wall area, two, three, or four centres are often seen massed together, and forming a common group-centre for the growth-lamellæ. The first feature which occurs to one in looking at fig. 29B is the absence of any large trabeculæ in the thin part of the septum, like those in *Heliastræa*, corresponding to the prominent parts of the ridges. The trabeculæ in *Goniastræa*, so far as they can be clearly distinguished, have a diameter of ·03 millim. to ·04 millim., the smallest I have yet had occasion to describe. At the same time the surface

ridge has a diameter of about ·15 millim. Sometimes the centres of calcification appear in transverse section even closer together than ·03 millim., and then they may be looked upon as almost coalescent. Short rows of such closely-placed centres produce the elliptical appearance represented in fig. 29A. The application of higher magnifying power, however, shows that the elliptical centre is in reality a combination of centres. It follows that the ridges on opposite surfaces of the septum in *Goniastræa* are structurally composed of several very small, uniformly-developed trabeculæ (*cf.* fig. 18D).

Correlated with the small size of the trabeculæ is the fact that the granulations on the ridges seldom correspond to a fascicle of fibres emerging from a single trabecula; they usually represent the coalesced fascicles passing out from the ridge-series of trabeculæ. Examples of small and large granulations can be studied in the accompanying sections.

Transverse sections of the septal pali offer nothing different from the septa. One or two ridges may be included in a single palus, and the structural appearance is the same as in the septal ridges.

Transverse Section of Wall (= Pseudotheca).

The thick parts of the septa coalesce laterally to form the wall. The trabeculæ in the mural part of a septum are much larger than those in the thinner calycinal portion. Fig. 30A shows three septa in the mural area, the middle septum in the figure being short. It will be observed that the growth-lamellæ (*cf.* fig. 30B) arrange themselves in concentric form around the axes of the trabeculæ, and the fibres radiate out freely in all directions. One might say radial symmetry of the fibres distinguished the large trabeculæ of the mural area, while bilateral symmetry was characteristic of the minute trabeculæ in the rest of the septum.

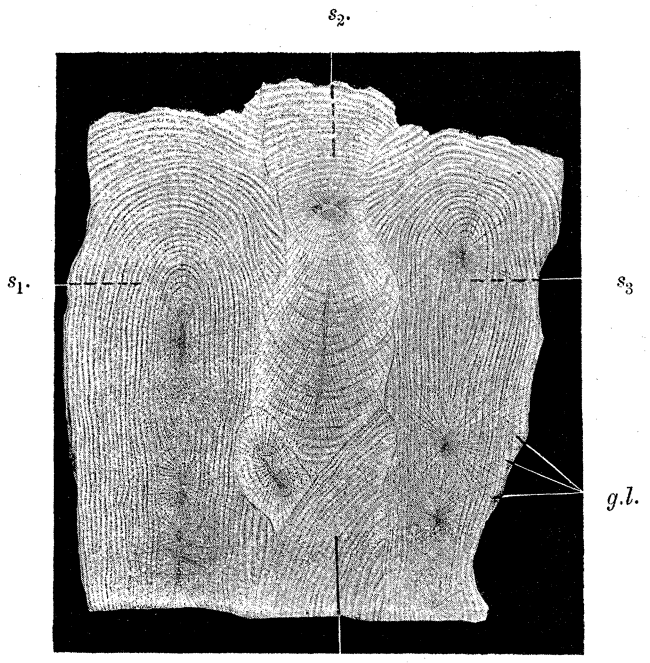
A well-developed dissepiment rests across the inner point of the short septum in fig. 30A. It is frequently seen that the close application of the dissepiments to short septa helps to make the wall stronger and thicker.

Tangential Longitudinal Section.

Fig. 31 presents a tangential vertical section through one septum, which has cut three adjacent ridges. The ridges lettered *a* and *c* happen to have been cut where granulations are present on the opposite surfaces; the ridge *b*, on the other hand, is cut at a smooth part of its course. The fibres within the granulations necessarily arrange themselves in the form of a large fascicle, since they are laid down originally at right angles to the planes of successive growth-lamellæ. The fascicle is all the more marked in *Goniastræa*, since the shape assumed by the granulation is extremely conical.

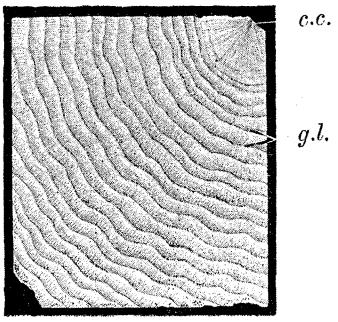
Later, in studying *Siderastræa*, granulations will be observed which have a flattish

Fig. 30A.



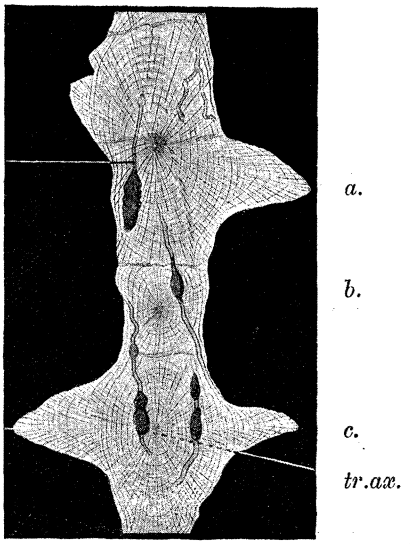
Transverse section of the wall area between two adjoining calyces of *Goniastræa*; large, compound trabeculæ are present in the septa ($s_1 s_2 s_3$), and thickened dissepiments (*d.*) add farther stability.

Fig. 30B.



A small portion of fig. 30A seen under very high microscopic power. *c.c.*, centre of calcification; *g.l.*, growth lamellæ, edged by dark bands (*cf.* p. 125).

Fig. 31.



Septum cut lengthways. The septal ridge "*c*" shows an almost *transverse* section of the ridge trabecula with granulations on opposite surfaces. *tr.ax.*, trabecular centre or axis; *h*, hypha of a fungal growth.

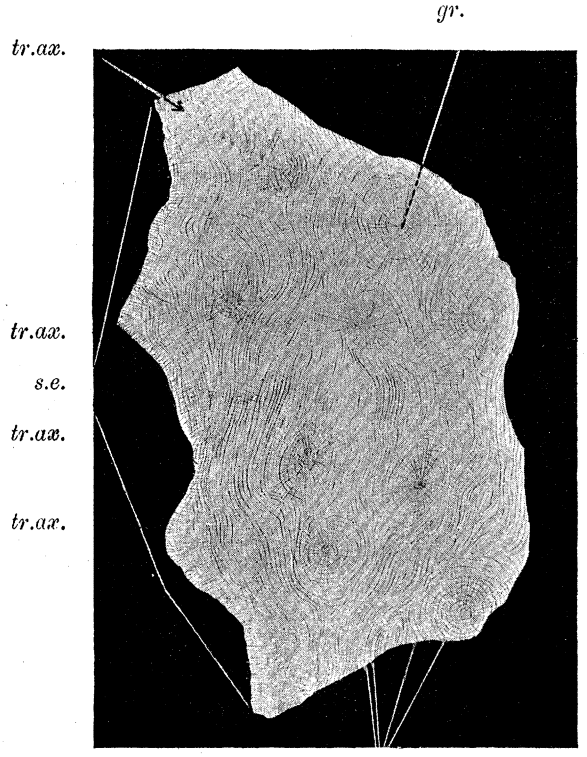
or gently rounded shape, and in which the fibres are almost parallel with one another. It is in the case of such blunt, broad granulations that a tendency arises for the granulations of adjacent ridges to unite and form "pseudo-synapticular" bars across the septal surface. In *Goniastræa*, however, although the base of the granulations may practically span the whole diameter of a surface ridge, the granulation itself tapers off and remains always isolated from its neighbours.

A few fungal hyphæ have been introduced into the figure, in their relative proportions. The growth of fungi and algæ disfigured a large number of the thin sections in this and other genera. Farther drawings are given below (figs. 33A, 33B).

Radial Longitudinal Section.

The radial longitudinal sections through *Goniastræa* septa were especially interesting. The specimen mainly examined was a perfectly fresh one, and showed the

Fig. 32.

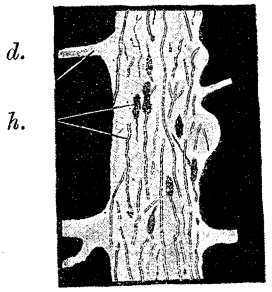


Longitudinal section parallel with the septal plane. Four trabecular axes (*tr.ax.*) run from their apices at the septal edge (*s.e.*) obliquely downwards through the section, and the latter thus meets four different "ridge" series of granulations (*gr.*); growth-lamellæ (*g.l.*).

calcareous lamellæ in mostly unaltered conditions. The surface section of a few ridges in fig. 32 shows the general distribution of the lamellar lines, although it was scarcely possible to reproduce them in a freehand drawing in all their fineness of structure.

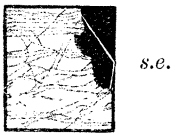
The ends of the crystalline fibres mark out the edges of growth-lamellæ like rows of beads. In places where the heads of granulations have been rubbed off by polishing, a series of concentric lamellæ still gives evidence of the characteristic conical shape of the lamellar deposit. The polishing has the effect of showing the growth-lamellæ of a granulation as it were *in ground plan.*

Fig. 33A.



Vertical section of septum penetrated with fungal growth.

Fig. 33B.



Section parallel with septal plane. *d.* dissepiment; *h.* fungal hyphæ; *s.e.* septal edge.

Figs. 33A and 33B are given to illustrate fungal growth in coral skeletons. Fig. 33A is a tangential longitudinal section of one septum of *Goniastræa,* which is penetrated by fructifying hyphæ. Fig. 33B is a part of a radial longitudinal section of a *Mussa* septum, in which near the edge the hyphæ almost give the appearance of a regular canalicular system in the skeletal parts. I have also had occasion to observe the extreme frequency of algal and fungal growths penetrating *fossil* specimens.

Summary of the Microscopic Sections.

Summing up briefly the results which may be deduced from these fine sections of *Goniastræa,* we find :—

(1.) *That* Goniastræa, *like* Mussa *and* Heliastræa, *has septal ridges, each of which is composed of a number of trabeculæ.* At the same time the upper edge of the septum is not deeply toothed in *Goniastræa*; the teeth are flat and have blunt points. Yet the structure shows conclusively here as in *Mussa* and *Heliastræa* that the septal invagination is notched out into a series of main pouches (corresponding to the teeth), and that in each pouch a number of active areas of calcification are marked out. Calicoblasts are deposited around these areas, and the minute trabeculæ are formed. As thickening proceeds, the original distinction of separate trabeculæ becomes rapidly lost in *Goniastræa,* and the large granulations which form correspond usually in diameter to the whole diameter of the pouch, respectively ridge.

(2.) *That* Goniastræa, *like* Mussa *and* Heliastræa, *and unlike* Galaxea, has a

wall mainly formed by thickening of the septa, and still further thickened internally by dissepimental deposit.

(3.) *Goniastræa*, unlike *Mussa* and *Heliastræa*, has not a deeply-toothed septal edge.

This feature is probably correlated with a tendency in *Goniastræa* and its allies to have paliform continuations of the septa. Each such palus has precisely the same microscopic structure as the septum, and is morphologically a specially large tooth of great importance in fission. The identity of the microscopic structure in septum and palus is important, as it at once distinguishes the pali of *Goniastræa* from those of the Trochocyathus group of Turbinolidæ.

In the *Goniastræa* palus one, two, or more trabecular ridges may be present. It is, in short, a pronounced form of the septal continuations in many Astræidæ which give rise to a so-called "spongiose" columella (*cf. Rhabdophyllia*).

Montlivaltia.

Although it is not my intention in this paper to include detailed microscopic sections of fossil genera, I am of opinion that the important fossil genus *Montlivaltia* has a septum whose structure is nearest to those above described as of *compound* or radio-symmetric *trabecular* type. Hitherto *Montlivaltia*, *Thecosmilia*, *Rhabdophyllia*, have been classified in the Lithophyllaceæ, E.H., along with *Mussa*; according to their microscopic structure, however, they resemble more closely typical genera belonging to the Astræaceæ, E.H. (= Astræinæ, Klz. + Meandrininæ, Klz.). They have, like *Heliastræa*, ridges of equal width on the septal surfaces, culminating in conical teeth at the upper edge. Moreover, each ridge is marked out by a series of prominent granulations corresponding to successive segments of growth.

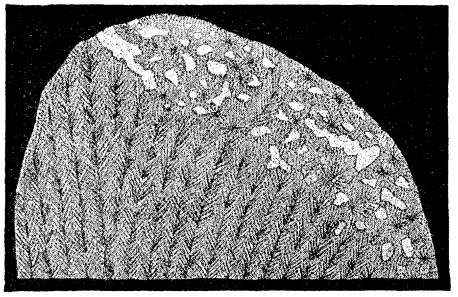
Figs. 34A and 34B are sections made from the Triassic species *Montlivaltia norica*,* Frech, and from the Cretaceous genus *Montlivaltia rudis*, E.H., respectively. Both sections I made in order to see finer details of microscopic structure than were already published. The state of preservation was not sufficient to permit of the identification of all the microscopic details which I had been able to observe in recent genera.

Corresponding to each pair of superficial ridges, one trabecular axis is present in transverse section. Fibres are radially arranged around this trabecular axis (ideal), passing at once from the median plane upwards and outwards towards the surfaces. Sometimes I could observe that the fibres were grouped in definite fascicles, whose origin in the median plane was marked by an individual point. The "point" seemed sometimes lighter, sometimes darker than the fibrous structure, according to con-

* This species is described for the first time in Frech's "Monograph of the Corals of the Zlambach Strata" ('Palæont.,' 1890–91, pp. 9 and 10).

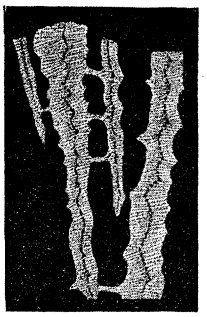
ditions of fossilization. It may be that those "points" indicate the axes of smaller trabeculæ acting as compacting tissue between main trabeculæ (*cf. Heliastræa*).

Fig. 34A.



Longitudinal section parallel with the septal plane. Each trabecula is seen to be a series of fascicles (*cf.* figs. 10, 17B, 25).

Fig. 34B.



Transverse section of alternating thick and thin septa. Zig-zag appearance of median "dark line" (*antea*, pp. 116, 117).

Very often longitudinal sections through fossil *Montlivaltias* and *Thecosmilias* present *irregularly dispersed* dark points in the axial region of the trabecula. This appearance has been observed in more pronounced degree also in sections of *Cyathophyllum* and its allies. They apparently represent organic cell-matter, originally intermixed with the fibrous deposit at active centres of deposit. The greater crowding of the "dark points" in the axial area agrees with the explanation given above for similar appearances in recent types (*antea*, p. 139).

Importance of the Direction of "Axes of Calcification" in a Septum.

It will now be readily understood that when a transverse section cuts a series of trabeculæ almost perpendicularly to their axes, it shows a series of central regions, darker or lighter, as the case may be, around which the fibres radiate. Each central region represents the axis of a trabecula (in general language an axis of calcification), and may show one, two, or several "points."

If, on the other hand, a transverse section cuts trabeculæ very obliquely, it will be in reality more a longitudinal section of the individual trabeculæ, although it cuts transversely through the septum. Then each trabecular axis will be represented by a longish series of central points, or by an apparently continuous central "short line." A zig-zag position of the "lines" is produced when the rows of granulations on the opposite surfaces of the septum alternate slightly in position. This is an appearance which is very commonly shown in transverse sections cut through the septa of such Eusmilinids and Turbinolids as are "striated" on the septal surfaces.

It is therefore necessary to compare carefully the position which "striæ" or "ridges" take up on the septal surface. As an example, the "striæ" on the surfaces of a septum of *Turbinaria* are almost horizontal with the edge of the septum, while

those on the surfaces of a *Galaxea* septum are variably oblique to the septal edge. The transverse section of the septum will show in the median plane an interrupted, often zig-zag series of short axes of calcification in the case of *Galaxea*. In *Turbinaria*, on the contrary, the transverse section will show in the median plane one line of calcification, comparable with that seen in a longitudinal section *parallel with a stria* in *Galaxea*.

In other words, the growth-segment of the *Turbinaria* septum is composed of a single trabecula with a single axis of calcification. This is the direct homologue of a "septal spine" which is pointed horizontally inwards in the calyx of a Palæozoic coral. The *Galaxea* septum is more complicated; in each growth-segment a number of trabeculæ are represented by a number of trabecular parts. These are added at the growing edge, any one of them being the homologue of a "septal spine." The segmental parts may be inclined to the vertical at all different angles, from oblique to horizontal.

There are again a number of Eusmilinid and Turbinolid genera, in which the septa are described as "smooth," having no striæ or ridges on their surfaces, although they may have granulations. Take, for example, *Euphyllia*. The surface of the septum is dotted with minute granules. By using a strong hand-lens, the granules are seen to occur in the course of delicate striæ or ridges which are perpendicular to the septal edge. About five or six striæ may be counted in 1 millim. The form of the striæ is broad, the granulations rounded, whereas in *Galaxea* the striæ are knife-edged and the granulations sharply pointed.

A transverse section of the septum *Euphyllia* has been published by BOURNE.* It is described by him as composed of parallel fibres arranged on the opposite sides of one continuous median axis ("centre") of calcification. Actually, however, this "centre of calcification" is made up of a number of centres, very closely placed, and elliptical in outline. The fibres emerging from those small elliptical axes are practically parallel, each group corresponding to the broad-shaped stria on the surface. The fibres are not obliquely placed with reference to the axes of the striæ, but are almost horizontally oriented. In other words, the deposit is laid down from the first by the lateral flaps of the septal invagination, and not at the upper edge where the flaps meet. The absolutely smooth edge of the septum finds in this fact a simple explanation.

The septa of *Euphyllia*, therefore, although finely striated on their surfaces, show two important features of distinction from the septa of types hitherto discussed :—

(1.) Smooth upper edge.

(2.) The fibres are directed almost horizontally outwards from the median plane of calcification to the opposite surfaces.

These correlated features suggest that the septal invagination is not frilled along

* BOURNE, "On the Anatomy of *Mussa* and *Euphyllia*, and on the Morphology of the Madreporarian Skeleton," 'Q. J. M. S.,' August, 1887, Plate 3, fig. 7.

its upper edge. At the same time, the two flaps are not quite smoothly opposed to one another, but are very faintly fluted in the same manner as observed in *Galaxea*, but with the convexities broader than the intervening furrows.

We may then recognize in the septal structure of *Euphyllia* a number of trabeculæ, parallel with one another and of uniform proportions; the axis of each being elongated in the plane of the septum.

CHAPTER III.—CLASSIFICATORY CHARACTERS OF THE ASTRÆIDÆ, E.H.

General Method of Growth.

1. *Compactness of the Septum.*

The invaginations of the aboral body-wall are formed in long radial lines. The flaps of any one of the radial folds fall into a corresponding paired system of pleats within which the calcareous fibres are deposited. The upward growth of the polyp takes place periodically, and at each period of growth a new edge is added to the septum. The addition is composed of small groups of fibres within each pair of the pleats, each edge-group is attached lengthwise to the similarly-shaped group formed in the preceding period of growth. And thus the continuous vertical series of fibrous groups arise, for which I have used the name of "trabeculæ."

Not only is the edge-group attached lengthwise to its predecessor, it is also attached sideways to the neighbouring edge-groups in course of formation at the same time. In other words the whole of the new tier of edge-groups which is added to the septum during a single growth-period is *firmly compacted before the close of that period.* The compact tier of edge-groups (= trabecular segments or parts) makes up one complete growth-segment of a septum.

By this feature of *compactness* in the method of growth, the Astræidæ are distinguished from the Pseudoastræinæ, Pratz, from the Lophoserinæ, E.H., and from the Eupsamminæ, E.H. In all these sub-families, and more rarely in the Funginæ, the tier of trabecular parts is not a compact septal segment. On the contrary, the edge-groups are not coherent with one another originally, and it is only towards the close of a growth-period that they may be to some extent attached together. Pores are left primarily between the adjacent groups, although in subsequent growth-periods calcareous tissue may close up some of these pores.*

Two factors therefore determine the compactness of the Astræid septum—(1) the complete coherence of each new tier of trabecular parts as it is laid down; (2) the precise serial succession of each new tier upon the foregoing, so that successively-formed trabecular parts are in line with one another (*cf.* Table, p. 252).

* Klunzinger mentions that pores may occur occasionally in the septa of Astræids. They are, however, of rare occurrence, and never show the definite structural relations to a growth-period described above for those sub-families in which the septa are typically porous.

2. *Compactness of the "Dissepimental" Floor.*

At the close of each growth-period in typical Astræids, the basal portion of the aboral body-wall situated between the radial invaginations deposits a layer or floor of calcareous dissepiments (Querblätter). These are usually convex in form, with the convex surface upwards. The aboral wall draws itself up gradually during the period of active deposit at the septal edge, forming during its updrawal the arched dissepiment. Finally the period of "pause" sets in, and the body-wall between the septa remains supported on its many-arched floor, which is then completed and thickened.

The formation of dissepiments therefore keeps pace with the addition of new tiers of trabecular parts along the septal edges. Each new platform of the dissepiments is as much above the platform previously formed as is the new septal edge above the preceding. The distance between two successive dissepimental floors is the measurement also of the additional height attained by the septa during a single growth-period.

The last-formed floor of dissepiments is *always some distance below the septal edges.* Usually some five or six septal growth-segments are present between the dissepiments and the growing edges of the primary septa. This fact allows lateral thickening of the septal growth-segments to go on during the interval which elapses between their first laying down at the septal edge and the ultimate withdrawal of the body-wall of the polyp. Complete withdrawal of the body-wall from any particular tier of trabecular parts in a septum is of course marked by the formation of a dissepimental floor at the horizon just above it.

One reason why the primary and secondary (sometimes also the next cycles in large calyces) septa are usually much thicker than the septa of intermediate cycles is because they extend to a greater height above the dissepimental floor. Consequently lateral thickening goes on during a greater number of growth-periods.

Another reason is that the fibrous deposit made during any single growth-period is itself thicker on the main septa than on the intermediate.

The formation of a complete basal layer of dissepiments at each period of growth is a highly distinctive feature for Astræidæ. In the Funginæ, Thamnastræinæ, Lophoserinæ, Eupsammidæ, the basal support is afforded in the main by cross-bars, "synapticulæ," over which the body-wall still descends in canaliculate fashion. As upward growth causes the aboral wall to be withdrawn from lower to higher horizons of synapticulæ, an occasional flat dissepiment may be formed between adjacent synapticulæ. But in none of these sub-families do we find a definite succession of compact dissepimental floors as in the Astræidæ.

On the other hand, the basal deposit is also a means of distinction, within certain limits, between Astræidæ and Turbinolidæ. The Astræidæ are mostly colony-building forms, and grow to various heights. The Turbinolidæ are all simple forms,

and the majority are extremely short. Basal deposit in them is limited to a solid outfilling of the lower part of the calyx. Without doubt, the solid deposit is added to during the successive growth-periods, just as in Astræids, but there is no free space left by which one may distinguish periodic additions.

There is a group of genera included by EDWARDS and HAIME among the Astræidæ —the Trochosmiliaceæ, E.H.—in which the only feature of distinction from Turbinolidæ is the occurrence of dissepiments. The latter, however, are said, in many of the genera, to be "very scanty." On the other hand, zoologists have frequently described certain recent simple corals as Turbinolids in which a few dissepiments are present.

As a matter of fact, the distinction is not one which can be sharply made in nature, since all transitions are found between Trochosmiliaceæ with a rich development of dissepiments, and Trochosmiliaceæ with solid deposit in the base of the calyx, and but few dissepiments in higher horizons. I shall have occasion, later, to point out other features in which the Trochosmiliaceæ show more affinity with the Turbinolidæ than with the Astræidæ. So far it is clear that, *with regard to their basal deposit*, the simple corals belonging to the Trochosmiliaceæ afford types transitional between the families Astræidæ, E.H., and Turbinolidæ, E.H.

3. *Theca and Epitheca in Astræidæ*, E.H.

The "theca" of the Madreporarian coral is one of the most vexed questions which come under discussion, and I shall have to refer to it again and again in the course of the present paper.

On looking at the drawing of *Mussa* (p. 137, fig. 22), it seems very simple to distinguish a theca upon which the edge-zone of the polyp is applied from an epitheca. The latter is formed as rings round the theca by the downward lip of the edge-zone. Again, in *Heliastræa*, the theca is clear enough, marking out almost equal septal and costal halves of the radial structure. An epitheca is apparently absent in *Heliastræa*. It is, indeed, absent around individual polyps of the colony, but there is a common epitheca at the base of the whole colony of polyps. The same is true of *Goniastræa* where a common epitheca surrounds the whole colony, and the individual polyps have a theca only. A single branch of the *Mussa* corallum is the homologue of the whole massive corallum of a *Heliastræa* or *Goniastræa* colony, in so far as each is surrounded by an epitheca similar in origin, similar in structure.

Take again a *simple* Astræid coral, *e.g.*, one of the most familiar of fossil Astræids, *Montlivaltia*. There an epitheca surrounds the simple calyx, identical in structure with that of the branch of *Mussa* or the colony of *Goniastræa*. *But there is no theca.* The same observation may be repeated for branching colonies of *Thecosmilia*, *Calamophyllia*, *Cladophyllia*, &c. Each branch represents in these cases an individual polyp which laid down epithecal rings outside of and surrounding the septa.

It is the same in many Turbinolidæ, in the majority of which an epitheca is

present, either as thin rings or as a more solid and often ornamental deposit exterior to the septa. Authors have sometimes called this deposit theca, sometimes epitheca, and sometimes have with justice got out of the difficulty by calling it both.

The essential difference which may be said to distinguish "theca" from "epitheca" is that the theca, or wall, must be structurally associated with the peripheral ends of septa, whereas the epitheca is in no structural connection with the septa, but is a continuous concentric deposit exterior to all the other skeletal structures of a calyx.

Following this distinction, both simple and colony-forming Astræid genera may be said to have *always an epitheca*: on the other hand, a *theca* may or may not be present in the "simple" genera, while, in colony-forming genera, the branching types may be without a theca; the massive types always have a theca.

4. *Eutheca and Pseudotheca in Astræidæ*, E.H.

The terms "eutheca" and "pseudotheca" were introduced by HEIDER and adopted by ORTMANN (see below, pp. 310–314). A perfect "pseudotheca" has been figured and described above, under *Goniastræa*. It is a *theca wholly* composed of the thickened peripheral parts of septa. An "eutheca" has been described under *Galaxea*. It is a theca in which distinct wall-lamellæ are present between the peripheral parts of the septa. The two may grow at different levels of the calyx, but unite in course of growth; or they may grow abreast of one another, and have their centres of calcification continuous with one another. Amongst the Astræidæ, E.H., it is only in the sub-family Eusmilinæ that an eutheca is developed. In all the Astræinæ the theca is either a perfect pseudotheca, or a slightly-modified form, in which erectly-placed dissepiments or large septal granulations help to compact and thicken the wall (ex., *Heliastræa*).* Occasionally, pores are said to be left in the pseudotheca; in the eutheca I have never heard of unfilled spaces. Typically, however, the theca of Astræinæ may be regarded as compact. In this feature it contrasts with the porous wall of the *Madreporaria perforata*, E.H., and also with the Pseudoastræinæ and Funginæ, in which a porous synapticular wall is present.

THE SUB-FAMILIES ASTRÆINÆ, E.H., AND EUSMILINÆ, E.H.

The Eusmilinæ, E.H.

The basis of distinction for the two sub-families of the Astræidæ rests at present on the external features of the septum. The septum of the *Astræinæ* genera is said to be toothed or spined at the upper edge, and the lateral surfaces of the septum are

* The original genus *Astræa* of LAMARCK coincides with the *Favias* and *Heliastræas* of later authors. EDWARDS and HAIME describe the septa in one of the most common recent species of *Heliastræa* (*H. Forskælana*, E.H.) as cribriform in structure; yet the same authors give *compact* septa in their diagnosis of the sub-family Astræinæ ('Corall.,' II., p. 286). All such pores are of intertrabecular position, and serve to show that the limiting-line between Astræidæ and Fungidæ cannot be very sharply drawn,

marked by a fan-shaped system of ridges, or by rows of granulations placed perpendicularly to the septal edge. The Eusmilinid septum, on the other hand, is described as smooth-edged, the lateral surfaces *frequently* bearing granulations placed parallel with the upper edge.

The types examined in detail above do not carry out these features of distinction. *Goniastræa*, an Astræinid, has a septum which has faintly-marked ridges on the lateral surface, and very slight indications of teeth at the edge. *Galaxea*, ranked as an Eusmilinid, has also a septum with striated lateral surfaces, and slightly serrated edges. In neither are granulations prominent; they are in both cases placed along the striæ, and are, therefore, perpendicular to the septal edge. It may be said, and with justice, that *Galaxea* is altogether out of place among Astræidæ, since it has a well-developed cœnenchyme. Even if *Galaxea* be removed, the same difficulty remains. I have seen plenty of species of *Stylina* with serrated edges, and all have striated surfaces. The genera allied with *Stylina* have similar septal features. Again, the wall of these genera is a pseudotheca of as perfect a type as that of *Goniastræa*.

Lately *Astrocœnia* and *Stephanocœnia* have been transferred by some authors from the Eusmilinæ, in the neighbourhood of the *Stylina* group, to the Astræinæ, on account of their toothed septal edges. If only the serrated edge were to be considered, several more genera might have been transferred. But there are several other considerations, *e.g.*, the thecal and basal deposit, the symmetry of the septa in the calyx, the presence of a true columella, or a pseudo-columella, &c. Other authors, again, have laid no weight whatever on the nature of the septal edge (see DUNCAN, "Review of the Madreporaria").

The serrated edge is, however, an indication of structure. There would be no chance of mistaking a good transverse section through the septum of a serrated type, *e.g.*, *Galaxea*, *Goniastræa*, with a section through a type like *Euphyllia*, in which all the septa are perfectly smooth-edged.

The transverse section of the serrated type shows a number of distinct trabecular centres of calcification in the median plane of the septum, that of *Euphyllia* shows one plane centre of calcification, on both sides of which the fibres are arranged parallel with each other. Moreover, the fibres in the latter case are almost horizontal in position, indicating that they are laid down from the first by the *lateral surfaces of the two flaps*, whereas the obliquely-placed fibres in the serrated type indicate that the fibres are first laid down *along the actual edge of the septal invagination* (p. 155).

So far as I have been able to study the structure of the Trochosmiliaceæ, the septa agree with that described for *Euphyllia* in the main, *e.g.*, *Placosmilia*, *Circophyllia*. The disposition of the fibres is the same, and the marked "two-leaved" character of the septum. *Aplophyllia* and *Rhipidogyra* are colonial Eusmilinids, with confluent calyces, whose septa are also built on the type of *Euphyllia*.

All these Eusmilinids stand, therefore, in distinct contrast with the Astræinæ, while a number of genera, such as *Galaxea* and *Stylina*, which have hitherto been

erroneously classified as Eusmilinids, have septa with a structure, and with external features, resembling the more delicately built septa of certain Astræinæ, *e.g.*, *Goniastræa*.

It is clear, therefore, that the sub-family Eusmilinæ, E.H., includes within it two very distinct septal types, the one of which is practically identical with the *Turbinolid* type, while the other is more akin to the simplest *Astræid* type.

The two Turbinolid genera, of which transverse sections have most often been made, are *Flabellum* and *Caryophyllia*, and BOURNE'S section of *Euphyllia*, REIS'* section of *Circophyllia*, and other sections already published of Eusmilinids, may readily be compared with those of *Flabellum* and *Caryophyllia* (see Introd., the works of KOCH, FOWLER, NICHOLSON).

I propose to entirely break up the sub-family Eusmilinæ, E.H.

A. The simple corals, the Trochosmiliaceæ, may be united with the Turbinolidæ.† Many features, in addition to that of septal structure, speak for this alteration—the frequent poverty of dissepiments in the Trochosmiliaceæ; the presence of a lamellar columella, sometimes continuous with a main septum, and giving bilaterality of parts to the calyx; the presence in other cases of a large styliform columella; independent of the septa. Moreover, the habit of the corallum is very similar, the polyp increases its size not so much by adding to its height as by adding to its width. The calyx becomes, therefore, elongated and compressed in shape. In the meantime I shall retain EDWARDS and HAIME'S title name of *Trochosmilia*, only altering the tribe into a sub-family, *Trochosmilinæ*.

B. The fissiparous Eusmilinid corals, *Rhipidogyra*, &c., will be fully discussed in my "Monograph of the Upper Jurassic Fauna of Stramberg," shortly to appear. There the reasons are given for uniting them into a new family, the Amphiastræidæ. The recent genus *Euphyllia* is rather anomalous in many ways, but its nearest affinity seems to be with the fissiparous types of the Amphiastræidæ. The structural relations of the wall and septa are alike in both, also the fine structure and external appearance of the septa.

Type: Euphyllia.—The septum is an infold from the wall and has a two-leaved appearance, with a distinct dark line, often looking double, in the median plane. This continuous dark line may be looked upon as a series of very closely set centres of calcification, or as one long axis of calcification. The calcareous fibres radiate at a low angle outwards from the median plane to the surfaces.

It happens in some genera that secondary surface thickening gives rise to horizontal rows of boss-like granulations, each row marking a single growth-period of the septum. If we regard the infolded tissue in the median plane as originally one horizontally

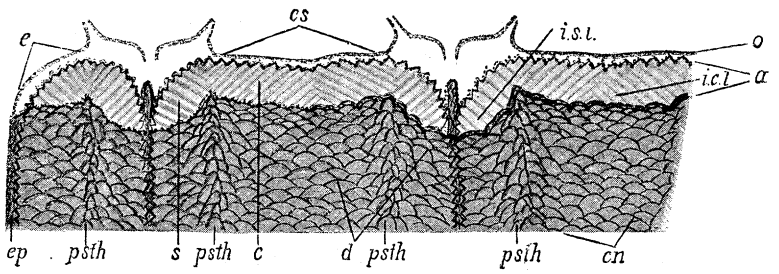
* REIS. See footnote below, p. 286.

† VERRILL has already suggested that a sub-family, Flabellinæ, be formed, including several of the Trochosmiliaceæ, with *Flabellum* and others of the Turbinolinæ, E.H., mainly on account of the fact that the tentacular disc is not stretched outwards beyond the wall.

placed axis of calcification, the length of the septum, with a single horizontal row of granulations, *corresponds* to a *single growth-segment* and is the morphological equivalent of a horizontally placed "septal spine" in Palæozoic forms; at the same time, moreover, the equivalent of either the *septum* or the *septal spine* in recent Madreporas.

The general resemblance of the corallum of *Euphyllia* to that of *Mussa* is entirely dependent on the fissiparous budding in both and cannot be regarded as an essential classificatory feature. BOURNE showed, it is true, that *Mussa* and *Euphyllia* were alike in the absence of "directive mesenteries." But FOWLER proved this feature in *Lophohelia*, an Oculinid, and HEIDER showed in *Madracis* that the position of the muscles in the mesenteries was very variable (see below, p. 290). BOURNE'S own suggestion was that their absence in *Mussa* and *Euphyllia* was merely an accessory feature correlated with the fissiparous mode of increase. *Euphyllia* has peculiarities not yet found in *Mussa* or any other Madreporarian genus. The ectodermal cells of the stomodæal tube have digestive functions, and the tube is drawn out into a number of convoluted channels, which lie in the visceral cavity. The endoderm, on the other hand, forms a highly vacuolated tissue, containing innumerable algal cells (*cf.* BOURNE, *loc. cit.*, 'Q. J. M. S.').

Fig. 35.



Typical *Stylinid* colony; letters as in fig. 2, p. 107; a columella is present in the middle of the calyx; the edge-zone extends horizontally—it is lettered "*cs.*" cœnosarc, for comparison with *Turbinaria*, fig. 56, and *Galaxea*; *psth.* pseudotheca; *ic. l.* intercostal loculus.

C. *The* Stylina *Group of Eusmilinid Genera.*—I propose to treat them as a separate family, the Stylinidæ, very closely related to a large number of the Amphiastræidæ. The early Mesozoic Stylinids are, farther, scarcely distinguishable from some colonial so-called "Rugose" genera. *Diplocœnia* has two "walls," and between them lies the broad dissepimental zone so characteristic of *Acervularia* and allied genera. *Cyathophora* and other Stylinids have central tabulæ. Again, the varying number of primary septa and the definite cyclical arrangement of the septa had already appeared in *Decacœnia*, *Pentacœnia*, and other young-Palæozoic types.

Galaxea.—This genus has a somewhat isolated position among recent Madreporaria. It has most in common with the Stylinidæ, but the presence of a true theca and the limited extent of the costæ lead me to place it only *provisionally* within this family.

The Astræidæ, E.H. (*excl. Eusmilinæ*).

The Astræinæ genera formed, in EDWARDS and HAIME'S classification, a well-marked sub-family which I would now regard as the sole representative of the family Astræidæ, E.H. The family would, if thus limited, include almost entirely colony-building corals in which neither "cœnenchyme" nor a "true theca" is developed. In other words, the adjacent polyps of a colony are united directly by their edge-zones, *e.g.*, *Heliastræa*, or the edge-zone may be scarcely developed and the adjacent polyps be united by pseudothecal thickening, *e.g.*, *Goniastræa*.

The leading features of the skeleton are :—

(1.) *Absence of cœnenchyme.*

(2.) The "wall" is pseudothecal in character, the septa always taking the main part in its construction. When no lateral thickening of the septa takes place, there is no "wall," and the septa are supported only by dissepiments.

(3.) A well-developed "*epitheca*" is always present surrounding individual branches of branching colonies, limited to the base in massive colonies. It is coalescent with the "pseudothecal" septal thickenings of calyces at the edge of the colony.

(4.) The *septa* may have either deeply or slightly-toothed edges, and the septa of the less-developed cycles in some genera may look almost smooth-edged. The lateral surfaces are always ridged and granulate, new ridges being introduced at one definite area in the septum, this is usually the area at which pseudothecal thickening of the lateral surfaces takes place. This area may be called the area of divergence, since the ridges diverge right and left from it to the septal and costal portions of the radial structures.

Microscopic examination shows that the septa are composed of a number of calcareous trabeculæ arranged compactly side by side. The trabeculæ usually form small fan-shaped groups corresponding to the individual ridges on the lateral surfaces of the septa. The calcareous fibres may be arranged with *bilateral* or *radial* symmetry relative to the trabecular axes of calcification. They are always originally deposited by the growing edge of the septal invagination, and are oriented therefore obliquely upwards and outwards from the trabecular axes.

The granulations on the septal surfaces follow the direction of the individual trabeculæ. If the latter form a broad ridge as in *Mussa*, each trabecula has its own distinct row of granulations, and the septal surface appears richly granulate. If the ridges are narrow, the granulations of the crowded trabeculæ coalesce and form one large granulation, *e.g.*, *Heliastræa*. Large granulations of adjacent septal surfaces may meet across the interseptal loculus and form a "pseudosynapticula."

(5.) The floor of the calyx is formed by regularly deposited *dissepiments*. A columella independent of the septa is rarely developed. But the inner ends of the longest septa are often drawn out as long teeth or pali and irregularly compacted to form a *pseudocolumella*.

Systematic Features of Generic Value.

Macroscopic features are :—

(1.) The shape of the septal edge, lanceolate, exsert, &c., and its minute details.

(2.) The constitution of the columella where such is present.

(3.) The characteristic form of the corallum.

Microscopic features are :—

(1.) The special structure of the ridges and granulations on the lateral surfaces of the septa.

(2.) The average distance from one another of the trabecular centres or axes of calcification in the median plane of the septum.

(3.) The uniformity of the trabeculæ in the septa, *i.e.*, if all have a single axis or paired fascicles, and are, on the whole, bilaterally symmetrical in their fibrous deposit, *e.g.*, *Mussa* ; or if all have a "group" axis with a wide circular periphery and have a radially symmetrical fibrous deposit *e.g.*, *Montlivaltia*. These are both uniform types. On the other hand, many types are not uniform in so far as they have some trabeculæ with radially symmetrical fibrous structure, and others with bilaterally symmetrical structure, *e.g.*, *Heliastræa*, *Goniastræa* (*cf.* p. 141).

Note on the Form and Increase of the Corallum.

In examining the Upper Jurassic corals from Stramberg, I found I could arrange a perfectly graduated series of specimens belonging to the genus *Thecosmilia*, beginning with the highly branched forms whose calyces were at the top of free stems, and ending with low massive forms in which the calyces remained either in contact with one another at their walls or appeared irregularly fissiparous. No author has given more attention to the features of budding and fission in classifying the Astræidæ than Duncan.* In his diagnosis of the genus *Thecosmilia* (*loc. cit.*, p. 81), we read, "Growth by fissiparity and rapid isolation, or by gemmation and subsequent fissiparity." However the fossil skeleton may appear, there can be no doubt that the living process in the polyp has one and the same result, whether the palæontologist calls it "gemmation" first or "fissiparity"! And it is hopeless to attempt to strain the same process for purposes of classification into two, hence I doubt the value of Duncan's sub-families. These are solely based on modes of increase and expressed as Astræidæ (1) *simplices*, (2) *reptantes*, (3) *gemmantes*, (4) *cæspitosæ*, (5) *confluentes*, (6) *agglomeratæ fissiparantes*, and (7) *agglomeratæ gemmantes* (Duncan, *loc. cit.*, p. 50).

In the same way as for *Thecosmilia*, one might arrange a graduated series of the

* Duncan, "A Revision of the Families and Genera of the Madreporaria," Linnean Society, London, 1884.

genus *Isastræa*, beginning this time with the typical massive form of the *Isastræa* corallum, in which calyces were clearly walled off from each other, and ending with a typical *Latimæandra*, in which few calyces have their own walls, most being arranged in confluent series, irregularly walled and winding. The individuality of the polyp is never so great in *Isastræa* as in *Thecosmilia*, since the Thecosmilian polyp at the end of a free stem carries on a much more independent existence than an Isastræan polyp on the surface of a compact colony. Again, although *Thecosmilia* may also have a massive corallum, the dignity of the polyp never descends so far as in that of a typical Latimæandroid. And we shall generally find that there is a certain standard of independence for each *genus*, which may be taken as a measure of the genus in placing it systematically. We may, in fact, use the form of the corallum and its habit of increase as a generic feature when we keep in view the *highest* degree of polypal individuality attained *and the lowest.* No sooner do we keep both ends of the scale before us than "gemmation" and "fissiparity" merge in one another. "*Fissiparity*" *I take to be simply a hastened development of buds under certain conditions and at certain periods of "vegetative growth" in the life of the coral.* And the buds, which form long meandroid series and never develop fully, probably perform in an Astræid colony the functions of a cœnenchymal area in "*Perforates*," namely, the rapid circulation of nutritive material throughout the colony.

Gemmation and Fissiparity.

As I have already said (*antea*, p. 147), all the forms of budding may be reduced to *intracalicular* and *extracalicular*, and these are merely varieties in the mode of vegetative increase. A bud may form in a colony at any part of the oral body-wall, in Astræidæ it forms usually on the peristome or above the lip of the calyx. If the bud is open to the main visceral cavity of the polyp, it is said to be intracalycinal; but if it forms just on the other side of the rim of the calyx and is open to the continuations of the cœlenteron on the outer side of the theca (the cœlenteral canals of the "Randplatte"), the bud is said to be extracalycinal or extracalicular. In the former case the appearance observed in the skeleton is called "fissiparity," as the tendency of the corallum is more or less meandroid; in the latter case, the appearance is called gemmation, and the tendency of the corallum is towards greater individuality of the calyces and branching growth.

The canalicular prolongations of the cœlenteron on the outer side of the calycinal rim may sometimes be very extensive in length, and may either hold closely to the wall of the calyx (*e.g.*, Astræidæ), or may spread over a wide interpolypal surface (*e.g.*, Stylinidæ, Oculinidæ, Eupsammidæ). Buds may form at any part of this extension, but then they are otherwise named—infracalicular, stolonal, cœnenchymal, &c. As I have said, in all cases the process is gemmation, and the same corallum may develop its buds anywhere. It is only where canalicular extrathecal continuations

are practically absent, that the polyp is limited to so-called "fissiparity," *e.g.*, *Goniastræa*, *Isastræa*.

Take as an example of the redundancy of budding which the coral may show, the following quotation from DUNCAN (*loc. cit.*, "*Astrangia*," pp. 66, 67): "There is no doubt that the species . . . . . vary in their method of gemmation. The corallites may entirely arise from the basal expansion, or some may come from the angles between corallites and even from the wall anywhere below the calyx. Some of these buds are accidentally placed, and have no intimate union with the parent; but others appear to be true infracalicular gemmations."

Sub-divisions of Astræidæ (= Astræinæ, E.H.).

The best basis on which minor sub-divisions of the Astræidæ can be made is probably that of the septal structure. The principal types of structure have been shown in chapter ii., they are: (1) *Montlivaltia* or *Thecosmilia*, (2) *Mussa*, (3) *Heliastræa*, (4) *Goniastræa*. At the same time the relation of the "edge-zone" (or costate part of the calyx) to the main visceral cavity (or septate part of the calyx) will be found in most cases to be a correlative feature of some importance.

(1.) *Lithophylliaceæ* (*pars.* E.H.).—Solitary or colonial; the buds develop as free branches, occupied by one polyp, seldom by a group. Epitheca is formed round each branch, pseudotheca is little developed.

The septal edges have equally developed, conical teeth, and the lateral surfaces of septa have uniform ridges, on each of which one main row of granulations is present. Genera: *Thecosmilia*, *Cladophyllia*, *Rhabdophyllia*, *Cladocora*, &c.

(2.) *Musaceæ*.—The buds develop as separate branches. Intracalycinal budding takes place within the mother-polyp of the branch, so that each branch is the seat of a small fissiparous polyp group surrounded by epitheca. Pseudotheca present, close to the epithecal rim of the calycinal group.

The septal edges have teeth unequally developed, and usually spiniform. The ridges on the septal surfaces are correspondingly variously developed. Each ridge has a broad surface on which numerous granulations are scattered.

Genera: *Mussa*, *Dasyphyllia*, *Isophyllia*, *Symphyllia*, *Ulophyllia*, &c.

(3.) *Astræaceæ*.—The corallum is massive. The buds develop as branches, which remain constantly attached at the rim of their edge-zones. The epitheca is limited to the base of the whole colony. Pseudothecæ are developed *well within each* of the individual calyces. The edge-zones are represented in the corallum by the broad costate portion external to the pseudothecæ of the calcyes. *The septal edges have equally developed*

teeth; prominent ridges are present on the lateral surfaces bearing larger and smaller granulations, the larger occasionally forming synapticulæ.

Genera: *Heliastræa, Confusastræa, Agathiphyllia, Stylastræa*, &c.

(4.) *Faviaceæ.—The corallum is never branching, always massive.* The edge-zones of polyps are extremely limited, and increase takes place almost wholly by *fissiparity* within the calyx. *The septa are only slightly toothed and the ridges on the lateral surfaces are extremely fine; granulations, small.*

The individual calyces may have *a distinct wall* (*ex. Favia*) *or a wall common to adjacent calyces* (*ex. Goniastræa, Isastræa*). The epitheca is well developed, limited to the base of the whole colony.

(5.) *Meandraceæ* (provisional, until the individual genera are microscopically examined).

The buds rarely develop individually; *long series of calyces are divided from neighbouring series by a common wall.* The septa may be deeply toothed, or very slightly. This tribe includes at present meandroid forms related to Astræaceæ and Faviaceæ, *i.e.*, according to their septal structure, the meandroid forms may be ultimately referred to one or other of these two tribes.

Genera: *Meandrina, Latimeandra, Diploria, Cœloria, Hydnophora*, &c.

There are few corals of solitary habit among the Astræidæ. At present several are classified as Astræidæ which have not the characteristic features; for example:—

Epistreptophyllum, a Jurassic genus which must be placed in the neighbourhood of the Eupsammidæ (*vide* chapter x., p. 303).

Leptophyllia, a Jurassic and Cretaceous genus which PRATZ has proved to belong to the Pseudoastræinæ (*vide* chapter v., p. 186).

CHAPTER IV.—FUNGIA AND SIDERASTRÆA.

FUNGIA.

The so-called "porous" *wall of* Fungia *is homologous with the* "compact" *wall of Astræid Types, and is like it, a* pseudo*theca.*

The genus *Fungia* has many points of interest. It was to denote the calcareous bars in the interseptal loculi of *Fungia* that EDWARDS and HAIME originally applied the name of "synapticula."* Again, the developmental history of *Fungia* is remark-

* EDWARDS and HAIME, 'Coralliaires,' 1857, vol. 1, p. 66, "Sometimes septal granulations become very large, coalesce with those of the continuous septa, and thus give rise to small solid bars, which divide each interseptal loculus into a series of small spaces communicating with one another. The presence of these solid bars, which we call *synapticulæ*, characterize the family Fungidæ, and has not been observed as yet in any other group of the class of Madreporaria. It is in the genus *Fungia* that synapticulæ have the greatest development, as in that genus they sometimes extend in the form of almost continuous curved lines from the bottom of the interseptal loculi to within a small distance of the free edges of the septa."

able. The young polyp possesses an upright, cup-shaped theca, with marked bilateral symmetry of the septa. But, as it becomes larger, the corallum develops in discoid form, until the theca rests almost horizontal with the base, and the growing exsert tips of the septa are to be found at the periphery of the disc (*cf.* BOURNE,* *loc. cit.*, Plate 24, figs. 3–8). No sign of the original bilateral symmetry is retained in the mature corallum, the septa being radially arranged. The theca has the same general relations to the cœlenteron and mesenteries as that of other Madreporaria. According to BOURNE, the theca, or wall, is "formed from the fused ends of contiguous septa, as is stated by G. v. KOCH to be the case in the lateral thecæ of other Madreporaria."

This statement is perfectly correct, yet the wall is homologous, strictly speaking, only with a "pseudothecal" wall such as the Astræids possess.

A general impression obtains that the porous nature of the wall of *Fungia* at once distinguishes it from the compact wall of Astræidæ, or even from that of the more nearly related Lophoserinæ, E.H. The apertures in the *Fungia* wall are, however, of small moment. If we removed the dissepiments between the thick peripheral portions of the septa of many Astræids (*e.g.*, *Heliastræa*, *Mussa*), we would have numerous apertures left in the so-called "compact pseudotheca." Such apertures would be the exact homologue of those in the *Fungia* wall, which are simply occasional interseptal spaces not sufficiently filled up by the basal deposit. This happens very readily, since the basal deposit in *Fungia* takes exclusively the form of synapticulæ, *i.e.*, rod-like bars, instead of flat, or arched dissepiments. In the Lophoserinæ, on the contrary, dissepiments are well developed in addition to the synapticulæ.

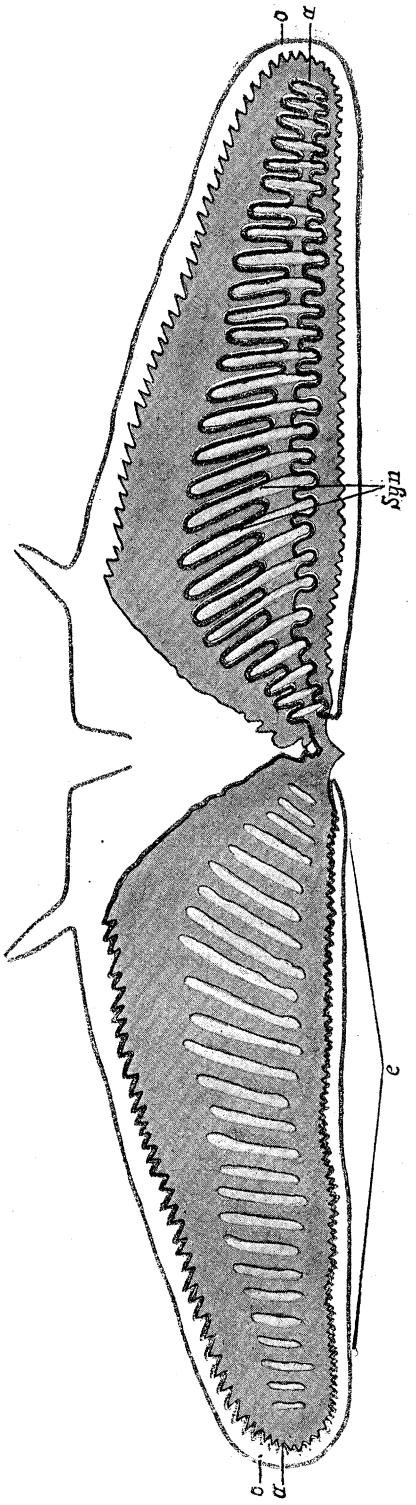
Fig. 36 presents a diagrammatic section through the corallum of *Fungia*, designed to show the relations existing between the aboral body-wall of the polyp and the skeletal parts. Comparison should be made with the similarly designed section through *Mussa*.

The Synapticulæ are formed within Interseptal Invaginations of the Aboral Body-wall.

BOURNE has given in the paper quoted above a series of figures illustrative of the attachment of the mesenteries to the body-wall. "All are firmly attached by their upper border to the peristome," the primary and secondary mesenteries being attached at their inner border to the stomodæum, the remaining orders being of "constantly decreasing length." The mesenteries radiate freely in the interseptal spaces near the upper margin, that is, above the upper ends of the synapticulæ, but are naturally interrupted in the main portion of the interseptal loculi by the presence of the synapticular bars (*cf.* BOURNE, *loc. cit.*, pp. 302–303). Exactly how this

* BOURNE, "The Anatomy of the Madreporarian Coral *Fungia*," 'Q. J. M. S.,' 107, January, 1887.

Fig. 36.



FUNGIA. The oral (*o.*) and aboral (*a.*) body-wall are doubled round, so that the part corresponding to the edge-zone (*e.*) of *Mussa* is here found on the basal surface *syn.* synapticulæ (*cf.* pp. 168–171). This diagram is to be compared especially with fig. 22. Two *non-cœnenchymatous* types, *Mussa* and *Fungia*, are represented in this way for the sake of comparison with *cœnenchymatous* types, *e.g.*, *Galaxea*, fig. 2, and Turbinaria, fig. 56.

interruption takes place is not clearly explained by BOURNE; possibly his view is best rendered in his subsequent paper ("The Anatomy of *Mussa* and *Euphyllia*," *loc. cit.*, p. 47). There he writes, "The manner in which the mesenteries may be pierced, as it were, by outgrowths from the walls of adjacent septa is well shown by the form of synapticula in *Fungia*. In this form processes arise from the walls of the septa which grow towards similar processes from the contiguous septa, and, meeting them, fuse with them to form synapticulæ."

It is true that the synapticulæ grow out as septal processes, though their fusion in *Fungia* is ordinarily brought about by the development of a new centre of calcification; but the important point is that they *neither "interrupt" nor "pierce" the mesenteries*. As I show in fig. 36, the part of the body wall to which the mesenteries are attached becomes gradually more and more invaginated, raised up on the growing ends of the synapticular bars, but still descending to the base of the polyp between the bars of any one interseptal loculus.

BOURNE did not make a special study of the skeletal, but of the anatomical relations, and his views with regard to the synapticulæ rested chiefly on previous observations made by EDWARDS and HAIME and by DUNCAN.* He says, in fact, at the conclusion of his paper that he "can offer no explanation of the origin and significance of the synapticula. Physiologically they seem to serve as stays or buttresses giving solidity and coherence to the corallum."

The structural support which they give is possibly their main function, in this respect they take the place of the dissepiments of Astræidæ. Their growth-relations with the other skeletal parts are precisely similar to those which I have demonstrated for dissepiments in the foregoing Astræid types. The first-formed synapticular floor in fig. 37 is lettered "S_1," the last-formed synapticular floor is lettered "S_{28}." The whole figure represents a *Fungia* septum placed vertically, instead of in its natural horizontal position. This I have done in order to make the comparison with the septum of Astræids more simple and to bring out the analogy between the successive "synapticular bars" of *Fungia* and the successive dissepimental floors of Astræidæ (*antea*, p. 157). Growth in the *Fungia* septum goes on not only at the growing apex of the septum but throughout its entire length (resp. height). So that the earlier-formed synapticular bars are constantly being added to as fast as the edges of the septum grows upwards. Their upward extension keeps pace steadily with the growth in height of the septa. The particular curve which is formed, if one draws a line, on the septal surface just above the uppermost ends of the whole series of synapticular bars, is at about the same distance from the septal margin throughout its whole length and is parallel with it. It corresponds, therefore, to a curve following a row of dissepiments in an Astræid polyp (*cf. Mussa, Heliastræa*).

What is then the particular advantage to the Fungid polyp of having synapticular

* DUNCAN, "Observations on the Madreporarian Family of Fungidæ," 'Journ. Linn. Soc.,' 17.

bars as a skeletal support instead of dissepiments? I believe the main advantage to be that, by this means, an *increased endodermal surface is afforded within the visceral cavity.* The synapticular invagination of the body-wall produces an elongated fold of the soft parts in the course of growth and gives rise to visceral canals on both sides of the synapticular prop. If a dissepimental floor took the place of the synapticular bar at any horizon, the surface of endoderm would be very short, whereas in the synapticular union there is a double endodermal surface from the upper part of the synapticular bar to its base. The advantage is analogous with that which is attained by highly *crimped* and *folded* or *pitted* flaps of the septal invaginations as compared with smooth flaps; or again, by invaginating the basal body-wall over a complicated columella, spongiose or paliform; again, by a highly canaliculate cœnosarc, as in *M. porosa,* in place of the smoothly extended cœnosarc of *Galaxea.*

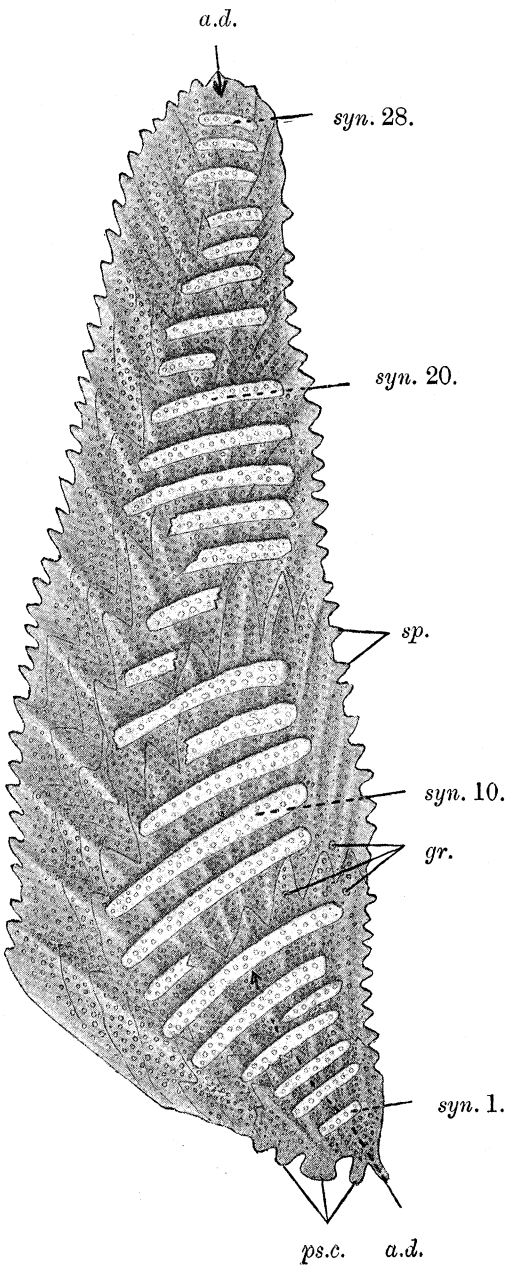
In Fungids, the increase of the visceral surface plays at any rate two *rôles* in the existence of the polyp. *First,* the larger assimilative area means more rapid digestion of the food-material introduced into the visceral cavity. *Second,* the canalicular form of the continuity of the peristomal soft parts with the thecal and basal affords the possibility of a more highly differentiated muscular system within the polyp, while it necessarily gives firmer attachment of the polyp to the skeleton. The genus *Fungia* itself, owing to its unusually large dimensions, shows those features best, but the skeletal structure of the small *Siderastræa* or *Lophoseris* polyp points to a similar significance of the synapticulæ.

The Septa.

The *thinner* septa of *Fungia* have a wavy margin with extremely fine teeth, and the surfaces are closely covered with granulations. Thicker and thinner parts of the septum may be distinguished near the edge and parallel to it, the thicker parts bearing larger granulations. The thinner parts mark the limit between successive growth-segments. The *thicker* septa are deeply toothed and have ridged surfaces; the ridges thicken as they become more remote from the septal edge and are continued as the synapticular bars. Each synapticular bar therefore represents coalesced ridges on the adjacent surfaces of two septa. The important macroscopic features of a thick septum are shown in fig. 37. The figure is represented purposely in a position at right angles to its true position in the corallum in order to facilitate comparison with the similar foregoing figures of Astræids. The "area" from which the septal ridges diverge may be seen to extend almost vertically in the plane of the septum—that is in the same direction as in *Galaxea, Mussa,* &c. (*antea,* figs. 3, 15, 22, 28). It is only the deformation in shape undergone by the growing *Fungia* polyp (*antea,* p. 168) which renders the true *inner* edge of the septum the apparent *upper* edge in the mature corallum, and the true *outer* edge of the septum the apparent *base.*

The zig-zag markings, more or less parallel with the septal edges, denote, as

Fig. 37.



Septum of *Fungia* represented in a vertical position instead of the horizontal position assumed in nature. The area of divergence (*a.d.*) of the trabecular ridges is thus seen to follow a line in the septal plane rather nearer the outer or "costal" edge than the inner or "septal" edge of the septum (*cf.* fig. 15).

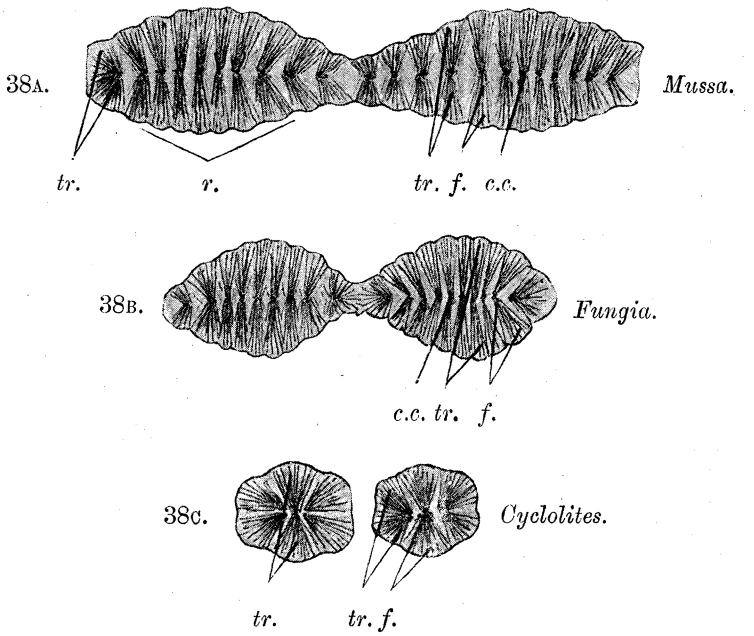
sp. = spiniform teeth of the costal edge.
syn. = synapticulæ in ascending series.
gr. = granulations.
ps.c. = pseudo-columellar teeth.

before, successive periods of growth, and define the limit of successive *growth-segments* in the septum.

It may be observed that granulations are scattered alike over the septal surface and the synapticular bars. The granulations on the synapticulæ can only be actually seen at their upper parts, where coalescence has not yet taken the place of the synapticulæ on the adjacent faces of two septa. In fig. 37, the granulations are for the sake of uniformity carried out along the whole synapticular bar.

The general resemblance of the septum of *Fungia* to that of an Astræid, more particularly one with broad ridges and irregularly scattered granulations, like *Mussa*, is sufficiently demonstrated by the figure. The fine structures of the ridge is also in the main comparable with that of a ridge in *Mussa* (*cf.* fig. 38). A diverging system

Fig. 38.



Comparison of transverse sections (diagrammatic, *cf.* fig. 18) through three characteristic septal types; *Mussa*, the septal ridges (*r.*) are elongate, and the centres of calcification (*c.c.*) widely spaced; *Fungia*, ridges more elliptical in outline, and the centres (*c.c.*) more closely packed; *Cyclolites*, ridges rounded, centres (*c.c.*) in one group, so that six fascicles (*f.*) form here a "compound trabecula."

of trabeculæ composes the ridges in both cases. The trabeculæ in *Fungia* are, however, arranged more as a parallel group, only the lateral trabeculæ diverging to any extent sideways. In fig. 38 nine or ten trabeculæ are represented in a single ridge of *Mussa* and *Fungia*, and the fascicles of fibro-crystals are bilaterally arranged with reference to a row of calcification centres (ideal axes) in the median plane of the septal ridge. For comparison, the ridge of *Cyclolites* is given. This genus is a typical Thamnastræid, whose septa has a fenestrated porous structure (fig. 69). The single "trabecula" (PRATZ) is the homologue of a trabecular ridge. Several fascicles are

present, but they are radially arranged around one main axis, and the ridge assumes rounded contours.

The trabecular structure can be demonstrated in *Fungia* without the use of the microscope. When a septum is warmed and then thrown suddenly into cold water, the calcareous laminæ flake off in various planes. The removal of the superficial laminæ shows that what appeared a rough, granulate ridge on the surface, is in reality a symmetrical group of trabeculæ. The individual trabeculæ are marked out by slight grooves from one another. Successive groups of trabeculæ are present, each of which is precisely homologous with the growth-segment of a septum of *Galaxea* or a "ridge" of *Mussa* (figs. 18A, 18B). The only differences are, 1st, that the length of the group in *Fungia* is greater relatively to the breadth; and, 2nd, that some six or seven of the trabeculæ in *Fungia*—those in the middle of the whole group—are parallel in direction. Lateral trabeculæ bend out somewhat obliquely, and form the means of coalescence with those of adjacent ridges. The number of trabeculæ in one ridge of *Fungia* is from eight to twelve.

The grouping of the trabeculæ in *Fungia* is intermediate between that which is observed in *Mussa* and that characteristic of the genera belonging to the Pseudo-astræinæ, Pratz. In the latter, each septal ridge is grooved in the manner described for *Fungia*, but the trabeculæ are all parallel in direction. None bend out obliquely to meet the trabeculæ of adjacent ridges (*cf.* Pratz' figures, 'Palæontographica,' *loc. cit.*, 1882, plate 27). The absence of obliquely-diverging trabeculæ is the cause of the porosity of the septum in those types (ex., *Cyclolites*, *Microsolena*, &c.). On the other hand, it is the presence of diverging trabeculæ in *Fungia* and *Siderastræa* which renders their septa compact like the septum of Astræids. The very thin septa of *Fungia* are, however, said to be sometimes porous, apparently due to less regular development of the diverging trabeculæ. But in all the specimens I happened to examine, all the septa were compact.

I represent the transitional stages shown by *Mussa*, *Fungia*, *Cyclolites* diagrammatically in transverse section (fig. 38). The *group of trabeculæ* in *Cyclolites* makes up one *rounded*, nodulose septal ridge, and it was to this ridge that Pratz applied the term "trabecula." It may be looked upon as a *compound* large trabecula (*vide antea*, p. 141), formed round several centres of calcification massed together in the median plane. The radial symmetry of the calcareous fibres in the compound trabecula, is distinctive from the bilateral symmetry of fibres in a simple trabecula.

The nodular swellings, with more or less *circular* outline, in the course of a Cyclolites trabecula, correspond with successive growth-periods, each "knot" representing one group of radiating fibres around crowded centres. *Fungia* and *Mussa* show similar groups, but the centres are not massed together. They are disposed in a row, and the fibres form a broad ridge with *elliptical* outline.

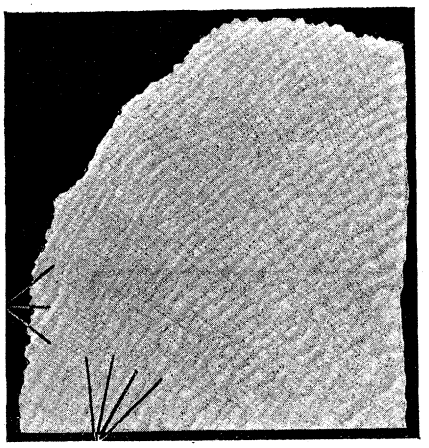
Comparison of the Cyclolites "trabecula" with the *large* compound trabeculæ in *Heliastræa* (*cf.* figs. 24, 26), or in *Montlivaltia*, shows that it fundamentally agrees

with them in structure. It will be readily understood that the broadening out of a "ridge" is correlative with *compactness* of a septum, whereas its narrowing to the nodulose "Cyclolites" form leads to a *porous* condition of the septum between its ridges.

Microscopic Sections.

The fundamental facts of the fibrous structure are the same as in Astræidæ. The fibres are laid down in fine growth-lamellæ. The cut edges of growth-lamellæ are well seen in fig. 39, a finely-polished surface slab of part of a *Fungia* septum, under

Fig. 39.



Section horizontal with the septal surface.
g.l., wavy "dark bands" of the growth-lamellæ.
f.c., fibro-crystals of the lamellæ crossing the "bands" in direction.

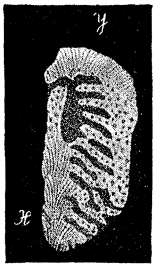
high magnifying power. The uneven polishing has exposed successive lamellæ and their fibres.

All the fascicles in *Fungia* take origin in the median plane of the ridge at the ideal axes of the several trabeculæ. They grow upwards for a short distance and then bend sharply outwards towards granulations on the surfaces of the trabeculæ. That this is the course followed may be deduced from comparing sections made longitudinally, in radial and in tangential direction.

Fig. 40C shows (11 times magnified) a longitudinal *radial* section in which one septum has been cut for the greater part near the median plane; but towards the synapticulæ (*i.e.*, on the right hand of the figure) the section has passed obliquely towards the septal surface and the synapticulæ. Fig. 40D gives another part of the same section where it had passed entirely through the first septum and the synapticulæ and entered the adjacent face of the next septum. The direction of the section through the two adjacent septa is shown in figs. 40A and 40B.

Both of the figs. 40C and 40D show that, wherever surface planes of the septum are met, or the planes immediately subjacent, the fascicles are cut almost perpendicularly to their axes. It may, therefore, be deduced that in those planes the axes

Fig. 40A.

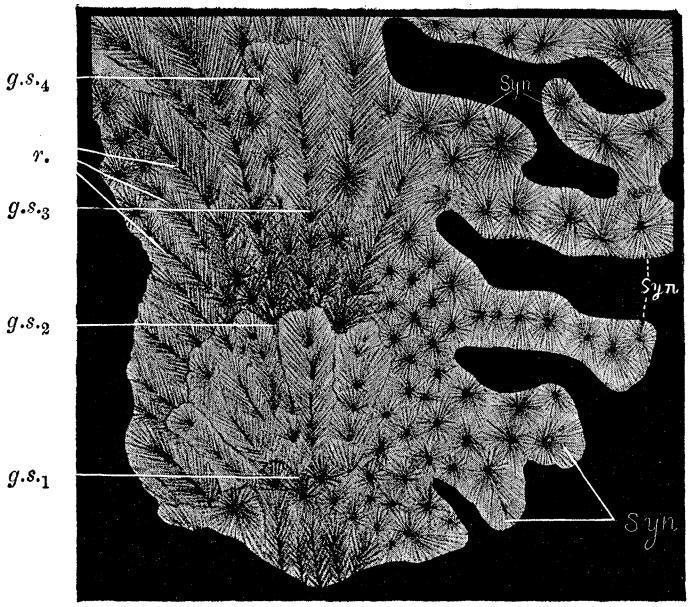


Small drawing to show the positions of the sections represented in fig. 40C ("x" in drawing) and fig. 40D (= "y").

Fig. 40B.

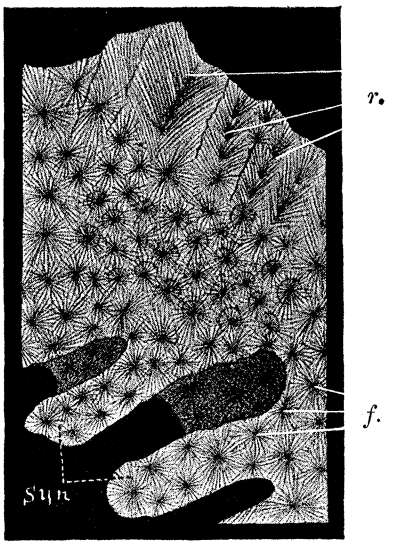
Small diagrammatic drawing to show how the plane of polishing in fig. 40A passed through two adjoining septa and the synapticulæ between.

Fig. 40C.



Section passing obliquely through a septum into the interseptal loculus with synapticular bars (*syn.*). Four growth-segments (*g.s.*) are indicated by fans of diverging trabecular ridges (*r.*), a single "syn." corresponding to each.

Fig. 40D.



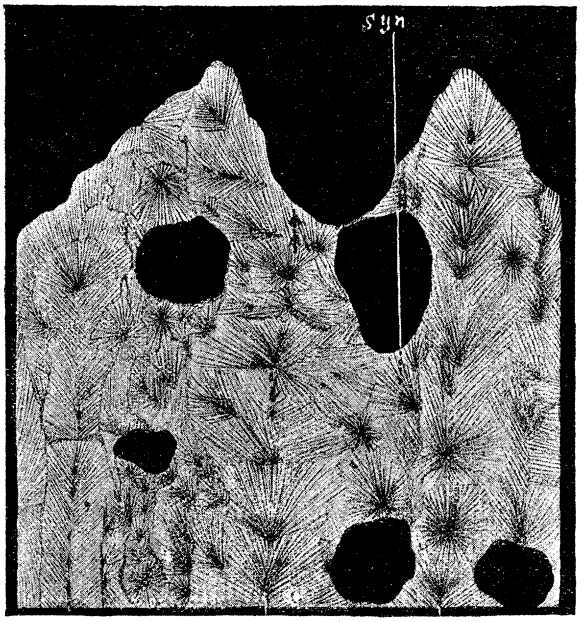
Same section continued through the interseptal loculus to the adjacent septum *f.* = fascicles cut across.

of the fascicles bend almost directly towards the surface. On the other hand, in the inner planes of the septum, the axes of the fascicles are met lengthways for some distance. They produce here the appearance (already familiar in figures of *Galaxea*,

&c.) of a more or less continuous line, representing the obliquely-cut axes of successive fascicles. We have in this fact a proof that the fascicles develop at first in an obliquely upward and outward direction with reference to the middle line or "ideal axis" of an individual trabecula (*cf. antea*, fig. 25, p. 143).

A *tangential* section (18 times enlarged) is drawn in fig. 41, including three septa and two interseptal loculi, occupied in part by synapticulæ. Passing into the synapticulæ are fascicles which have their origin in the septum, at a plane near the septal surface. Those fascicles may either not grow sufficiently beyond the surface, or may

Fig. 41.



s. *syn.* *s.* *syn.* *s.*

Tangential section of Fungia. *s.* = septa; *syn.* = synapticulæ. Independent centres of calcification are present in the synapticulæ.

not happen to meet an oppositely placed fascicle. In either case, *one or more new fascicles develop in the interseptal loculus*, and form a means of coalescence between the fascicles growing out from the septum. The new fascicles are constituted precisely like the septal fascicles and bear evidence, therefore, of their origin in a specially invaginated pouch of ectoderm.

As growth advances, new interseptal fascicles are formed in the same vertical line as the foregoing, and thus the small invagination of the basal body-wall, in which the first interseptal fascicles developed, lengthens out until the body-wall becomes invaginated over the whole, long synapticular bar. The continuity of the synapticular bar is in a direction at right angles to the direction of apical growth of the septum (*cf.* fig. 119).

In a tangential section of the *Heliastræa* septa (*antea*, fig. 27), and again in tangential sections given, by PRATZ, of Pseudo-Astræinæ genera, pseudosynapticulæ and dissepiments are present. It will also be frequently seen that, where the fascicular outgrowths from septa do not succeed in bridging the interseptal loculus, a small dissepiment is laid down between them by the basal body-wall, *as it withdraws from lower to higher horizons* of the corallum. But the basal body-wall in *Fungia never withdraws itself* completely from the lower horizons; it forms instead these extra, cylindrical invaginations of the body-wall between septal invaginations.

To this ingenious device are mainly due the large proportions which the discoid corallum may obtain, as well as the characteristic and peculiar skeletal feature of the series of synapticular bars in the interseptal loculi.

The Growth Relations of Fungia.

A microscopic surface section through granulations shows that the corresponding fascicles have a diameter varying from ·16 millim. to ·25 millim., and on the synapticulæ the fascicles have sometimes a very large diameter, measuring as much as ·35 millim. The fascicles of *Fungia* have, therefore, throughout the corallum a much larger size than those of the Astræid types, which have been studied above. Probably the fascicles thus measured represent coalesced fascicles from the central and parallel placed trabeculæ in a ridge.

At the exsert apical portion of the septum, where the additional height (apparently length) attained during a growth-period is always greatest, the measurements in *Fungia* gives fairly definite results. The growth-segment of a single ridge measures, then, from 1·2 millim. to 1·5 millim. in height, the maximum width at the surface of the same growth-segment is 1·5 millim., its diametric thickness at a non-synapticular portion a little over 1 millim. at synapticular portion 1·6 millim. Hence the growth-segment may be regarded as fairly cubical in dimensions, although its actual form is notched at the base, and rounded or pointed at the apex.

The synapticular thickening is at the *bases* of adjacent growth-segments, hence the curve of any one synapticular bar bends convexly, so as to be parallel with the exsert apical portion of the septum. In this relation to the growing edge, it simulates the dissepimental floor of the Astræid polyp. Compare the last-formed synapticular bar with the exsert margin of the septum in fig. 37, and the same relations will be observed as those shown by the last-formed dissepimental floor and the septal margin in figs. 2, 15, 22.

SIDERASTRÆA.

The Presence of Synapticulæ and the Lateral Coalescence of Septa within the Calyx.

The genus *Siderastræa*, although in outward appearance resembling certain colony-forming Astræids, has been ascertained to be like the Fungidæ in its tentacles and

soft parts.* A careful examination of the microscopic skeletal structures would suffice to determine this relationship.

The calyces are small, united with one another, pseudothecal, have compact radial structures, and a paliform pseudocolumella, in so far having a general resemblance, therefore, to *Goniastræa* (*cf.* below, fig. 42). But while *Goniastræa* has *dissepimental basal structures* and a *wall* formed by *septal thickening* at the area of divergence, *Siderastræa* has well-developed *synapticulæ* representing both *basal* and *tangential* structures. Dissepiments are also present here and there, but they have not in *Siderastræa* the definite growth-relations which they have in Astræids. On the other hand, the synapticulæ are an essential part of every growth-segment, in the same way as demonstrated above in the case of *Fungia*.

Again, in the inner parts of the calyces, where the septa approach each other more closely, their surfaces actually coalesce (*cf.* fig. 43A), and groups of septa are formed. The same coalescence takes place in *Fungia* and in the Lophoserids, and is a marked feature, above all, in the Eupsammidæ. The Astræidæ, on the other hand, never show marked septal grouping, but only an irregular columellar meshwork of septal ends in genera like *Rhabdophyllia*, with "spongiose columella." The direct lateral coalescence of the septal surfaces belonging to different septal cycles is homologous with the synapticular union of septa. It is, moreover, a skeletal feature specially characteristic of synapticulate Madreporarian types. It may be said in opposition to this that septal grouping occurs also in some of the Turbinolidæ. Later parts of this paper will show that the Turbinolidæ present in their calycinal features a striking resemblance with the Madreporaria perforata, E.H.; and the lateral, quasi-synapticulate coalescence of septa to form Eupsammid-looking septal groups is not one of the least of their features of resemblance.

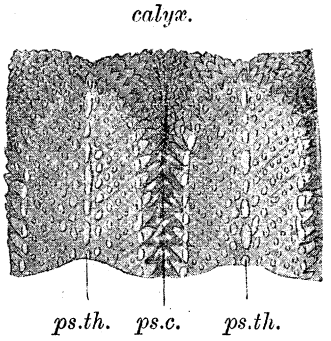
Fig. 42A is drawn as if looking into the interior of one calyx of *Siderastræa* and the adjoining halves of two other calyces, seen in longitudinal section. The septal surfaces are exposed and show parallel ridges on which large synapticular granulations mark the successive growth-parts of each ridge. The teeth of the ridges are prominent; their shape is broad and blunt-edged, like the teeth of the Pseudo-Astræinæ and of *Fungia*.

Comparing this figure with fig. 37, a septum of *Fungia*, the direction of the ridges will be seen to be the same. In *Fungia* they diverge from an area in the septum, in *Siderastræa* the area of divergence is at the wall between two calyces. The granulations belonging to any one septal segment in *Fungia* are those which unite and form a continuous bar on the surface of the septum. The latter runs therefore in a direction at right angles to the ridges. In the Palæozoic genus *Heliophyllum* the

* DUNCAN refers to the researches of AGASSIZ and POURTALES on this genus; *vide* "Revision of the Families and Genera of the Madreporaria," p. 184. The same author rightly separates the genus *Siderastræa* from the two genera *Astræomorpha* and *Mesomorpha*, with which PRATZ had united it under his group of Pseudoastræinæ Irregulares.

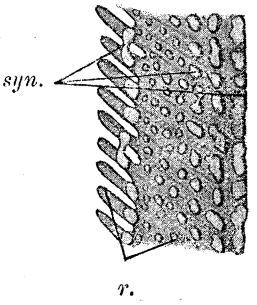
"carinæ" on the septal surfaces are structurally homologous with the bars on *Fungia*, but adjacent bars do not meet across the interseptal loculus in *Heliopyllum*. In short, the carinæ do not act as synapticulæ. Also in a few Jurassic genera carinæ are present which do not form synapticular union of septa.

Fig. 42A.



Skeletal parts of *Siderastræa ps.c.*, pseudocolumella of calyx, *ps.th.*, pseudotheca between calyces.

Fig. 42B.



Septal surface showing the direction of the ridges (*r*), and the position of the large synapticular granulations (*syn.*).

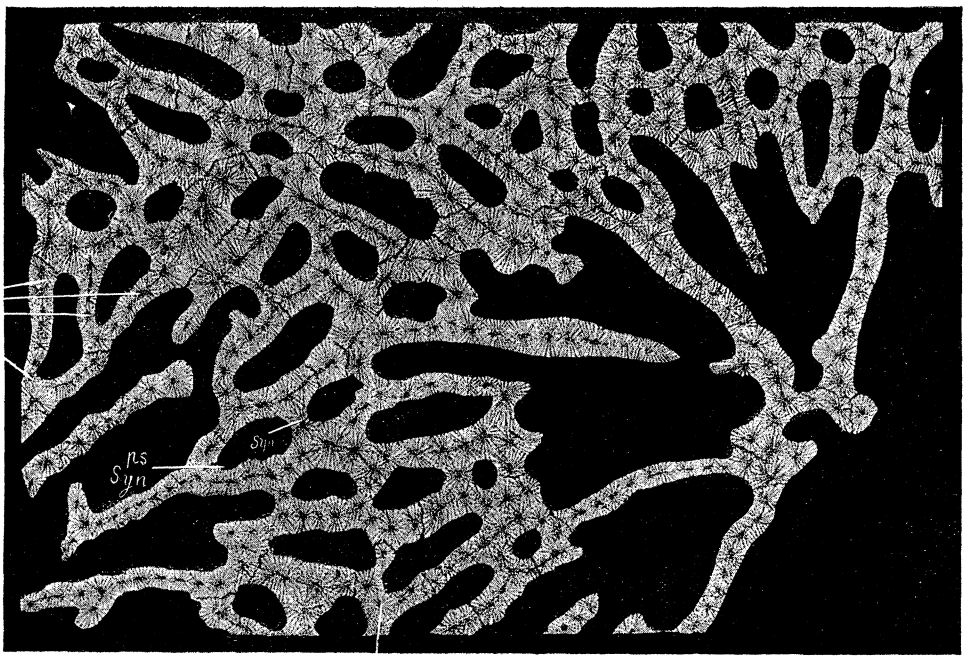
In *Siderastræa*, there is scarcely any tendency for the granulations to unite across the ridges of the same septum. Only at the wall and the centre of the calyx occasional short bars are formed on the surface of neighbouring ridges. On the other hand, the granulations of adjacent septal surfaces meet in the interseptal loculi and form characteristic vertical series of synapticulæ. This is the typical form of synapticulæ, where large granulate eminences meet *at intervals*. The *continuous* synapticular bars or carinæ in *Fungia* are quite exceptional.

Towards the centre of the calyx, where the septa stand very close to one another, direct lateral coalescence of the septa may be said to take place, as the granulations are scarcely perceptible. Where the distance between adjacent septa becomes greater, *i.e.*, nearer the periphery, the granulations of adjacent surfaces meet without the intervention of a new "synapticular" centre of calcification. This particular form of synapticular coalescence is called "pseudosynapticular," and has already been mentioned as an occasional occurrence in the calyces of *Heliastræa*. At the periphery of the *Siderastræa* calyces where the septa are most distant from one another, the introduction of new synapticular centres of calcification is the rule. The granulations on the septal surfaces are in short seldom sufficiently developed to bridge the whole space at the mural part of the calyces, and new invaginations of the aboral wall between them give rise to new centres of calcification. The resulting skeletal bridge is called a "true synapticula," and is the homologue of the synapticular bars in *Fungia*.

The transverse section (fig. 43) of a few septa of *Siderastræa* shows the various forms of *interseptal* skeletal support just enumerated; (1) lateral coalescence of septa,

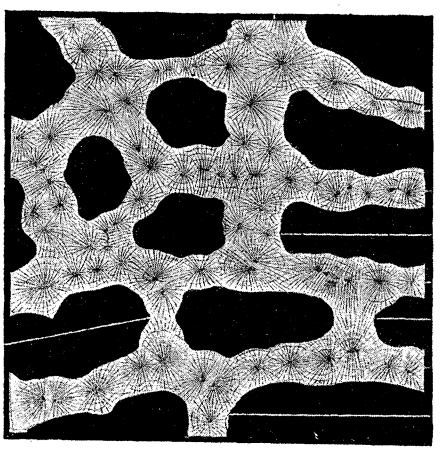
(2) pseudosynapticular, (3) synapticular. In all cases the morphological significance is the same. It is the building up of a basal support leaving canalicular spaces for downward prolongations of the visceral cavity of the polyp. In this respect, *Side-*

Fig. 43A.



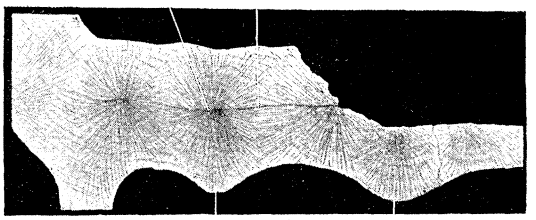
Transverse section through calyces of *Siderastræa*. The synapticular "wall," or pseudotheca (*ps.th.*) is seen between three adjacent calyces: *syn.* synapticula; *ps.syn.* pseudosynapticula; *co.se.* lateral coalescence of septa, *s.* septa.

Fig. 43B.



Transverse section; enlarged drawing of a pseudothecal part of the same section as fig. 43A.

Fig. 43C.

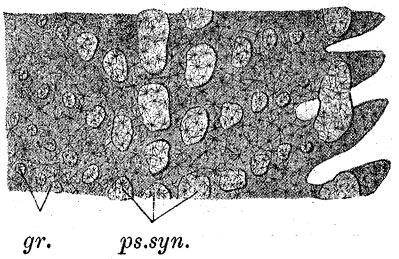


One septum (high power). *gr.* granulations; *cr.* a crack in the section along the median plane.

rastræa is like *Fungia*, and stands in sharp contrast with Astræids in which the basal support is laid down as a continuous closed platform of dissepiments.

The same section illustrates the microscopic structure of the septa of *Siderastræa*. They are composed of a number of trabeculæ, in which the fibres are *radially* arranged around a central axis. Fig. 43c is a more highly-enlarged septum, showing the tendency of the septa to split along the median planes. When dust accumulates in such an artificial crack, it naturally presents all the appearances of a "*dark line.*" This drawing indicates also the cut edges of the series of growth-lamellæ as lines running across the radiating calcareous fibres. Now and then two centres of calcification are present diverging from one another in the median plane. Then the trabecula appears double and is elongated in outline. The individual trabeculæ of *Siderastræa* may be compared with large trabeculæ, showing radial symmetry of fibres in *Heliastræa* (*cf.* fig. 24A), or with the central closely-parallel group of trabeculæ in a septal ridge of *Fungia* (*cf.* fig. 40).

Fig. 44.



Longitudinal section parallel with the septal plane; pseudosynapticulæ (*ps.syn.*), an enlarged form of granulation (*gr.*).

The trabeculæ, in any one ridge of *Siderastræa*, may, as in *Fungia*, be placed obliquely and diverge from one another *in the plane of the septum.* This it is which makes the septum both in *Fungia* and *Siderastræa* typically compact, distinguishing them from the septa in the Pseudoastræinæ, Lophoserinæ, and Eupsamminæ.

In the radial group of fibres (transverse section, fig. 43c), corresponding to individual trabeculæ in *Siderastræa*, smaller fascicles of fibres are often distinguishable. These have the same relation to the large granulations on the lateral surfaces of the septa as I have described above for *Fungia*. Fig. 44 is a microscopic view of a fairly thick surface preparation of a *Siderastræa* septum. The emergent ends of fascicles are seen to coalesce in quite indefinite number at the granulate (pseudosynapticular) parts of the septum. If this view of microscopic structure be compared with figs. 42A and 42B, it will be seen at once that the series of granulations follow the individual septal ridges. Fig. 44 shows the microscopic structure of granulations and of pseudosynapticulæ formed by the coalescence of several fascicles.

As I already took occasion to mention in the historical account (*antea*, Introd., p. 103), PRATZ observed a certain indication of smaller groups of fibres (= fascicles)

passing outwards from the axis of the trabeculæ in *Cyclolites* and allied genera. He thought they possibly corresponded to the small surface granulations which he called nodules ("Knötchen")—a few small granulations uniting to form the "pseudo-synapticula." PRATZ, however, made no farther research in this direction, and, therefore, failed to recognize the full significance of the successive "nodular" groups as the *individual growth-parts of the trabeculæ representing successive growth-periods of the polyp* (*antea*, p. 156).

When that general fact is recognized we can follow the trabecular growth-part in its various forms, narrow and bilaterally symmetrical, large and radially symmetrical, throughout every great group of the Madreporaria. In *Siderastræa* the average measurements of a trabecular growth-part are as follows:—

Height (or length)	= ·22 to ·28 millim.
Width at surface	= ·11 „ ·14 „
Diametric thickness	= ·10 „ ·16 „

Classificatory Relationship of Siderastræa.

The microscopic structure of a single trabecula is, as we have seen, identical in the genus *Siderastræa*, and in genera belonging to the sub-family Pseudoastræinæ, PRATZ. *Fungia* on the other hand shows secondary thickening in the form of new centres of calcification developed on the side surfaces of the septa in connection with the synapticular granulations. This is, however, a feature correlated with the low form of the *Fungia* corallum, and the fact that the soft tissues remain in the canalicular portions of the cœlenteron throughout the life of the polyp; it is, therefore, not a feature in itself of classificatory distinction between *Fungia* and *Siderastræa*. In spite of the dissimilarity in the form of the corallum in those two genera, the agreement in all essential structural features is undoubted. Recapitulating briefly, the septa both of *Fungia** and *Siderastræa* are typically compact, and have granulate surfaces, the miscroscopic structure showing that the septa are composed of trabeculæ which may diverge from one another in the space of a single septal ridge; whereas, in the Pseudoastræinæ, the trabeculæ composing a septal ridge are absolutely parallel throughout the whole course of that ridge. The only mode by which adjacent ridges can coalesce in the latter case is by means of elongation of the fibres in the septal plane. This elongation takes place at regular intervals between successive growth-periods in the Pseudoastræinæ, and the result is a series of regular pores in the septum. Secondary calcareous deposits may afterwards fill up the septal pores. *Fungia* and *Siderastræa*, by means of obliquely set trabeculæ, form septal segments which actually grow compactly.

* DUNCAN notes that the septa of the higher orders of *Fungia* are often perforate; I have seldom seen apertures, they are at any rate never present in the regular series characteristic of Pseudoastræinæ.

While this difference in the septal structure is the chief feature distinguishing the two genera under discussion from the Pseudoastræinæ, there is also the second distinction, which PRATZ had observed in his classification of Pseudoastræinæ into minor groups—the presence or absence of new centres of calcification to bring about the coalescence of the granulations across septa loculi. PRATZ noted in *Siderastræa* that coalescence took place sometimes with intervention of new centres of calcification, sometimes without; in the characteristic Pseudoastræinæ types (Pseudoastræinæ regulares = allies of *Thamnastræa* and *Microsolena*) coalescence in all cases took place directly between granulations, the latter form of coalescence PRATZ called *Pseudosynapticular*, the former *Synapticular*. The fine structure of *Fungia* was unknown to PRATZ, but it is now clear from the sections given above that *Siderastræa* agrees with *Fungia* and differs from the Thamnastræids and Microsolenids in respect of the coalescence. In other words, that the basal body-wall of *Siderastræa*, like that of *Fungia*, may be specially invaginated between the septa. Fascicles of fibres are then formed within the invagination similar to the fascicles formed in every small "pit" of the septal invagination of the body-wall.

Those two features lead me to classify Siderastræa rather in the immediate neighbourhood of Fungia than in that of the Pseudoastræinæ. My result differs here both from PRATZ and from DUNCAN; the latter may indeed be said to have been influenced directly by PRATZ. DUNCAN'S family of "Plesiofungidæ" includes the genera which PRATZ examined and referred to a sub-family, Pseudoastræinæ regulares and irregulares, the only change made by DUNCAN being to break up the sub-group "Pseudoastræinæ irregulares." He still left, however, the three genera belonging to the sub-group in the immediate relationship of the main group. The three genera are *Siderastræa*, *Astræomorpha*, *Mesomorpha*. *Siderastræa* is, as I have said, nearly related to *Fungia*. *Astræomorpha* and *Mesomorpha* are both fossil genera, and most probably are related with the *Madreporaria perforata*, E.H. They are dealt with in Part II., chapter v. of this paper.

True and False Synapticulæ (PRATZ).

The original definition of the term is quoted above ("*Fungia*" foot-note, p. 167), and may be seen to refer only to the *macroscopic* appearance of the coalescence of opposite granulations. This definition held good until PRATZ made the distinction based upon microscopic investigation of a true synapticula composed of one or more centres of calcification, and a false synapticula in which no new centre of calcification was present, but the fibrous "nodules" of the septa were merely elongated. Since EDWARDS and HAIME had defined "synapticula" as an elongation of the granulations (= "nodules"), PRATZ' "*false* synapticula" corresponded to the actual words of EDWARDS and HAIME'S definition. But the "sense" of the original definition was made clear by EDWARDS and HAIME in their application of the term in the first place

to the synapticulæ of *Fungia*. And accepting the "sense" of the original definition and its application by those authors to Fungids, Lophoserids, &c., PRATZ invented the term "pseudosynapticulæ," for the manner of coalescence which he observed throughout a number of genera, and *which did not agree, microscopically considered, with the manner of coalescence typical of Fungids, Lophoserids, &c.* From that time forward there has reigned a kind of scepticism in the literature with regard to the distinction made by PRATZ and expressed in his terms of "*True Synapticula*" = "Synapticula" (E.H.), and "False Synapticula" = a microscopic appearance not characteristic of the "synapticular bars" of *Fungia* which EDWARDS and HAIME had quoted as an example of their use of the term Synapticula.

Although PRATZ himself must have been acquainted with the microscopic structure of the "true synapticula," he referred to it only in a few passing words in his work, and gave no figure to demonstrate any difference. Neither was his explanation of the "true synapticula" very clear. He said a process grew out singly from one septum towards the adjacent side of the neighbouring septum and fused with it, new centres of calcification having built up the calcareous process in the course of its interseptal extension. This is partly right, such synapticulæ occur very often in perforate corals, Eupsammidæ, Poritidæ, &c., but as it happens, the synapticulæ of *Fungia* are quite different, they are formed partly as septal outgrowths, partly as an interseptal continuously-growing calcareous bar.

ORTMANN did not agree with PRATZ in recognizing a structural difference between true and false synapticulæ. He writes:—"Special centres of calcification do not exist for the synapticulæ, hence there are no 'true' synapticulæ in the sense described by PRATZ, and *all* structures which have hitherto been called synapticulæ must, according to PRATZ himself, be termed synapticulæ."*

I find, however, that it is highly convenient to have the distinctive term of pseudo-synapticula where granulations meet directly.

"True" synapticulæ have various forms of development. In *Eupsammia* they attain an independence of development, and a morphological significance still greater than they present in *Fungia* and *Siderastræa*.

CHAPTER V.—THE FAMILY FUNGIDÆ.

PRATZ' DISPOSITION OF SUB-FAMILIES.

The detailed microscopic investigations carried out by PRATZ on early Jurassic representatives of the family of Fungidæ led that author to draw up a table of classificatory features for the various sub-families. His sub-divisions are Pseudo-

* ORTMANN, "Die systematische Stellung einiger fossiler Korallengattungen und Versuch einer phylogenetischen Ableitung der lebenden Steinkorallen," 'Neues Jahrb. für Mineral. u. Geol.,' 1887, II., p. 185.

astræinæ, Pseudoagaricinæ, Funginæ, Lophoserinæ (Agaricinæ), Merulininæ.* He bases the classificatory features of the three last-named sub-families upon the data of previous authors (DANA, VERRILL, EDWARDS and HAIME). The first two sub-families are, however, treated from what may be called an original standpoint in the classification of fossil corals, and embody the main results of the microscopic and morphological research made by PRATZ himself. Although, as I have said, PRATZ took Jurassic genera as the basis of work, he included also Triassic, Cretaceous, Tertiary, and recent genera in smaller number. The genera *Coscinaræa* and *Siderastræa* are indeed the only two recent genera included. For the features of *Coscinaræa* he relied upon information given him by KLUNZINGER; while *Siderastræa* received but a brief examination and was not directly compared with Fungidæ and with *Fungia*. Again, in accordance with the then generally accepted idea that *Madreporaria aporosa*, E.H., had little connection with *M. perforata*, E.H., PRATZ nowhere institutes a comparison of any type, fossil or recent, with the Eupsamminæ. On the other hand, the trabeculate porous character of the septa in the Poritinæ induced him, without any microscopic or closer investigation of typical genera, to place the sub-family Poritinæ, E.H., under his sub-family Pseudoastræinæ, together with *Microsolena* and other fossil members called Pseudoastræinæ regulares. I mention this last fact because it is possible it may have influenced NEUMAYR in writing of "*Microsolena*," as building a "bridge to the Poritidæ" (*cf.* below, p. 306).

Proposed Emendation of the Sub-family Pseudoastræinæ, PRATZ.

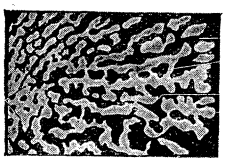
As the microscopic slides of PRATZ were placed at my disposal, I feel in a position to review the table of classification which he founded upon them. The only modifications which strike me as advisable concern the recent genera, and one or two fossil genera which my examination of recent Eupsamminæ leads me to regard as more nearly allied with Eupsamminæ than with Pseudoastræinæ. These fossil genera are classified by PRATZ as Pseudoastræinæ irregulares, and along with them he places the recent *Coscinaræa*. The type genus *Haplaræa* (Jur.), shows microscopically and macroscopically marked similarity with the genus *Eupsammia* (*cf.* transverse section, fig. 45), *Diplaræa* is allied with *Haplaræa* (fig. 45), *Meandraræa* has, on the other hand, the character of Lophoserinæ (this genus will be fully diagnosed in my "Monograph of the Stramberg Coral Fauna"), while *Coscinaræa* has most in common with Eupsammidæ.

On these considerations I propose to annul the Pseudoastræinæ *irregulares*, PRATZ,

* The general features of *Merulina* seem to agree with those of the Fungidæ. KLUNZINGER groups it as an Astræid in his sub-family Meandrininæ. It is possibly better to include it under the Funginæ on account of the porous, echinulate basal surface as well as the occurrence of true synapticulæ in the interseptal loculi; a more detailed examination is necessary before its systematic position can be stated with certainty.

and to recognize the Pseudoastræinæ *regulares*, PRATZ, consequently as the *complete* sub-family. I exclude from this sub-family the genus *Thamnaræa* and the Poritinæ, E.H., both of which had been included by PRATZ.

Fig. 45.



Transverse section of *Haplaræa*, showing spongiose columella, septa with pores (*p.*) and united laterally by true synapticulæ (*syn.*), also a pseudothecal wall with pores (*ps. th.*).

Comparison of Pseudoastræinæ, PRATZ (= *Thamnastræinæ*) *with the Astræidæ.*

A typical septum representing PRATZ' sub-family is given below (fig. 69); a comparison of a transverse section of the component trabeculæ with *Fungia* and *Mussa* has been already made (fig. 38). But the nearer details must be referred to in PRATZ' work ('Palæontographica,' 1882). The characteristic structural features common to Astræinæ, E.H. (= Astræidæ, *antea*, p. 163), and Pseudoastræinæ may be enumerated as follows :—

(1.) In each radial structure there is a "line of divergence," from which individual trabeculæ pass obliquely upwards in opposite directions—inwards and upwards towards the centre of the calyx, outwards and upwards away from the centre of the calyx.

(2.) This line of divergence coincides with the position of the peripheral thickening which gives rise to the "wall" of the calyx. The thickening is partly brought about by outgrowths from the septa, partly by oblique and vertical placing of inter-radial structures.

(3.) The latter are dissepimental and pseudosynapticular in character.

(4.) The septum and costa ("radial structure") is composed of trabeculæ, whose microscopic structure is like that described for *Goniastræa*, &c., above. Coalescent fascicles of fibres form a large granulation, corresponding to each growth-part of the trabecular ridge. These large granulations, by meeting adjacent granulations from neighbouring septa, form a series of "pseudosynapticular" bridges across the interseptal loculus. Occasional pseudosynapticular union is present in *Heliastræa* and other Astræidæ.

Differences from Astræidæ :—(1.) *In the microscopic constitution of the individual growth-part.*

The neighbouring trabeculæ of a single septum do not grow upwards in contact

with one another throughout a growth-period. In other words, not all the calcareous fibres of a fascicle have a fairly equal length, but some grow much longer than others, and only the long fibres project sufficiently to meet those of the trabecular growth-parts on either side in the septal plane. In this way, practically a circular granulation is formed, projecting outwards all round the trabecular growth-part. Sometimes the projection may be at the upper part, or may wind spirally round the segment. In some cases the fascicles are sufficiently large to retain distinctness during the development of the granulate projection, and one can see that the latter is made up of a ring of smaller granulations, *each of which corresponds to the emergent end of a single fascicle* (ex. *Cyclolites*, figs. 38 and 69). Those are the "*regularly grouped calcareous nodules*," of which, as PRATZ says, the trabecula is composed, and he identifies the "nodules" ("Knötchen," PRATZ) with the "sclerenchymatous nodule" of EDWARDS and HAIME. It is clear that in the expression of EDWARDS and HAIME the whole growth-part was meant. The tiny "knobs" on the surface of a nodule are identical with the single fascicles, two or more of which have been microscopically proved by me to compose a "growth-part" in all types of Astræidæ and Fungidæ discussed above.

The unequal elongation of the fibres in the fascicles of Pseudoastræinæ genera produces the characteristic bush-like appearance of the fibres in longitudinal sections of trabeculæ, each bush corresponding to the part added during a single growth-period. The group of fascicles in Astræinæ has a more elongated axis and equal development of fibres for a single growth-part. As a result of the different mode of growth, the septa in Astræidæ are compact, or seldom leave a space between trabeculæ, while those of Pseudoastræinæ are originally *fenestrated*. Secondary compacting tissue may fill up the original fenestrations left between adjacent trabecular growth-parts.

(2.) *Difference in the regularity of the pseudosynapticulæ in interseptal loculi.*

The granulate ring of each growth-part which projects into the interseptal loculus is developed so uniformly along the whole horizontal series of growth-parts corresponding to a growth-period, that they tend sometimes to coalesce as continuous bars along the septal surface. Another still more frequent tendency is for the adjacent granulate projections to meet and give rise to a vertical series of interseptal uniting-rods, here *pseudosynapticulæ*.

Connection of Pseudoastræinæ with Fungidæ.

The features of difference from Astræinæ are precisely those which justify the systematic position of the Pseudoastræinæ, PRATZ, *as an ally of the Funginæ and Lophoserinæ, E.H., and a sub-family of the Fungidæ.*

Although later deposit renders the septa in Lophoserinæ usually compact, they are for the most part laid down as a series of non-compacted trabecular growth-parts.

The same is sometimes true of the smaller septa in *Fungia* and in a general way of the Eupsammidæ septa.

The tendency to the formation of continuous bars along the septal surface is especially characteristic of *Fungia* as well as of genera in other sub-families of Fungidæ.

The interseptal uniting-rods in these three sub-families may be produced as in Pseudoastræinæ by prolongation of the fascicular fibres belonging to septal growth-segments, or they may be due to the insertion of new fascicles. In the latter case, as I have pointed out above, they are formed in special invaginations of the aboral body wall and are "true synapticulæ."

It would seem, therefore, that the fossil sub-family Pseudoastræinæ has a microscopic structure of skeletal parts varying little from that of Astræinæ, but these variations indicate that the living polyp had an arrangement of its body-wall and internal tissues like that of recent Fungidæ. There is no recent representative of the Pseudoastræinæ. The period of the highest development of the sub-family was Up. Jurassic: a period in which the recent Fungids, Lophoserids, and Eupsammids were still, so to speak, in the nursery of their existence.

Frech's *alteration of the name of Pseudoastræinæ to Thamnastræinæ.*

Frech recently objected to the names of Pseudoastræinæ and Pseudoagaricinæ given by Pratz, and altered them to Thamnastræinæ and Astræomorphinæ respectively, at the same time referring them to a special family Thamnastræidæ instead of Fungidæ, under which Pratz had placed them ("Kor. Fauna der Trias.," 'Palaeont.,' vol. 37, 1890, p. 59). Both the names Thamnastræidæ and Thamnastræinæ had already been used in the literature, the former by Reuss in 1864, the latter by Becker in 1875. Frech made no comment on previous use; he accepted Pratz' systematic grouping, changing only the nomenclature.

The only point wherein he mentions disagreement with Pratz has regard to the distinction of true and false synapticulæ. He writes: "The (true) synapticulæ have their origin by complete coalescence of pseudosynapticulæ; at the same time the anatomical difference is visible only in the case of relatively few very well preserved specimens. According to Ortmann, moreover, the said distinction is untenable, since a line of fusion (Trennungsnaht) is always present." Frech, therefore, unites the Pseudoastræinæ regulares and irregulares, Pratz, under the title Thamnastræinæ, Frech.

Pratz, however, did not distinguish the two branches of his sub-family on the basis of the synapticulæ alone. The main feature to which he drew attention in giving the adjectival names "Regulares" and "Irregulares" was the *difference in the microscopic structure of the septa.* He defined Pseudoastræinæ regulares and irregulares as follows:—

P. regulares, PRATZ.

"Trabecula built up of regularly (symmetrically) grouped calcareous nodules coming into contact with each other at fairly regular distances, by means of which rows of pores are formed, running vertically to the septal edge, and more or less *regularly* distributed.

Neighbouring septal surfaces bound together by *Pseudosynapticulæ* and traversæ (dissepiments)."

P. irregulares, PRATZ.

Trabeculæ built up of numerous fine, calcareous nodules, grouped without symmetry, and united irregularly (*regellos*) with one another. Intratrabecular spaces (pores), therefore, of very different size and spacing (Anordnung).

Neighbouring septa united by *true synapticulæ* in addition to traversæ (dissepiments).

If now for the "calcareous nodule" in these definitions the fibrous fascicle be read, and each *group* of fascicles be understood to represent a distinct growth-part of a trabecular ridge, it will be seen that the definitions given by PRATZ have been fully corroborated by my work. PRATZ' *definition of P. irregulares gives, in fact, the main features of the Eupsammidæ, by which they may be distinguished from Pseudoastræinæ regulares* (*cf.* below, 'Table of Classification,' p. 252, "Successive" and "Contemporaneous Growth-parts"). The distinctions so carefully worked out by PRATZ are, therefore, fully justified, and I regard it as a backward step to unite the two sub-groups under the one sub-family Thamnastræinæ. Moreover, I have already shown that PRATZ had right in distinguishing two kinds of synapticulæ—the pseudosynapticulæ of the "Pseudoastræinæ regulares" and the true synapticulæ present in Funginæ, &c.

Astræomorphinæ, FRECH.

The limits of FRECH'S sub-family Astræomorphinæ coincides precisely with those of PRATZ'S sub-family Pseudoagaricinæ. Under this sub-family the Triassic genus *Astræomorpha* and the recent genus *Siderastræa* were included by PRATZ; two genera which I do not regard as nearly related.

FRECH, at the same time, speaks of *Astræomorpha* as the ancestral genus from which sprang three of the four genera belonging to the Triassic family Spongiomorphidæ (*loc. cit.*, p. 70). He writes:—"The most peculiar type (of the Spongiomorphidæ) is undoubtedly *Stromatomorpha*. Precisely this genus is found already in the *Muschelkalk* together with *Astræomorpha*, from which last-named genus the three other genera (*Spongiomorpha*, *Heptastylopsis*, *Heptastylis*) are descended ('sich ableiten lassen')." On a later page, however, there is more reserve in the author's expressions: "The origin of the Spongiomorphidæ from the Astræomorphinæ is in so far problematical, since both appear together for the first time in *Muschelkalk*. Probably both spring from the same unknown ancestral type" (*loc. cit.*, p. 73).

FRECH then gives a diagram in which he shows the possible connection of *Actinacis* as well as of the *Perforata* related with *Turbinaria*, with the Spongiomorphidæ and Astræomorphinæ. "The *Turbinarias* are descended from some form related to *Heptastylopsis*" (a Spongiomorphid).

The general result which may be drawn from FRECH'S work is, therefore, that the Spongiomorphidæ include the ancestral type of *Turbinaria*, and are intimately related with the Astræomorphinæ, hence more distinctly with the companion sub-family Thamnastræinæ,—these terms being used in PRATZ'S sense of Pseudoagaricinæ and Pseudoastræidæ respectively. As PRATZ included *Porites* under the Pseudoastræinæ, we have a very large tree of relationship and descent, including most of the *Madreporaria perforata*, E.H. and the ancestral forms of the Fungidæ, together with a family Spongiomorphidæ of an entirely aberrant character.

With this result I entirely disagree. My reasons will appear during the course of the present paper.

The genera closely related to *Cyclolites*, *Thamnastræa*, and *Microsolena* are those which properly belong to the sub-family Thamnastræinæ, and for them it is unnecessary to erect a special family Thamnastræidæ. They are nothing else than the early Triassic representatives of our Fungidæ.

The genus *Siderastræa* has a very clear line of descent within this family. On the other hand *Astræomorpha* seems to me to come from an entirely different origin, and to have structurally more resemblance with *Porites* than with *Siderastræa* or any other Fungid.

Lophoserinæ, E.H.

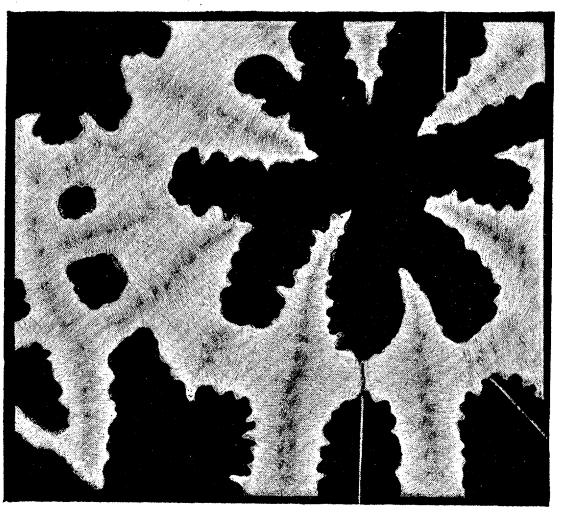
The affinity of the Lophoserinæ, E.H., with the Thamnastræinæ (BECKER, *em. aut.*), and with the Funginæ, E.H., is fully recognized. The considerable development of pseudosynapticulæ is a feature of resemblance with the Thamnastræinæ. But their distribution in the calyx and the occasional occurrence of true synapticulæ is a point of difference. Again, the basal surface of the corallum has the same smooth or epithecate character in Lophoserinæ as in Thamnastræinæ.

In the structural features of its septa, the Lophoserinæ are intermediate between the Funginæ and the Eupsammidæ. The septa may be compact and composed of well-developed septal ridges and regular trabeculæ, as in *Fungia* and *Siderastræa*. Or it may have irregular pores, arising from interruption of the calcification around trabecular axes, as in the case of the Eupsammidæ. The centres of calcification are more closely and less regularly set in such types of Lophoserinæ, and in many cases the opposite fascicles are zig-zagged in position.

Fig. 46 is a transverse section of adjoining calyces of *Lophoseris*, showing the close setting of the fibrous fascicles in the septa, the highly granulate outline of the septal surfaces, also the occurrence of both pseudosynapticulæ and true synapticulæ. Fig. 47 is a transverse section made through a thickened pseudotheca, between two rows of

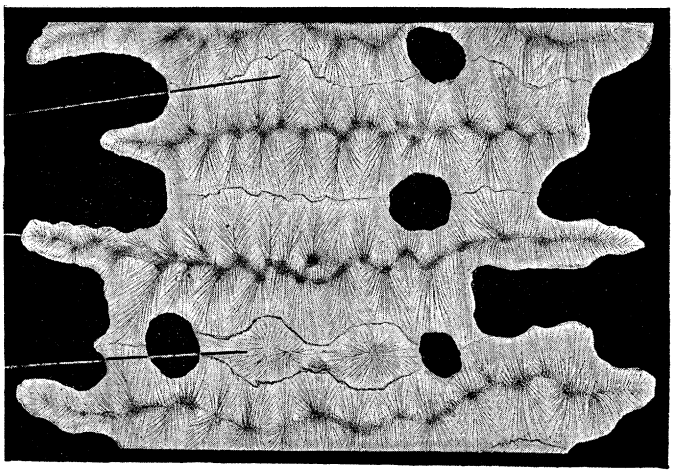
calyces in a meandroid type. A comparison of this microscopic section with fig. 52, *Eupsammia*, shows the points of agreement in the crowded centres of deposit and pseudothecal thickening. The figured specimen of *Eupsammia* was scarcely so well preserved as that of *Lophoseris*.

Fig. 46.



Transvesre section of a calyx of Lophoseris—true synapticulæ (*syn.*), and pseudosynapticulæ (*ps.syn.*). form the pseudotheca;—septal granulations (*gr.*) correspond with the "centres of calcification."

Fig. 47.



Transverse section through a much thickened pseudotheca, continued growth of the synapticulæ and pseudosynapticular granulations having blocked up a large part of the interseptal loculi.

CHAPTER VI.—EUPSAMMIA; SYSTEMATIC POSITION OF THE EUPSAMMIDÆ

EUPSAMMIA.

The Sub-kingdom M. Perforata, E.H.

All the generic types previously described in this paper have been chosen from the sub-kingdom "Madreporaria Aporosa," E.H.; in *Eupsammia*, however, we have a representative of the *Madreporaria perforata*, E.H.* The *M. perforata* were subdivided by EDWARDS and HAIME into two families, the *Madreporidæ*, in which the porosity of the calcareous skeleton was comparatively little developed, and the *Poritidæ* with a highly reticulate skeleton. Since their classification, published in "Coralliaires," various alterations have been suggested. The three sub-families of the Madreporidæ, the Eupsammineæ, Turbinarineæ, and Madreporineæ, have especially been sorted and re-sorted. One author groups Turbinarineæ with Poritineæ, another regards Turbinarineæ as distinctly related to Madreporineæ, but removed from Eupsammineæ, the Poritineæ themselves have been classified (in part) with the Thamnastræidæ. Generally speaking, the Eupsammineæ have been held aloof from much controversy, at the same time that, by reason of repeated research of *Astroides calycularis*,† their features were becoming known in the greatest detail.

Canalicular System in the Interseptal Loculi.

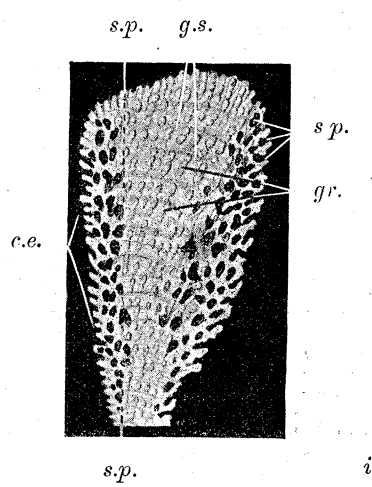
The Eupsammineæ have porous septa, a synapticular wall, and, in colonial types, a canaliculate cœnenchyme. I examined chiefly the skeletal structure of the genus *Eupsammia*. Fig. 48 is a drawing of the septal surface of *Eupsammia trochiformis*, E.H., an Eocene species, with simple corallum. The septal pores are present chiefly at the peripheral part of the septum and near the columella; others, which were originally present in the septum between these two areas, have been subsequently filled up. Secondary thickening goes often so far as to completely transform the lower half of the corallum into a solid mass. The stages of growth are easily observed on this septum, also the relations of the granulations to the growth-segments (*cf.* p. 110). A transverse section (fig. 49) near the lip of the corallum shows the septa coalescing here and there by means of synapticular cross-bars. Where the interseptal loculi are narrow towards the columella, the inner ends of the septa belonging to the higher orders coalesce directly by one of their lateral surfaces with the adjacent lateral surface of a longer septum. Groups of septa are thus firmly united with one another, and skeletal strength is attained in this manner instead of by the development of compact wall and dissepiments as in the Astræidæ.

* See EDWARDS and HAIME, "Coralliaires," especially vol. 2, p. 5, and vol. 3, pp. 89 and 90.

† Ref. Introd., LACAZE DUTHIERS, v. KOCH, v. HEIDER.

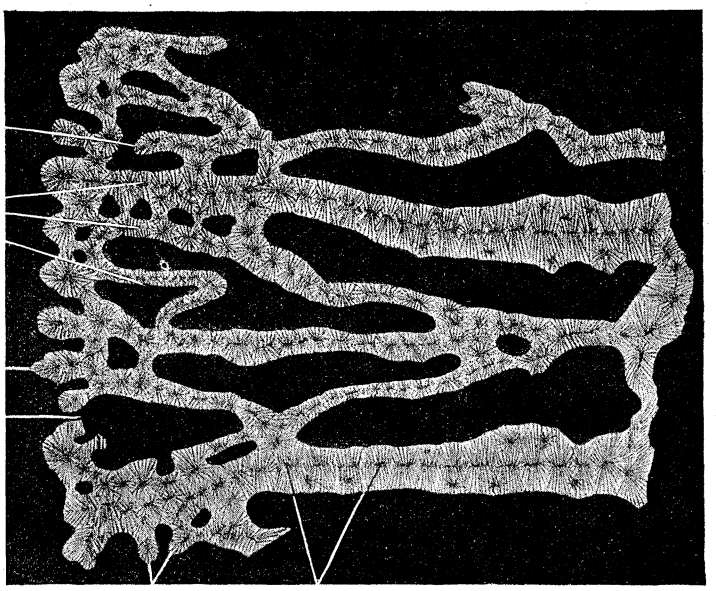
Whilst this mode of skeletal interseptal support at once indicates the nearer affinity of the Eupsammids with Fungids (*cf. Siderastræa*) and Lophoserids than with Astræids, an important difference may be at once observed between the arrangement of the interseptal supports in Eupsammids as compared with the arrangement characteristic of the previously-discussed synapticulate families. In *Eupsammia* the

Fig. 48.



Septum of *Eupsammia trochiformis*, E.H.; *s.p.*, septal pores at the inner (columellar) and outer (pseudothecal) regions; *c.e.*, costal edge of septum; *g.s.*, a growth-segment of septum with its curving series of granulations; *gr.*, granulations in other growth-segments.

Fig. 49.



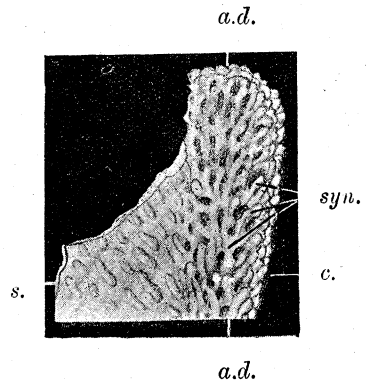
Transverse section *Eupsammia*; *s.*, septa united by the synapticular network; *s.p.*, septal pore near the periphery; *c.*, costa; *ic.p.*, intercostal pore; *c.c.*, centres of calcification.

synapticulæ are *not arranged in vertical series, but alternate with one another, or are quite irregular in position.* The canalicular system in the interseptal loculi is more highly involved than in the Fungids and Lophoserids, it is a branching network of channels instead of simple, smaller channels extending downwards from the cœlenteron into the intersynapticular spaces.

The most complicated development of this synapticular network is found near the costal portion of the simple corallum of *Eupsammia*. There the inter-radial loculi are originally widest, and the basal body-wall of the polyp is invaginated in an entirely irregular fashion. Within an oblique or erect-growing invagination an erect synapticula develops, it is again united crossways with similar synapticula, which need neither be in the same radial nor in the same tangential line as its neighbour. Fig. 50 is a drawing of the branching synapticular network in an interseptal loculus near the periphery of the calyx. This is only a more irregular manner of invagination

of the body-wall at the base of the growing polyp than we have hitherto had occasion to observe. In the Turbinarinæ and Madreporinæ the *cœnosarcal* part of the body-wall frequently forms a similar irregular synapticular network in the inter-radial loculi of the "cœnenchyme."

Fig. 50.



Enlarged drawing of septal surface (broken at left-hand side), showing the branching synapticulæ (*syn.*), and its part in the formation of rows of tubercles between the costal continuations of septa; *s.* septum; *c.* costa; *a.d.* area of divergence.

The Area of Divergence.

In the description of foregoing genera of the Astræinæ and Fungidæ, I have pointed out that all longitudinal ridges observed on the surfaces of the *radial* structures are directed in opposite ways towards the septum and towards the costa, and also that a pair of ridges take their origin simultaneously from a line at the periphery of the calyx. The whole peripheral line, or "area" of divergence of the ridges, becomes in those foregoing types much thickened, and helps to form a "pseudothecal" wall. The farther development of a ridge takes place by the end-to-end attachment of new "segments of growth" until the full length of the ridge is attained. The completed ridge is comparable to a calcareous chain composed of links of various shape and form, viz., the growth-segments of the spiniform or nodular ridge, as the case may be.

Only in the case of *Lophoseris* and, generally speaking, the Lophoserinæ, we found that the trabecular chain of individual parts was occasionally interrupted. In other words, that the successive growth-parts were not always directly joined up end-to-end with one another, although the ridges, otherwise in point of origin and direction, agreed with the Astræinæ and Fungidæ. *Lophoseris* displays in this respect a decided approach to *Eupsammia*.

Referring again to the surface drawing of the septum of *Eupsammia* (fig. 48), it will be seen that horizontal growth-curves pass over the septum. The curves are more strongly marked at intervals in the septum corresponding to successive growth-periods. The granulations on the septal surface form, on the whole, curves which follow the intervals between these thicker, more strongly-marked growth-curves.

Considered vertically, however, the series of granulations is interrupted at the peripheral and inner areas of the septum by irregularly-shaped pores. We may look upon the series of granulations as the superficial form assumed by a successive series of growth-parts belonging to a large trabecula. The irregular shape of the septal pores in *Eupsammia* is due to the fact that the growth-parts of one trabecula may be disconnected, and also the growth-parts of adjacent trabeculæ. When the spaces thus left run into one another, naturally irregular pores arise. Moreover, since the secondary outfilling has no definite relation to the structure, the original pores may, in the course of time, be irregularly diminished in size.

New trabeculæ are inserted at the periphery, and a distinct area of divergence is there observed (*a.d.* fig. 50). In *Eupsammia*, however, there is not simply the divergence of one septal and one costal trabecula; but a definite fan-group of trabeculæ is formed at each new growth-period. The new trabecular parts are placed alternately between those of the foregoing growth-period, and two or three new trabeculæ take origin at the "keystone" part of the arch.

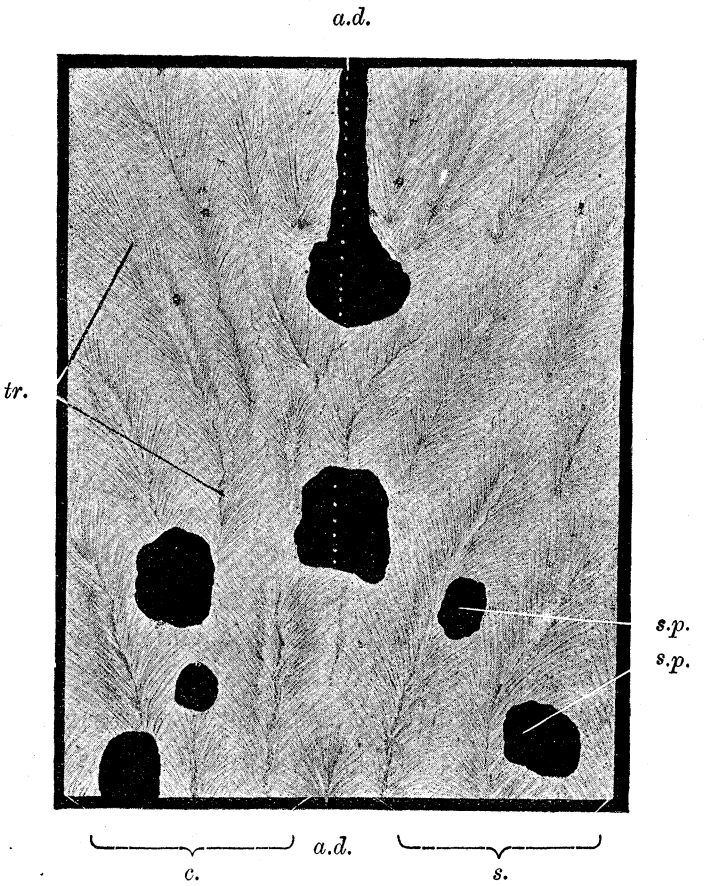
One might almost say that towards the columella a second area of divergence is present, with alternating position of the successive trabecular parts like that in the main peripheral area. The trabeculæ are directed on the one side towards the columella, on the other slantingly upwards into the prominent exsert expansion of the septum. This inner expansion of the septum is, however, a generic feature and is associated with the almost turbinate shape of the simple corallum of *Eupsammia trochiformis*. It may be compared with the cristiform lobes of the septa in a few Astræids and in a large number of Turbinolids.

Microscopic Structure.

The radial longitudinal section, fig. 51A, is cut parallel with the septum and passing through the area of divergence at the periphery. It shows that the "septum" is made up of trabeculæ with long, radiating fibres, and that the divergence of the trabeculæ distinguishes a *costal*, or outer, from a *septal*, or inner edge. These are once more the same essential features as we have already observed in the radial structures of Astræid and other coral types. Each trabecula corresponds in width to a single granulate ridge on the septal surface (*cf.* fig. 48). The trabeculæ are usually composed of short series of fascicles. Interruptions in fascicular growth take place and leave skeletal pores, which correspond to intervals between growth-periods. More seldom a continuous series of fascicles forms, and a compact trabecula is built up through two or more growth-periods. This occurs specially at or close to the area of divergence, where the septum is always strongest. The ends of the fascicles bend outward from the median plane into a tangential direction and are then continued as a synapticular structure or into granulations. Apertures are left in the septal plane above the parts at which the trabeculæ ends bend outwards. Fig. 51B is a radial

longitudinal section cut very near the surface of the septum and passing through its entire breadth from columella to wall. The fascicular ends of the trabeculæ are cut almost transversely since they bend outwards near the surface. The synapticular network is drawn in lighter tone against the darker ground of the septum. This will be understood by comparison with fig. 50 above.

Fig. 51A.



Eupsammia: section parallel with the septal plane, meeting trabeculæ only at part of their length, the tips of the trabeculæ bend outwards from the plane of section; *a.d.* area of divergence; *s.* septum; *c.* costa; *s.p.* septal pores—*two* of a curve of *four* pores indicating the limit of one growth-segment at this peripheral region.

A transverse section (fig. 52) shows the pores occurring in the septal plane, and, corresponding to them, calcareous synapticular structures on either side. The section includes the peripheral costal area of several septa, but the large amount of secondary thickening has almost filled up the originally canaliculate system of synapticulæ. The centres of calcification are extremely close in the median plane of a septum so that each surface-ridge corresponds to several inner centres of calcification. At the same time fascicular grouping of the fibres is clearly seen, and the axes of fascicles bend outwards from the median plane into the middle of surface granulations.

The growth-lamellæ curve very regularly round definite centres at the first laying down of the septum. But, as successive growth-periods follow, the primary in-and-out curving of the innermost layers becomes lost, and larger curves, *much less regular*, make themselves evident. It is this fact which in *Eupsammia* gives to the innermost growth-layers a certain distinctness from the subsequently developed layers. They appear in sections as a lighter band on both sides of the median centres, while the fibres beyond them, although having their crystallographical axes generally speaking in the same direction, seem opaquer. The opacity is due to frequent variation in the particular form of the curves of successive lamellæ, and a consequent crossing of the fibres.

The "Dark Line" of the Septum.

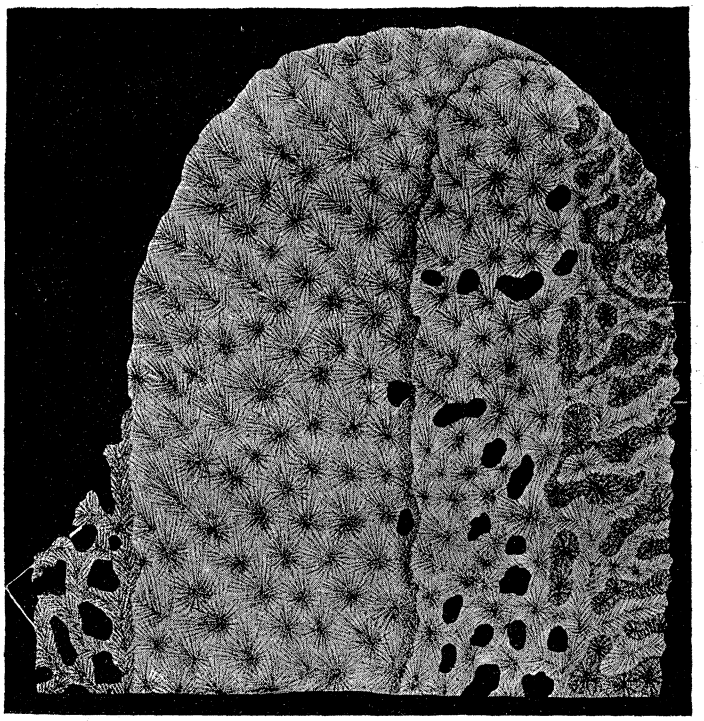
The microscopic sections indicate above all the smoothness of the growth-lamellæ in contradistinction to the crimped and corrugated lamellæ which we have studied in Astræinæ and in Fungidæ. The leaf-like apposition of successive lamellæ is much more easily demonstrated in *Eupsammia*, although here, and indeed in all Madreporarian types, the septum is composed of fibrous layers from the middle plane to the surfaces. The median lighter band, corresponding to the deposit of the septal margin, represents the "dark line," the "primary streak," and "primary septum" of KOCH and other authors. It cannot, however, be *structurally* distinguished from a "lamellar stereoplasm" in the sense of those authors, since the so-called primary septum is itself lamellar. It is the *close and at the same time elongate setting of the centres of calcification* in *Eupsammia* which gives the appearance in ordinary thick sections of a median line in the septum.

We have in all hitherto examined cases precisely the same general structural relations in the septum; *the individual differences in the various types consist in a varying distance from one another of the original centres of calcification around which the flaps of the septal fold lay down their first growth-lamellæ.*

The "True" Synapticulæ of Eupsammia compared with Pseudosynapticulæ.

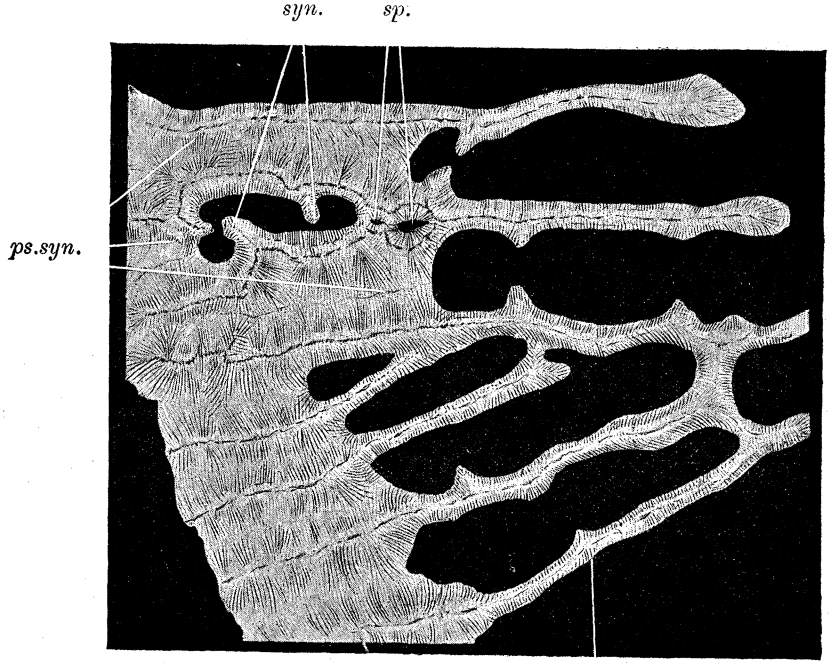
Correlated with the smoothness of the growth-lamellæ is another feature, externally apparent, the smoothness and bluntness of the marginal apices of the septal ridges and also of the synapticular growths. The septal edge of *Eupsammia* can scarcely be called toothed in the acceptation of the expression for Astræinæ, much less is it "spined" or "serrated." It is knobbed or nodular, the nodule having an elliptical outline with its *long axis set across*, and not along the septal plane. Very often (where the fibrous rows have bent out from subjacent horizons and continued to grow as upright synapticulæ) small knobs are present on one side or both of the septal knobs. These smaller knobs or nodules are synapticular growths, each with its own centre of calcification. And two or three such nodules may bridge the interseptal

Fig. 51B.



Section parallel with the septal plane, but cut nearer the surface than 51A—hence the outward-bent tips of trabeculæ are met almost rectangularly. *col.*, columella; *syn.*, synapticular network, seen as if projected against the darker-looking septum behind (*s.*).

Fig. 52.



Transverse section *Eupsammia*, showing secondary thickening filling up the interseptal loculi. *s.*, septum; *syn.*, synapticula; *ps.syn.*, pseudosynapticula; *sp.*, interseptal space.

space. As these nodules are frequently connected with each other by this mode of *bending* of the rows of fibres, now into upright, now oblique, now horizontal direction, one may look upon a synapticular bridge as growing out from one septum to the next. PRATZ seems to have had this particular form of synapticula in view when he gave his definition of the "true synapticula" (*antea* p. 185). I am led to this opinion by the fact that these synapticular knobs of *Eupsammia* outwardly resemble the component "nodules" of a trabecula of *Cyclolites*, *Microsolena*, and other genera of the Pseudo-Astræinæ examined by PRATZ. PRATZ did not identify the structure of the *nodule* of *Cyclolites*, &c., with that of the Astræid *granulation*. Their identity is however demonstrated in the preceding parts of this paper, *since both "nodule" and "granulation" correspond with one or more fasicular groups of fibres extending towards the lateral surface of a septum.* Some of the synapticular knobs of *Eupsammia* are, on the other hand, formed in *special invaginations* of the basal body-wall of the polyp, and are homologous with the *new* centres of calcification introduced in the interseptal loculi of Fungids and Lophoserids and forming a coalescence of the adjacent *granulate* outgrowths. In *Eupsammia* the invagination does not continue as in the case of the synapticular "bar" of *Fungia* in a definite vertical direction, but ceases after the formation of a single synapticular growth. The next invagination arises in any direction obliquely to, or rectangularly outwards from, the foregoing.

Certain points of similarity with the Turbinolidæ.

Curiously enough, another Madreporarian family, apparently remote from the Eupsammidæ, has a very similar microscopic septal structure. In the *Turbinolidæ*, the axes of calcification in the median plane of the septum are also very closely set and the growth-lamellæ very smoothly apposed. An important difference however consists in the fact that a trabecular axis never bends out of the median plane in Turbinolidæ. There are therefore no septal granulations into which the axes of fascicular bundles of fibres bend. When a granulation forms on the septal surface, it covers a number of small centres of calcification in the median plane, from which practically parallel-placed fibres pass into the granulation. The fine structure of smooth-septate Eusmilinæ is essentially similar (*antea* p. 161).

The Turbinolidæ often resemble Eupsammia in another characteristic, the coalescence of septa at their inner ends often building a symmetrical figure. The genus *Turbinolia* itself shows this feature, and still more the genus *Deltocyathus* and other genera belonging to the Trochocyathus group. Such local coalescence can only be produced by the invagination of a part of the body-wall of the polyp, not in the direct radial line of the septal invagination, and is therefore homologous with synapticular invagination. It affords a means of support to the interseptal portions of the body-wall, and in the case of the short Turbinolid corallum, renders the customary dissepimental support less necessary. We have already studied an analogous case in Fungia.

Here, however, the points of similarity between Eupsammia and the Turbinolidæ end. Wall and septa of Turbinolidæ are *compact* and the mural ring of calcification is in continuity with the septal centres of calcification. I shall return to these distinguishing features of the Turbinolidæ in discussing the remaining so-called "Perforate" types:—*Turbinaria*, *Madrepora*, and *Porites*.

Systematic Relationship of the Eupsamminæ (E. and H.) to the Family of Fungidæ (Dana emend. Zittel.)

The Septo-Costal Area of Divergence.

In common with the Astræinæ and the Fungidæ, the Eupsamminæ possess radial structures in which a *thicker peripheral area* is the seat of divergence of the component septal and costal trabeculæ. Farther the extra thickness of this peripheral area is a *large constituent in the formation of a calicinal wall area.* Between the adjacent thickenings of the radial structures, a very small invagination of the basal part of the body wall is sufficient to form a compact wall. According to the particular shape of the invagination, an erect but flat-surfaced dissepiment may be formed or a roundish calcareous rod of synapticular character. The wall which is formed in this way may be said to be several growth-periods behind the septa in its original development.

These relations of walls and septa are characteristic of Astræinæ, Funginæ, Lophoserinæ, and Eupsamminæ, and are absent in the Turbinolidæ, Madreporidæ (excl. Eupsamminæ) and Poritinæ.

The Lophoserinæ more especially resemble the Eupsamminæ in respect of the non-continuity of the successive growth-parts in the septal trabeculæ. The irregular pores in the septa are thus explained in both Lophoserinæ and Eupsamminæ.

The nodulate shape of the individual trabecular growth-parts in the Eupsamminæ closely resembles that characteristic of Pseudoastræinæ, of *Siderastræa*, and of Lophoserinæ. In all these types, as well as in *Fungia*, the coalescence of septal ends with one another is frequent, and is associated with the general fact that the basal body-wall in this group forms small invaginations at any part of the interradial loculi.

As a rule, the *branching* colonies of Eupsammids tend to the simpler form of canalicular system observed in Funginæ and Lophoserinæ, and have not the complicated cœnenchyme of *Turbinaria*, *Madrepora*, and *Porites*.

Recapitulating briefly the most important features of *Eupsammia*, we have:—

(1.) The trabeculæ composing the septum often incompletely united with one another, as in Pseudoastræinæ, *Fungia*, *Lophoseris*, &c.

(2.) The individual growth-parts of any one trabecula not always attached end to end, although following each other in vertical succession. Where such an aperture is left *in* the trabecula, and it happens to be alongside of an aperture left between

two adjacent trabeculæ, an "irregular pore" appears in the septum. The Lophoserinæ show the same feature.

(3.) The fascicle of fibres has its axis in the median plane of the septum, but may bend out in *unpaired* fashion towards an interseptal loculus, and give origin there to a synapticula. This feature is, perhaps, the most characteristic for *Eupsammia* in contradistinction to the Lophoserinæ, Funginæ, and Pseudoastræinæ. To it is due the occurrence of synapticulæ, not in series above one another, but irregularly.

(4.) A great variety in the precise course and position of synapticular calcareous bars gives the skeleton of *Eupsammia* at its peripheral portion a certain resemblance with the involved meshes of cœnenchyme in *Madrepora* and *Turbinaria*. Again, the fact that many synapticulæ are directed obliquely inwards and upwards towards the calyx shows the independence of the synapticula and its analogy with the growth-part of a radial trabecula. The canalicular system of the Eupsamminæ, E.H., varies we may say between the less complicated *Fungia* type and the more highly differentiated "perforate" type, but it is the least constant of all features in the Eupsamminæ, and the last that may serve as a systematic basis.

(5.) From the above microscopic study of skeletal features, the genus *Eupsammia* will be seen to have much in common with the Fungidæ. It is very significant to find that the anatomical relations of another genus belonging to the Eupsamminæ show very marked affinities with those of Fungidæ. The species *Stephanophyllia formosissima* has been described by FOWLER ("*Madreporaria*, IV.," Q. J. M. S., February, 1888), who writes:—"In several respects *Stephanophyllia* exhibits a resemblance to the *Fungia* recently described by BOURNE. The plano-convex shape of the corallum, and the correlated basal position of the theca, are, of course, characteristic of both genera; besides this, a view of a complete mesentery shows that a few synapticulæ brace together the septa of this coral, and that between the synapticulæ the muscular pleatings of the mesoglœa are gathered into strong bundles in a very characteristic manner, hitherto described only in *Fungia*. The histological appearance of the craspedon is also similar, and characteristic in both forms. On the whole, *Stephanophyllia* appears to bring *Fungia* into closer relations with the Eupsammidæ than have been generally allowed."

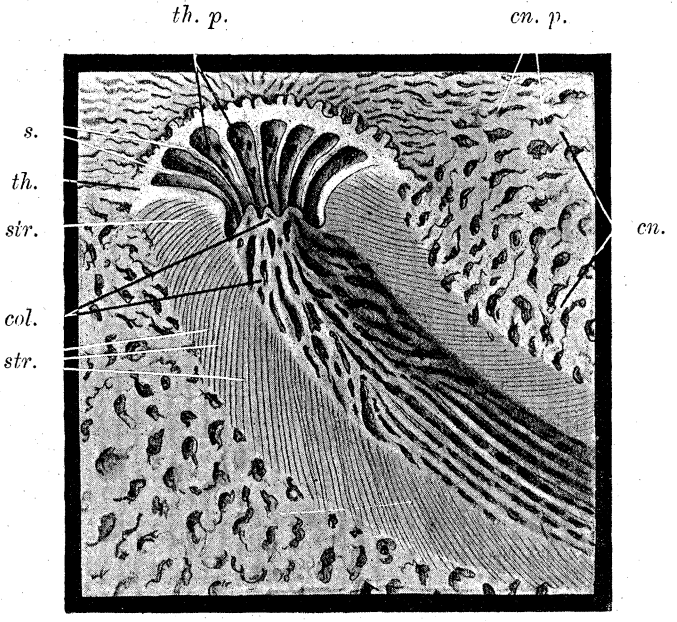
According to all the above results, the sub-family Eupsamminæ, E.H., deserves a systematic position as an independent family, the Eupsammidæ, allied with the Fungidæ. The relationship of the Eupsamminæ, E.H., to the Madreporinæ, E.H., and Turbinarinæ, E.H., is far more doubtful, as later parts of this paper will show. Amongst the *M. perforata*, E.H., it is the sub-family Poritinæ, E.H., which has most apparent resemblance to the Eupsammids, yet no clear evidence can be given that these two groups are nearly related.

CHAPTER VII.—SOME "PERFORATE" TYPES: TURBINARIA, MADREPORA, PORITES.

TURBINARIA.

Fig. 53. The species examined, *T. mesenterina*, LAM., has a low foliate corallum, the individual polyps grow very obliquely forming a calycinal tube of turbinate shape.* Fig. 53 is the drawing of a half calyx, presenting the surface view of two septa, and

Fig. 53.



Enlarged drawing of *Turbinaria mesenterina*, LAM.; *col.*, columellar pali; *th. p.*, thecal pores; *cn. p.*, cœnenchymal pores; *s.*, septa; *str.* striæ (septal trabeculæ).

the central pali and columellar area. The septa are compact and smooth, reminding one of the Turbinolid and Eusmilinid type in general. On the other hand, the wall is essentially synapticular in character, apertures being left in regular series and affording the means of communication between the canalicular cœnenchyme and the polypal cavities. During the life of the polyp the cœlenteron, or body-cavity within the theca, is continued into the extrathecal cœnosarcal tissue lining the complicated cœnenchymal network of skeletal canals.† The general relations of the hard and soft parts in *Turbinaria* may be studied in fig. 56.

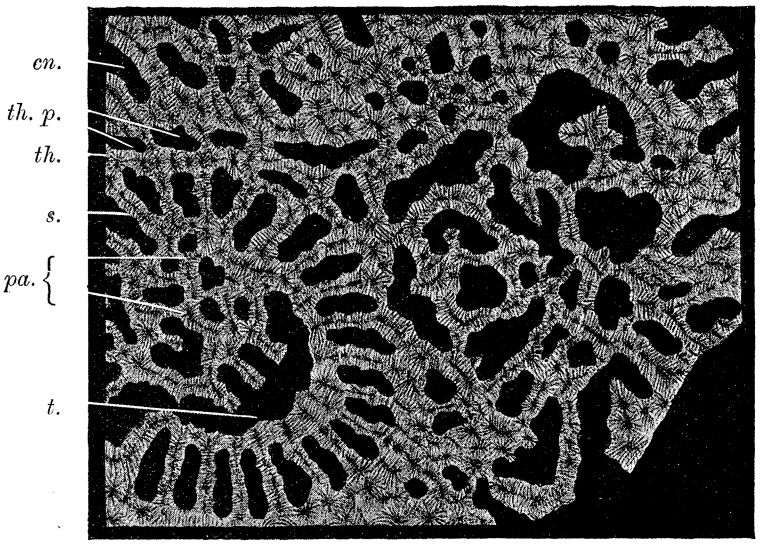
* A species nearly allied to *T. mesenterina* is figured by EDWARDS and HAIME in the "*Atlas* of Hist. Natur. des Coralliaires," Plate E, fig. 1A and 1B, *Turbinaria cinerascens*.

† The anatomy of the polypal parts has been worked out by Dr. G. H. FOWLER, "The Anatomy of the Madreporaria III.," 'Quart. Journ. Micr. Sc.,' August, 1887.

The Skeletal Parts of the Calyx.

Septa.—The lateral surfaces of the septa are striated, and on the striæ are occasional small granulations. The striæ are not arranged in the form of a divergent fan of ridges as in *Galaxea*, neither do they diverge from a peripheral area in the radial structure as in Astræids, Fungids, and also, if with a slight difference, in *Eupsammia*. But the striæ are placed almost horizontally with the upper edge of the septum so that the apex of the stria is directed towards the centre of the calyx. In a transverse section of the calyx usually only one or two striæ are cut in each septum, and the microscopic structure presented must therefore be compared, not with the *transverse* sections of Astræidæ, &c., but rather with any longitudinal, tangential section through a few striæ or trabeculæ in these groups.

Fig. 54.



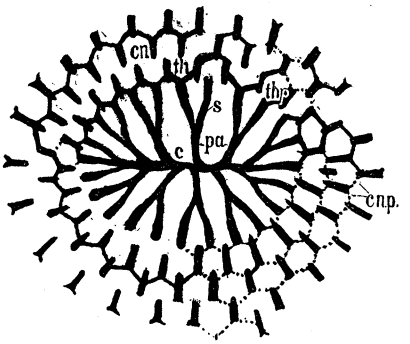
Turbinaria: transverse section showing the microscopic structure of septa (*s.*), their prolongations as pali (*pa.*) surrounding the columella, the theca (*th*), thecal pores (*th. p.*), and cœnenchymal interspaces (*cn.*), radial in direction; *t.*, an accidental tear in the section.

Fig. 54 shows the agreement of the microscopic structure of the septa with that already described for *Euphyllia*, in a less degree with that of *Eupsammia*. The dark band in the middle is composed like that in *Euphyllia* of very closely set centres of calcification. Similarly there are no fascicle-groups of fibres passing outwards from the median plane to the surface granulations. The growth-lamellæ are smooth, and only the outermost lamellæ show a less uniform deposit; the fibres become lengthened at some parts and not at others, and thus superficial granulations of small size occur on the striæ, bearing however a definite relation to particular series of calcification centres.

Septa, Pali, and Columella.—The paliform prolongations of the septa have the

same microscopic structure as the septa. They surround in buttress-like fashion a central lamellar columella, which is itself the continuation of one of the primary septa. A diagrammatic ground-plan of the septa, pali, and columella is given in fig. 55. The position of the columella in the long diameter of the usually somewhat

Fig. 55.



Ground plan of calyx (*T. mesenterina*). *c.*, columella, a continuation of one of the primary septa; *s.*, septa, primary and secondary septa unite as couples to form pali (*pa.*). The theca is formed by thecal and costal bars alternating with pores (*th.p.*); similarly the cœnenchyme (*cn.*). See p. 209.

elliptical calyx, as well as its crest-like prominence amidst the pali, gives a marked bi-symmetry to the skeletal parts, (*cf.* FOWLER, the position of the "directive" mesenteries is at the ends of the dividing plane of bi-symmetry in the polyp, *loc. cit.*, p. 87.)

An important feature represented in the figure, is the *origin of each palus from the coalescence of two of the principal septa.* This at once distinguishes the *Turbinaria pali* from the occasional paliform prolongations of single septa in *Goniastræa* and a few other *Astræid* genera, while it shows their resemblance with many of the Turbinolidæ in which rings of pali alternate in position with the septa. The coalescence of the septa to form the pali takes place according to a definite system. One primary and one secondary septum unite in couples all round the calyx. An exception to this is at the ends of the long diameter marked out by the crest, where the primary septum either remains solitary or unites with the secondaries on both sides. The primary which remains solitary bends sidewards, and then returns to the mid-line and forms the columellar crest. A long, leading septum with columellar continuation may be said to be one of the most characteristic features of the Eusmilinæ, ED. and H., and it is among genera of the same sub-family that we find lamellar pali in front of the principal septa, *e.g.*, *Dendrogyra*, *Pectinia*. Those are also, as I have already said, familiar in *Caryophyllia* and other Turbinolidæ (see also p. 272).

If we now bear in mind the similarity of the fine structure of the septa in *Turbinaria* with that of *Euphyllia* or of *Caryophyllia*, it will be admitted that the

skeletal parts of the calyx of *Turbinaria have many points of affinity with similar parts in the calyces of Eusmilinid and Turbinolid genera.*

A feature of smaller moment is the slanting away of the pali from the radial septal plane as they grow upwards and inwards. The same slanting growth is observed very often in the inner ends of septa (*e.g., Euphyllia*). It has in *Turbinaria* a certain significance, as the pali in winding round, become coalescent with one another by small synapticular bars, and considerable strength of the amphicolumellar structure is attained.

Between the septa and the pali a trench-like hollow is observed, which has its origin in the deep scallop between the inner ends of the coalescent pairs of septa and the corresponding palus. The mesenterial filaments descend into this skeletal trench within the polyp, and I have little doubt that the *Turbinaria "trench" is the functional equivalent of the "fossula" of Palæozoic Madreporaria.* To this I shall return in chapter ix.

Conflicting reports are often given in specific descriptions of pali-bearing forms, with regard to the actual number of rings of pali present. A section made near the growing lip of the *Turbinaria* calyx yields two rings of pali, a section at some distance below yields only one. The explanation is easily observed in a longitudinal section of the calyx. The pali starting from any given growth-horizon have already grown inwards and upwards to the main columellar crest when the next series of pali begin to develop. At the origin of the next series, the two rings of pali are clearly apparent, but subsequently the pali in the same radial line are united by secondary calcareous deposit, laid down by synapticular invaginations of the basal body-wall as the soft tissues are being slowly withdrawn from lower to higher growth-horizons. Similar observations may be made on the septal pali in Poritidæ and on the spines of *Madrepora.*

The so-called Synapticular Wall.*

In discussing the synapticular bars of *Fungia,* I referred to the attachment of the mesenteries to the polypal body-wall at the oral, lateral, and basal body-surfaces of the polyp. In *Fungia,* the lateral and basal body-wall of the polyp to which the mesenteries are attached is invaginated subsequently to the septal invaginations, the interseptal invaginations then keeping pace with the septal, but at a lower horizon of growth. A continuous synapticular bar thus takes origin over which the body-wall bearing the mesenteries is doubled into long folds lining canalicular continuations of the cœlenteron between adjacent synapticular bars.

* The term "synapticular" has been applied to the porous wall of "Perforates," no doubt because of the general resemblance between the skeletal bars of the wall and the synapticular bars between the septa in Fungidæ. But I think the term misapplied. The original use of "synapticula" was limited to a bar *uniting septa* (see p. 167), *and necessarily of later origin than the septa.*

The process in *Siderastræa* and *Lophoseris* is similar, but no continuous synapticular bar is formed. Separate synapticulæ are laid down in parts corresponding with the growth-periods of the polyp. Thus apertures are left unfilled, although the synapticular invagination continues to be withdrawn upward in a definite vertical direction.

In *Eupsammia*, still another variety is presented—new synapticular invaginations are made at each growth-period, and they are not above each other, but either alternate or may be irregularly placed. Such an arrangement denotes a much greater complication of cœlenteric canals than in the case of the vertical synapticular series or continuous bar.

One structural feature is, however, shown in common by all those types. It is that the invagination of the mesenterial portion of the body-wall takes place at *some distance below*, and is at first of *posterior date* to that of the septal and costal portions. Hence the parts of the mesenteries enclosed in the synapticular channels are continuous in the open interseptal loculus above the synapticular invagination. In other words, the mesenteries in the synapticular channels are merely the prolongations of the mesenteries in the upper non-synapticular part of the cœlenteron. Further, the mesenteries pass continuously over the synapticular wall into the "Randplatte," or edge-zone, of the polyp.

Turbinaria, on the other hand, at once distinguishes itself in the fact that, at the peripheral portion of each polyp where mural invaginations are formed, they form *contemporaneously with* or even *prior to* the invaginations in which septa are produced. This fact I have deduced from a series of sections. In all types mentioned above, the synapticulæ form subsequently to the septa, and microscopic sections show that the calcareous deposit around the septal centres of calcification serves as the starting-point of a synapticula, the prop on which the mesenterial body-wall temporarily supports itself in the course of its further invagination. In the converse case represented by *Turbinaria*, the sections show a *mural ring of calcification centres around the polyp, from which at certain points processes grow out and serve in their turn as the starting-points of septa.* I describe here merely the appearances of the section. A comparison between transverse sections of *Siderastræa* (fig. 43) or *Eupsammia* (fig. 52), on the one hand, and *Turbinaria* (fig. 53) and *Madrepora* (fig. 57), on the other, will explain the difference.

The same difference may be observed between the transverse sections of the wall and septa in an Astræid like *Heliastræa* (sub-family Astræinæ) and those of *Galaxea*, *Euphyllia*, or, still more, *Turbinolia*, *Flabellum*, and other genera belonging to the Turbinolidæ. There the invaginations homologous with the synapticular invaginations in the previously-mentioned types are continuous and give rise to a *compact wall*; yet the priority of the *septal* invaginations in the Astræinæ, and, on the contrary, the contemporaneity or the priority of the wall invaginations in the

Turbinolidæ, produce similar appearances in transverse sections, as have just been described for different synapticular types.

I find no statement in FOWLER'S paper on *Turbinaria* with regard to the time-relations of the development of radial and inter-radial structures of the polyp. But my own microscopic sections of the skeleton seem to me sufficient basis for my statement that the inter-radial invaginations at the mural area are at least not later than those of the radial structures. The wall "synapticulæ" are, therefore, at the same horizon in the calyx as the septa; they are no longer basal in position. In analogous cases a number of researches give clear evidence of a difference in the time-relations of the radial and inter-radial invagination (*vide* KOCH'S various papers on development).

The contemporaneous time-relations of the septal and mural invaginations in Turbinaria, together with the alternations in position of the mural and costal invagination at successive growth-periods, are, in my opinion, the main reasons which explain the "cutting-off" of the polypal mesenteries at the mural portion of the polyp from the cœnosarcal inter-polypal portions of the colony.

The Perforations in the Wall occur between successive Mural Bars.

Two successive stages of growth are represented in the diagrammatic ground-plan, fig. 54. In both stages the cœlenteron of the polyp is continuous with the cœnosarcal canals above the septa and between the adjacent mesenteries of two neighbouring pairs of mesenteries; in other words, the inter-mesenteric chambers of the polyp are extended continuously into the cœnosarc. At one stage represented in the figure, the mesenterial parts of the body-wall are invaginated at the periphery of the polyp, and mural supports are produced; at the other stage, the mesenterial parts of the body-wall continue freely across the mural area, but new costal invaginations are formed, corresponding in position to an ectocœle, *i.e.*, the part of the cœlenteron between adjacent mesenteries of two neighbouring pairs of mesenteries. This alternating mode of support at one stage by mesenterial invaginations, at the next by additional costal invaginations, produces the characteristic double series of apertures in the "wall" of *Turbinaria* between any two septa, and at the same time is seen to be necessarily correlated with the formation of costæ unrepresented by corresponding septa.

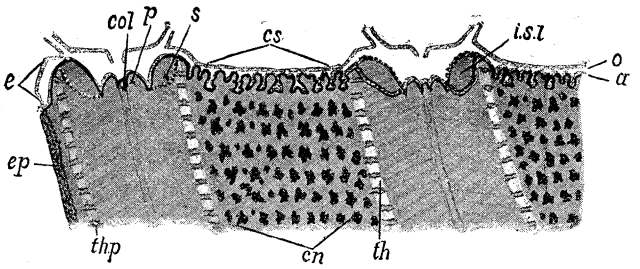
I may at once call attention to the similarity which the genus *Turbinolia* presents in the possession of *additional costæ*, as well as in the appearance of a *double series of dimples* on the outer surface of the compact wall between every two septa. An allied Turbinolid genus has a double series of pores in the wall (see below, p. 249).

TURBINARIA.

A Cœnenchymatous Reef-building Ally of the Turbinolidæ.

FOWLER writes ('Q. J. M. S.,' August, 1887, "Madreporaria," III.): "If we are justified in crediting the appearance of the tissues in *Stylophora*, *Madrepora*, and *Turbinaria*, which implies that the body-wall is supported upon the echinulations, it is not perhaps too much to infer that these relations are of *secondary significance and have arisen contemporaneously with the development of cœnenchyme for the support of the external body-wall*, owing to the inadequacy of the peripheral sections of the mesenteries to effect this support elsewhere than immediately round the theca (where this is exsert from the cœnenchyme)." I may also refer to BOURNE's General Remarks on the porous and aporose skeleton (*loc. cit.*, 'Q. J. M. S.,' August, 1887) which so far anticipate my results. The latter show that the presence of a porous cœnenchyma (of which the porous wall is simply the proximal calycinal part) in *Turbinaria* is itself of only secondary systematic importance. The features of the calyx are the basis on which classificatory relationship must rest, and the result of my investigations would go to prove *that Turbinaria is a specialized "Perforate" Turbinolid*, specialized in that part of the polyp which forms the thick wall and epitheca of its non-cœnenchymatous relations.

Fig. 56.



TURBINARIA.—Cœnenchymatous type; letters as in fig. 2, p. 107; a columella (*col.*), and pali (*p.*), are present; *th.p.* thecal pores, which open into those (black in the figure) of the cœnenchyme (*cn.*) (*cf.* p. 203). This diagram is given for comparison with the similarly-treated figs. 2, 22, 35, and 36.

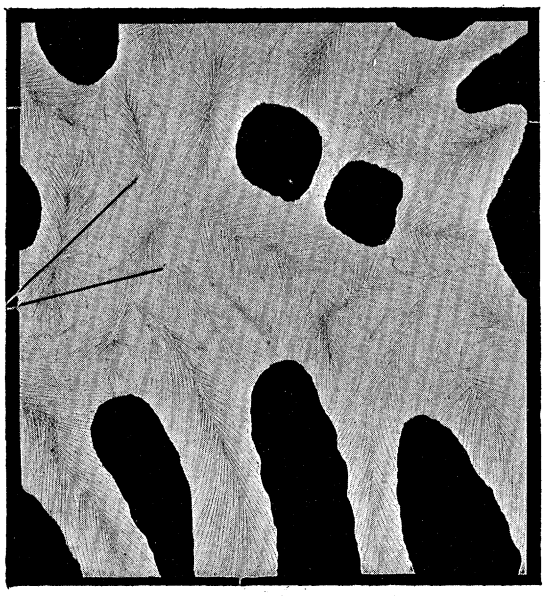
The skeletal parts of the Cœnenchyme agree in Microscopic Structure with those of the Calyx.

One can generally distinguish in the cœnenchyme *radial* or *costal* and *inter-radial* or *synapticular* centres of calcification; although, owing to the subsequent continuity of the original invaginations, the two are very often coalescent. Then the cœnenchyme may appear to be concentric in its arrangement, or variously irregular. The

greatest irregularity naturally obtains at the parts most remote from adjoining calyces, where the soft parts rest more or less loosely on the trough-like depressions of the cœnenchyme.

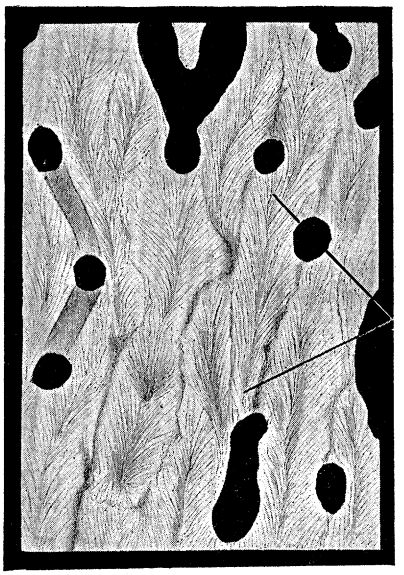
The details of microscopic structure prove that each so-called "echinulation" of the cœnenchyme, whether in a costal or synapticular position, is itself identical with a septum or a palus of the calyx. There is a dark line medially made up of closely set axes of calcification and originally of organic constitution, and on both sides of it, or around it (according as the echinulation is elliptical or circular in section), are smooth

Fig. 57A.



Transverse section through cœnenchyme between two adjacent calyces of *Turbinaria*. Median "darker line" (calcification centres) seen in the septa (*s.*) and also in the several trabeculæ of the cœnenchyme (*cn.*).

Fig. 57B.



Section longitudinally cut through cœnenchyme, showing the varying direction of trabeculæ (*tr.*) and the occurrence of pores.

growth-lamellæ in which the fibres are parallel with one another. Usually the "echinulation" of *Turbinaria* is laminate in form, and one can often distinguish that the lamina is composed of two or three striæ, and repeating, in fact, the septal structure. Fig. 57A is a transverse section through the cœnenchyme between adjacent calcyces; the trabeculæ are met in all possible directions. Fig. 57B is a longitudinal section through the cœnenchyme, showing the irregular slanting growth of the trabeculæ and the consequent irregular occurrence and shape of intertrabecular pores.

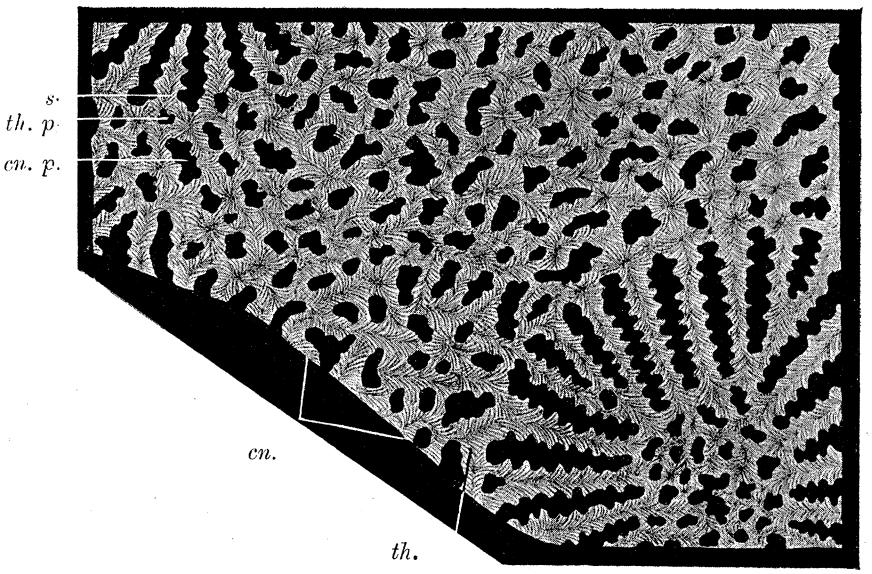
The echinulations of successive growth-periods are not necessarily above one another in position, hence the system of canals is very irregular, analogous, speaking generally, with the system obtaining in the mural area of *Eupsammia*. The cœnosarcal parts descend to very unequal depths within the canalicular system. In

the diagrammatic representation of the cœnenchyma given in fig. 56, it is impossible to show more than the general relations of calyx and cœnenchyma.

Actinacis.

The Cretaceous genus *Actinacis* has a fine structure of its skeleton, identical with that observed in *Turbinaria*. The transverse section, fig. 58, may be compared with fig. 54, a corresponding section of *Turbinaria*. The small part of the calyx at the left-hand corner of fig. 58 shows especially well the connection of septa and wall. Instead of a septum being continued through the wall as a costa, it appears to divide in two halves, which bend away from one another in the direction of the wall. Between the

Fig. 58.



Transverse section Actinacis; *s*, septa; *th. p.*, thecal pore, where a septum splits into two, to form mural bars; *cn. p.*, cœnenchymal pore in a line with the thecal pore.

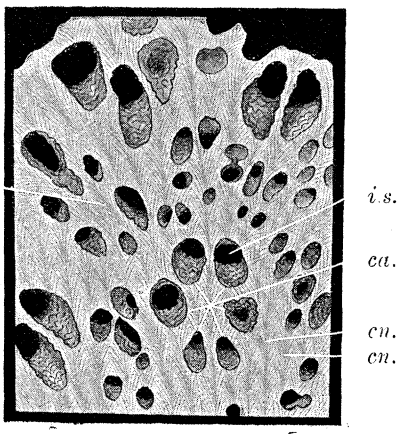
two halves a thecal, virtually a cœnenchymal, pore is present. These relations of structure in wall and septa are the same as in the Turbinolidæ, and, as I have already explained, can only take place when the upper edges of the wall and the septa keep equal pace in growth, remaining at one and the same height, or where the wall is prior in growth to the septa.

In my "Monograph of the Stramberg Corals," I have discussed the resemblances between *Actinacis* and the Jurassic genus *Thamnaræa*. The latter has hitherto been placed among the Pseudoastræinæ, Pratz, I believe erroneously.

Madrepora.

The anatomy of the *Madrepora* polyp, and the relations of the polypal and cœnosarcal soft parts to the coral skeleton, have been made the subject of a special memoir by Fowler.* Since, moreover, the coral skeleton is especially familiar in its general appearance to all, I shall at once enter into detailed structural features. A longitudinal section made near the surface of a branch is presented in fig. 59. A number of calyces are cut obliquely, still the general arrangement of six interseptal loculi can be observed in the calyces. The skeletal structures, calycinal or cœnenchymal, are seen in this drawing to be built up of trabeculæ with radially arranged fibres.

Fig. 59.



Longitudinal section passing obliquely through a branch of *Madrepora; ca.*, the six-septate calyces distorted by section; *i.s.*, an interseptal loculus; *cn.*, cœnenchymal trabeculæ.

I have explained under *Turbinaria* how the development of the mural invagination previously to the septal invaginations is correlated (1) with the introduction outside the polyp of new costal invaginations not represented by septa, and (2) with the invagination of those parts of the aboral body-wall of the cœnosarc which correspond to the mesenterial parts of the body-wall of the polyp. In these cœnosarcal invaginations synapticular structures form, which are practically side-growths of the costal structures (*antea*, p. 209). The same explanation may be extended to *Madrepora*, with the additional fact of a much more rapid tangential expansion of the polypal and cœnosarcal body-wall, and consequently the introduction at the mural part of the polyp of a greater number of costæ without relation to septa.

Unlike *Eupsammia*, no "area of divergence" is present between the septal and costal parts of the radial structures ("septa") in *Turbinaria* or *Madrepora*. Its absence is another feature correlated with the contemporaneity or priority in development of the wall-ring of calcification relative to the radial structures.

* Fowler, "The Anatomy of the Madreporaria," II, 'Q. J. M. S.,' August, 1886.

While the above observations are founded on the study of microscopic sections of the skeleton, they are in harmony with an important comparison which FOWLER has drawn between the anatomical relations of the cœnenchyme in *Rhodopsammia*, a cœnenchymatous Eupsammid, and *Madrepora* (*loc. cit.*, 'B. Anatomy').

In one of his best-known papers on Madreporaria, KOCH* remarks of *Madrepora*, "The skeleton shows already considerable thickening close to the calycinal opening, and it may readily be observed that the secondary introduction of peripheral secondary septa is of importance in the course of enlargement of the branches. The later thickening distinguishes itself clearly in cross-sections by its layers, and it fills out large spaces." The first part of this statement concerns the skeletal feature just discussed; the second part expresses again the general conception of a primary skeletal tissue, differing in structure from a secondary, viz., the *stereoplasm*, only the latter being looked upon as lamellar. I have already had occasion, under Astræidæ and Fungidæ, to prove that this conception is incorrect, and now, in *Madrepora*, although the appearance of the deposit towards the surface of any skeletal part varies in a higher degree than in any other Madreporarian coral which I have hitherto examined, I hope to show by microscopic sections that the *primary deposit as well as the "later thickening" is lamellar* in origin and structure, and that the *growth-lamellæ of Madrepora* from first to last are composed of *coalesced calcified calicoblasts*, which once represented living ectoderm.

Microscopic Sections.

A *transverse* section (fig. 60) through calyx and cœnenchyme shows at once the strong contrast to which KOCH referred. As in *Eupsammia*, a clearer band is apparent on both sides of a very dark "middle line" or "centre of calcification" in every skeletal structure; but the calcareous deposit beyond the clearer band has no longer its fibres oriented in the same direction as those of the clear band, they surround it in every possible direction. The continuous thecal ring of calcification, and its coalescence with septal and costal centres of calcification, is well shown in the same figure.

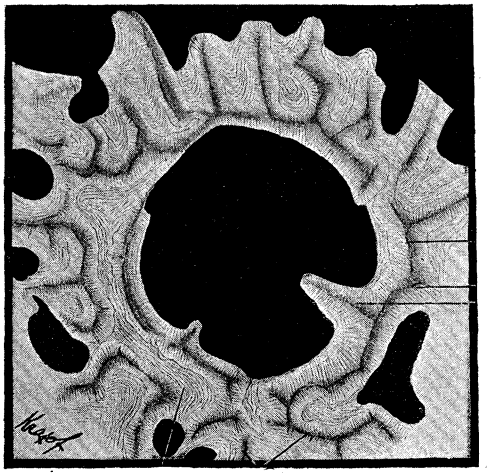
I shall at once compare *longitudinal* sections (fig. 61). The calyx is very obliquely cut, showing the main septum and the smaller one opposite it, met in longitudinal section. The contrast is again observed, and the fibres of the central area of calcification are seen to be more horizontally oriented than those of the so-called "stereoplasm." The central areas are continuous in the septa and in the thecal commissures, bearing out the statement above that the invaginations, both tangential and radial, *in* the calyx and *out* of the calyx, are contemporaneous in their origin as well as in the formation of their calcareous deposit. The outer lighter-looking fibres belonging to

* KOCH, "Ueber das Verhältniss von Skelet und Weichtheilen bei den Madreporen," 'Morph. Jahrb.,' vol. 12, 1886, p. 159.

the "later thickening" wind themselves in and about all the original centres of calcification, and their orientation becomes more oblique, in some parts it is almost vertically upwards.

Fig. 62 is a longitudinal section less obliquely cut than fig. 61, and shows better the variation in the direction of fibres at the original centres of calcification and at the outer parts corresponding to later periods of growth. At the right side of the figure the section has met the central part of the skeletal structures, and one sees the dark-looking areas at which the first layers of deposit formed. At the left side of the figure the section has passed deeper, the darker areas are polished away, and only the outer deposit is exposed. It is clear from the sections that the difference in the orientation of the calcareous fibres is associated with the rapid growth of the *Madrepora* corallum as well as with the constantly changing apical direction of growth

Fig. 60.



Transverse section (partly injured inside the calyx). The fibro-crystals close to the centres of calcification are met obliquely by the section.
Those of the secondary deposit (*sec.*) are met almost perpendicularly.

followed by the individual polyps of the branching-stock. The arrangement of the individual polyps around a leading mother-polyp in the colony is well-known, also the twisting of the polyps during growth.

Little need here be said of the *Madrepora* septum. Its agreement with *Turbinaria* is seen in the possession of a well-marked, darker central axis of deposit directed from the porous wall inwards (*cf.* also Part II., pp. 270, 279). The peculiarity of the septal apparatus of *Madrepora*, as compared with that of *Turbinaria*, is in the fact that a number of the smaller cycles of septa are represented by vertical series of spines.

These "septal spines" of *Madrepora* have each a single centre of calcification which

in some species appears as a ring at its base, in others has itself a broad base and narrow tip. Its variation in form is always correlated with some external difference of shape in the spine itself. The spines are developed in pocket-like invaginations extending from the aboral body-wall of the polyp which is apposed to the inner wall-

Fig. 61.

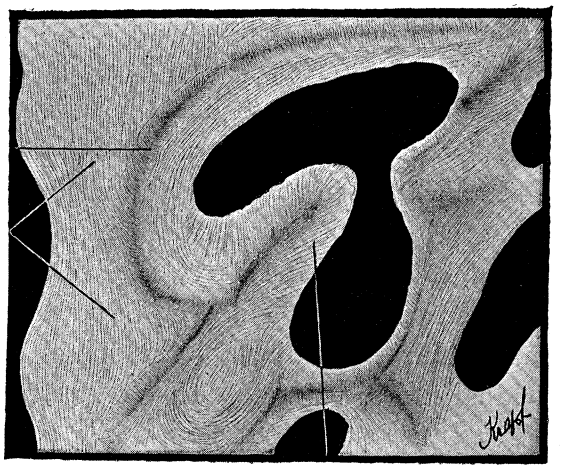
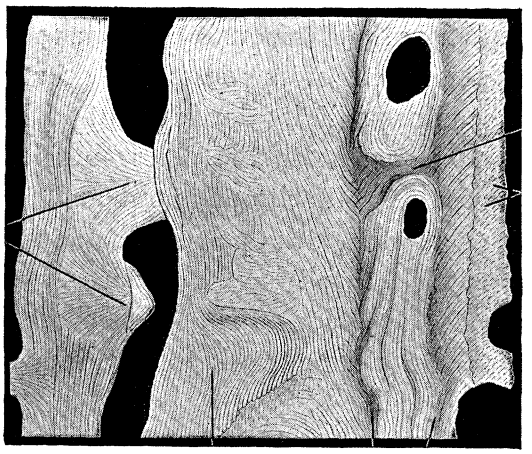


Fig. 62.



Longitudinal sections—fig. 61 obliquely cut, fig. 62 vertically cut: *m.s.*, main septum of calyx; *th.*, thecal centres of calcification; *sec.*, secondary deposit; *f.c.*, fibro-crystals of secondary deposit met across their axes; *c.c.*, centres of calcification in costæ; *syn.*, synapticulæ.

surface, and from the appearance of sections, I am inclined to think that the invaginated pocket of polypal flesh is not withdrawn, but dies out upon the skeletal structure to which it gives origin. The next spines may or may not be exactly above each other; they are all directed horizontally. This feature is very different from

the type of perforate radial structure observed in Lophoserids and Eupsammids. In those the successive spines (= trabecular growth-parts) are vertically or obliquely directed. When not in contact end to end, they still keep to a fairly definite vertical line of growth, and can be distinguished as a trabecular chain of individual growth-parts.

Madrepora may be said to display a kind of haphazardism in respect of its skeletal invaginations, more especially in its cœnenchyme, as if at any time and at any place a new invagination might appear. Sometimes an invagination shoots up in a radial line of costal spines, sometimes it is an invagination between two adjacent lines of costal spines, and again a flat smooth surface of the body-wall is busy laying down laminar thickening around and between the original invaginations. It is impossible to find in the cœnenchyme of the *Madrepora* corallum regular relations of growth governing *radial, tangential, and basal structures*, such as the growth-relations which I have elucidated for the Astræidæ, &c. One can, however, in a *single* costal series find nodular, pseudo-synapticular thickenings of the spines indicating the pauses in the growth of the individual series. But these pauses occur at *different horizons of two adjacent costal series and even of adjacent spines in a single costal series*, hence no regularity can arise in the position of pores in the skeletal structures.

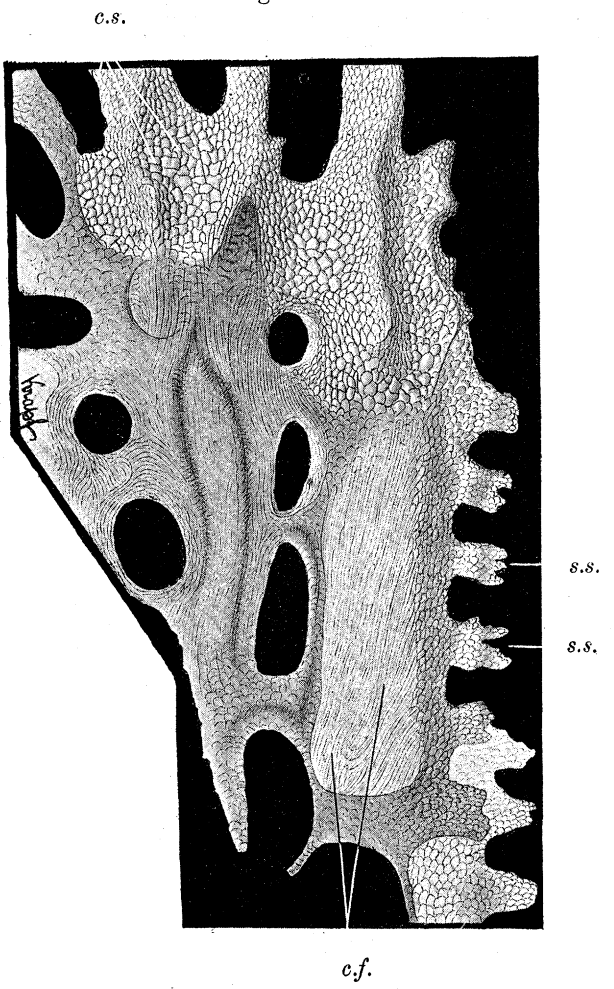
It will readily be seen how completely the unequal growth of a *skeletal* system of support replaces for the cœnosarc the support afforded in Astræidæ and Fungidæ by mesenteries extending from the polyp into the edge-zones or extrathecal parts of adjacent polyps. At the same time this unequal spinate system of growth outside the polyp is necessarily independent of the system of growth within the polyp, since the polypal wall is contemporaneous in its development with the septa and both wall and septa are anterior in development to the parts outside the polypal walls. For the same reason, viz., the contemporaneity of mural and radial invagination in the polyp, the mesenteries are shut within the polyp. The wall grows upwards as rapidly as the septa, and the mesenterial loculi have therefore no opportunity of extending between septa over a lower-placed lip of the wall and forming an edge-zone continuous with the polyp. There can be no edge-zone, in short, where wall and septa are contemporaneously developed.

The Calicoblasts.

The calicoblasts at the growing apices of skeletal spines in *Madrepora* must, to judge from the rapid growth of the corallum, undergo the changes of calcification very rapidly. They appear also to be less completely calcified than in the case of corals where the invaginated layer retreats slowly and uniformly, and rests for a longer period in any particular position. This I take to be the reason why the original fibrous deposit at the central areas of calcification in *Madrepora* are so much intermixed with organic matter, and seem so opaque in sections.

The vertically directed fibres have a chequered appearance, not unlike striated muscle fibres, and measure ·006 millim. in diameter. Each such fibre represents a section through growth-lamellæ, the chequering of the fibre indicating the "bands" of contact between successive calicoblasts. This is proved by fig. 63, which shows the scale-like appearance of the calicoblasts composing the long fibres. Frequently finer

Fig. 63.



Longitudinal section of *Madrepora* (partly decalcified); *c.s.*, calicoblast scales in decalcified portion; *c.f.*, calcareous fibres; *s.s.*, septal spines covered by the constituent scales of the growth-lamellæ.

fibrils are seen within the main fibres. The figure represents a thin section of *Madrepora* which has been slowly decalcified round the edges. In the decalcified portions the fibres are seen to break up into the constituent cells or calicoblasts. At the right hand of the figure a longitudinal series of septal spines are seen, projecting horizontally into the lumen of the calyx. The rest of the figure passes vertically through the cœnenchyme. This section is of great importance, as it wholly confirms what I explained in *Galaxea* above, that the calcified calicoblasts belonging to successive

lamellæ unite to form the long and apparently continuous fibres which radiate outwards from the centres of calcification to the skeletal surfaces.

In structure and origin, therefore, the "later thickening" is identical with the primary deposit. But it remains as a typical feature of *Madrepora*, that the *primary fascicles are laid down in a number of ectodermal pockets entirely separated from one another.* Around those small calcareous fascicles, the body-wall is enveloped and the cœlenteron is drawn out into a labyrinth of canals; secondarily, the body-wall winds itself upwards on the primary skeletal supports, during which process some parts may remain inextricably caught, and continue for a time only in living connection with the polyp, while others may be completely withdrawn. In either case, the direction of the calcareous deposit, which is, in the primary fascicle, obliquely outwards from the centre, veers more and more into an upward direction, and gives rise to the long fibres parallel with the direction of growth at different parts of the *Madrepora* branch.

The relations of the porous wall and cœnenchyma are essentially alike in *Madrepora* and in *Turbinaria*; the small size of the calyces in *Madrepora*, and the diminution of the septa frequently to mere spines projecting inward from the wall, are features probably correlated with the branching, and at the same time twisting, growth of the *Madrepora* corallum. Well-developed septa in *Madrepora* have the same structure as septa of *Turbinaria*. Above all the almost constant feature in *Madrepora* of the continuation of one of the primary septa to form a columella, yielding a plane of division in the polyp between bilaterally symmetrical halves, is a strong point of resemblance in the calyces of *Madrepora* and *Turbinaria*. The development of an efficient cœnosarcal system of canals seems to have done more towards the degradation of the calyces in *Madrepora* than in *Turbinaria*. Yet there can be little doubt that both types are specially-modified reef-living Turbinolid allies, especially adapted for the fluctuations of tide and depth, and having replaced the compact wall-thickening of the deep-sea Turbinolid by a light framework of interpolypal skeletal canals.

Porites.

Its General Structure.

I shall be able to curtail my description of *Porites* by frequent reference to the foregoing pages on *Madrepora* and *Turbinaria*. The relations of wall and septa are the same in *Porites* as have been described for those two types. Centres of calcification are continuous in wall and septa, and the deposit is laid down in both at the same horizon of growth. The shape of the wall in *Porites* is more zig-zag in form than in *Turbinaria* or *Madrepora*; in other words, the mural bars are not exactly tangential to the septa in position, but form acute angles with them. The other ends of the mural bars meet usually with, sometimes without, the intervention of a costa. The costa then props the body-wall at that part during the course of a

growth-period; at the close of the period a new pair of mural bars develop, and so on.

The pores of the wall in *Porites* are therefore produced according to the same process of growth as in *Turbinaria*. A comparison of the ground-plan of *Porites* (fig. 64) with that of *Turbinaria* (fig. 55), will show the similarity in the structural

Fig. 64A.

c.

Fig. 64B.

th. col. p. s. th. c.

Ground-plan of two different types of *Porites*. *th.*, theca, zig-zag in shape; *c.*, costa; *s.*, septum; *p.*, palus; *col.*, columella.

plan of the two calyces. This is especially clear with regard to the calycinal pali in both forms. In *Turbinaria*, the pali grow upward from the fused ends of a primary and a secondary septum, the same is true of *Porites*. But the pali in *Porites* are small and round and not lamellar, hence a transverse section may cut one, two, or even three pali in the same radial line, the individual pali having taken origin successively and attained various stages of growth. As explained under *Turbinaria*, subsequent calcareous deposit may block up the spaces originally present between the pali and septum in one radial line and give the appearance of one continuous compact radial structure extending from the mural area to the centre of the calyx. Then the radial structure looks very like an Astræid septum, and the resemblance is still more heightened by the fact that the individual pali appear on the lateral surfaces like ridges jutting out from the compacting calcareous tissue.

On the other hand, even after a secondary deposit of calcareous tissue has been laid down, it may happen that apertures are left unfilled between the septum and pali. Thus, in systematic descriptions, the radial structure in *Porites* has usually been regarded as *perforate*, and PRATZ placed the Poritinæ, E.H. (*loc. cit.*, 'Palæontographica,' 1882, pp. 122–123), amongst the Microsolenid members of the Pseudoastræinæ.

According to my examination, the *septum of Poritidæ* is small, either rounded or lamellar in shape, *and its relation to the pali is precisely the same as the relation observed in* Turbinaria, *or that which may be observed in pali-bearing Turbinolidæ.*

Moreover, the zig-zag nature of the wall in *Porites* is paralleled by the genus *Paracyathus* and others belonging to the Trochocyathaceæ, E.H.

Tangential expansion of the mural area is again in *Porites*, as in *Turbinaria* and *Madrepora*, accomplished by the introduction of new costal invaginations (see fig. 64). It will be seen from the ground-plan of the calyx that any two mural bars coalescing

with a radial structure bear the same relation to it as any two adjacent septa bear to the palus between them. The tangential expansion of the calyx follows in fact the same system throughout, and a mural ring of thickening might in some cases arise round the pali, in which case the "septa" would be looked upon as "costæ."

The costæ present between adjacent polyps are placed *opposite every angle* of the zig-zag mural ring. Secondary thickening not only tends to solidify the wall, but frequently produces in addition an outer ring of thickening, halfway between adjacent polyps.

Its Microscopic Structure.

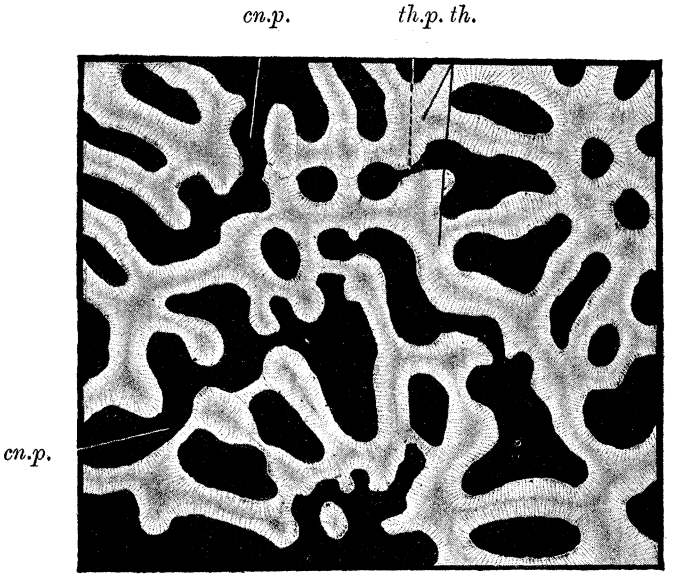
Figs. 65 and 66 are made from the uppermost portions of the corallum of *Porites incrustans* (DEFR.). Looking at a transverse microscopic section, first with hand lens only, a loose tissue is seen in which *radial* lines of structure are much less pronounced than in Astræids. The cause of this is that we have not in *Porites* one continuous broad calcareous structure, but a series of compound trabeculæ varying little in size and shape. It may be observed (1) that the series is apt to deviate from a definite radial line, (2) it is thinner and thicker, much like a string of beads, (3) between adjacent radial series numerous cross-bars (synapticulæ) are present, whose fine structure exactly repeats that of the septal trabeculæ themselves.

It follows that such a section represents a closely-knit, spongiose skeletal tissue, built, however, on a *regular trabecular* system. The network of the corallum is all the more striking, since the skeletal parts of the radial series grow vertically upwards, and the synapticulæ are placed horizontally between them (*cf.* fig. 65).

Stronger magnifying power shows short, dark axes of calcification, both in the radial series of trabeculæ and in the synapticulæ. Fascicles of fibres are gathered around the axes of calcification and radiate horizontally outwards to the surfaces of the skeletal parts (*cf.* fig. 66). The synapticulæ are seen in transverse section to have almost the same areal dimensions as the cross-sections of the trabeculæ.

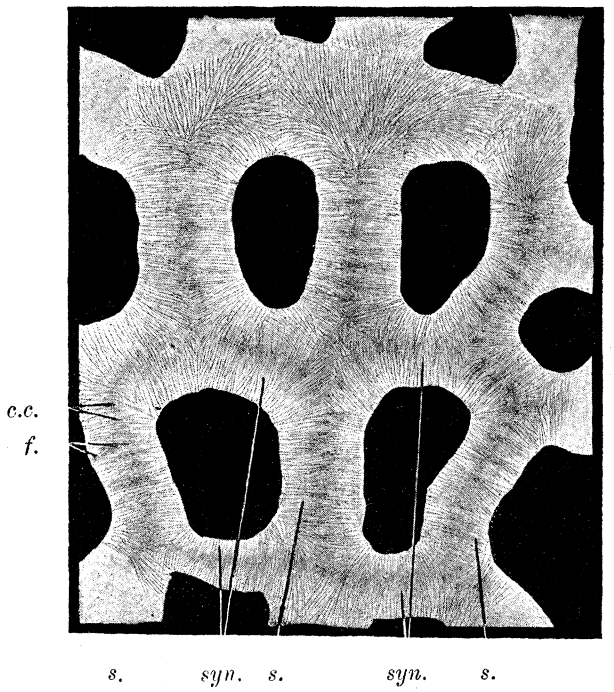
The longitudinal section (fig. 66) shows the general arrangement stated above, of vertically-directed trabeculæ and synapticulæ placed at right angles to them. The position of the short, dark axes of calcification corresponds to the different directions of growth; those in the trabeculæ of the radial series being vertically placed, in apical succession, those in the synapticulæ being horizontally placed, and the whole synapticula including one axis of calcification of *equal length with any one of the axes of calcification* in the radial trabeculæ. The fascicles of fibres in the radial trabeculæ lie horizontally, since they are placed at right angles to the axes of calcification. In the synapticulæ, the fascicles are directed also at right angles to the axes, that is, they radiate upwards and downwards in the section. It may be concluded, from a comparison of the transverse section of the synapticulæ, that in the actual synapticular bar, the fascicles radiate in all directions, from the axes of calcification to the rounded surface.

Fig. 65.



Transverse section Porites incrustans. *th.*, theca; *th.p.*, thecal pore; *cn.p.*, cœnenchymal pore. Pali are seen in front of septa, or in various stages of fusion.

Fig. 66.



Longitudinal section, showing the precise similarity of structure in septa (*s.*), and synapticulæ (*syn.*). In both, the fascicles (*f.*) bush out circularly around the calcification centres (*c.c.*).

It is readily demonstrated in the sections that the individual fascicles are essentially the same in origin and structure as the fascicles in other types, for example, *Galaxea*. Alternating light and dark bands cross the fascicles and indicate successive growth-lamellæ. The chief difference is that in *Galaxea* the long axis of the fascicle is mainly in the median plane of the septum, the uppermost end fascicle then bending out laterally towards a granulation. Whereas in *Porites*, the fascicle takes merely its origin in the middle line, its whole length is in a rectangular direction. The darker-looking "centre of calcification" in *Porites* represents the organic remnant, not of one fascicle or pair of fascicles, originated during a single growth-period, but of a *number* of fascicles formed radially around an axis during a single growth-period of the trabecula. So much of a trabecula as occurs between two successive synapticulæ represents one growth-part of a radial structure. The interesting relation is therefore demonstrated that all the *radial* skeletal structures of *Porites*, *pali*, *septa*, *costæ* (all of which are here merely special names applied to *trabeculæ* of the same structure, according to their particular position in the calyx), as well as *the synapticulæ, are composed of growth-segments precisely similar in size, shape, and structure.*

Each synapticula is one *horizontal growth-part*, developed for the most part contemporaneously with the vertical growth of the radial trabeculæ. This is shown by the position of the synapticulæ with reference to the series of growth-parts in the trabeculæ. Each new synapticula is interposed at the interval between two successive growth-parts in a trabecula, and during their simultaneous growth the fibres become mixed at the coalescent areas of the horizontal and vertical deposit. I look upon the cross-bars of *Porites* as *tangentially* placed growth-parts of equal rank with *radially* placed growth-parts, meriting the name of "synapticulæ," inasmuch as they are regularly disposed along the interradial loculi and coalesce with the radial structures. Yet, unlike the "mural bars," they are not placed opposite each other in adjacent loculi so as to form a continuous ring of thickening.

Its Systematic Relationships.

If we now compare *Porites* with *Eupsammia*, a certain resemblance obtains, which is due merely to the fact that the growth-parts of the septal trabeculæ are clearly defined throughout the whole corallum of *Porites*. This gives regularity to the general structure, and, when secondary deposit renders the septa and pali apparently one continuous surface, partly porous, partly compact, the resemblance to the *Eupsammia* septum is very great. A comparison of the microscopic sections, however, shows a very different fibrous arrangement within the trabeculæ, that of *Eupsammia* being undoubtedly much nearer the Fungidæ than it is near *Porites*. The latter agrees with *Turbinaria* and *Madrepora* and differs from *Eupsammia* in the contemporaneous time-relations of the development of mural and septal structures, and in the absence of an "area of divergence" at the periphery of the septum.

Again, comparing *Porites* with any typical genus of the *Pseudoastræinæ*, to which group the Poritinæ were referred by PRATZ, several features of difference are presented.

(1.) The fine structure of the trabecula is different, in so far as the fascicles of *Porites* are more horizontal in position, and spring from different horizons of the individual "growth-parts," instead of radiating out like a bush from the base.

(2.) The Pseudoastræinæ have their trabeculæ in a definite radial line corresponding to a continuous radial fold of the invaginated body-wall.

(3.) The canalicular system produced by trabeculæ and pseudosynapticulæ in the Pseudoastræinæ is solely of secondary origin, the pseudo-synapticular bars depending on elongation of the trabecular fibres during withdrawal of the soft parts. In *Porites*, on the other hand, the canalicular system is determined at once by the primary deposit; septal and synapticular "growth-parts" form simultaneously at the uppermost horizons of the coral.

If we could eliminate the factor of secondary coalescence, we should have in *Porites* a *primary reticulate skeleton, of which the individual pieces had been enveloped in polypal flesh, firmly enveloped, in definite relative positions crosswise and lengthwise.* It is the perfection of this primary reticulate skeleton which gives *Porites* the palm among the "Perforate" Madreporarians. I regard it as the most strongly specialized generic type among reef-builders. In spite of transitional forms among the Poritinæ and the ancestral type presented by *Litharæa*, it seems only right to place *Porites* and its congeners systematically in the rank of a special family. The Poritidæ need not be far removed from the Turbinarinæ and Madreporinæ, and all three must be looked upon as mixed types, at any rate related in polypal characters with various members of the compact Turbinolidæ.

CHAPTER VIII.—GENERAL REVIEW OF MACROSCOPIC AND MICROSCOPIC SKELETAL FEATURES.

CONCLUSIONS RELATIVE TO CLASSIFICATION.

The above comparative study of the skeletal parts and of their microscopic structure indicates that the sub-kingdoms of *Madreporaria aporosa* and *M. perforata* recognized by EDWARDS and HAIME, draws an arbitrary line of sub-division. If we were to base sub-kingdoms of the Madreporaria on the compactness or porosity of the skeletal structures, the families Turbinolidæ and Astræidæ would alone* be

* In giving the following summary, I limit my remarks here to the families which I have myself examined; the *Stylophoridæ*, E.H., and *Oculinidæ*, E.H., for example, are not specially discussed, although they are families belonging to the *M. aporosa*, E.H. The *Dasmidæ* may be regarded as degraded forms of Turbinolidæ.

correctly called *Madreporaria aporosa*, while the great majority of the Fungidæ would have to be included, together with the Madreporidæ, E.H., and the Poritinæ, E.H., as *Madreporaria perforata*. But such sub-kingdoms would be also entirely artificial.

Certain genera (*e.g.*, *Microsolena*), placed by EDWARDS and HAIME among the *M. perforata* (sub-family Poritinæ), were removed by PRATZ to the Pseudoastræinæ as a sub-family of the Fungidæ. The same author showed that, in spite of the regular fenestration in the original laying-down of the radial structures in those genera, the characters of the sub-family, as a whole, were intermediate between the Astræinæ and the Agaricinæ (Lophoserinæ, E.H.). Although PRATZ rightly appreciated the main features of the Pseudoastræinæ, he erroneously included several genera, *e.g.*, *Haplaræa*, *Thamnaræa*, *Porites*, *Siderastræa* in side-branches of this sub-family.

The Jurassic and Cretaceous genus *Haplaræa* may be regarded as an ancestral type of the *simple* Eupsammids. In *Haplaræa* the union of adjacent septal surfaces is both pseudosynapticular and synapticular. A certain tendency to form septal groups is also apparent, but is not a definite feature as in the Eupsammids. In the latter the synapticular union is mostly restricted to the peripheral area, while nearer the centre of the calyces the pseudosynapticular union (*i.e.*, union of adjacent granulations) is often replaced by the closer coalescence of the actual septal surfaces at non-granulate parts. This close coalescence it is which produces the septal groups, often symmetrically arranged, in the Eupsammids. Similar septal grouping is characteristic of the families Fungidæ and Lophoseridæ, both of them likewise "synapticulate" families. The ancestral Jurassic and early Cretaceous types of these three families are naturally less specialized than the later types, and such forms as *Haplaræa* are important witnesses of the originally common features of the stock. From the point of view of the palæontologist the most important "common feature" would be expressed as the *rich development of both synapticulæ and dissepiments*. From the zoologist's point of view the same feature could be expressed as the development of canaliculate downward prolongations of the visceral cavity of the polyp—*within* the polyp itself in simple forms, and both *within* and *without* the polyp in colonial forms. At the same time these canaliculate prolongations are definitely confined to the inter-septal and intercostal loculi, *i.e.*, they occurred in distinct lines radiating outwards from the central parts of the polyps, and extending (in colonies) without interruption into the cœnosarcal or interpolypal areas.

It is well known that no such canaliculate extension of the cœlenteron is present in the meshes of the skeleton in the Astræidæ and Turbinolidæ, nor indeed in the Oculinidæ or Pocilloporidæ. But it might be thought that the *Madreporaria perforata* of EDWARDS and HAIME had a similar system of visceral canals. This is not the case. Excluding the Eupsamminæ, E. H., from the *M. perforata*, E. H., there remain the Madreporinæ and the Poritidæ. The typical genera of the Madreporinæ

have been discussed in the preceding pages. Within the polyps there are no long canalicular prolongations, but a continuous deep visceral chamber. In the cœnosarcal areas there *is* a richly-developed canalicular system, which, however, is not restricted within definite uninterrupted radial lines, but constantly changes the relative position of its ramifications. With regard to the Poritinæ, E. H., I can say less, as no sufficient anatomical research has been made; to judge from the skeleton they seem to have a canalicular system equally developed within and without the polyp, but nowhere restricted to definite radial limits—in short, a system more complex and more highly differentiated than in any Eupsammid, Fungid, or Lophoserid.

Thus the canaliculate system in the skeletal meshwork of the Madreporinæ, E. H., and Poritinæ, E. H., is *not* homologous with that which characterises the Fungidæ and their allies (*cf.* Part II, pp. 261–263). The same end is reached for the vital processes of the coral polyps, but by different means. A "porous wall" is a necessary part of the means adopted by the Madreporinæ and Poritinæ, and is always developed *contemporaneously with the septa* in these groups, and according to one unvarying plan of structure.

On the other hand, in the Fungidæ and their allies, the radial structures (continuous septa and costæ) are first formed, and they determine the *subsequent* development of synapticulæ. At some particular part a wall-thickening is formed, partly by the septo-costæ, partly by the synapticulæ. But a wall is an afterthought, as it were, in these corals, and may be entirely absent (ex. Pseudoastræinæ), irregularly and incompletely developed (ex. Funginæ), regularly porous (ex. Funginæ), compact or porous (ex. Lophoseridæ), regularly or irregularly porous (ex. Eupsammidæ).

The two important skeletal features in the Fungidæ and their allies are therefore (1) the continuity of the radial structures from the centre of the calices into the costal or inter-calycinal areas; (2) the free upward growth of the radial structures previous to the laying down of any wall deposit. These two features are the correlatives in the skeleton of an anatomical feature in the living polyp, to which zoologists have lately been devoting more attention, viz., the presence of an edge-zone ("Randplatte") round the polyp. The edge-zone is the continuation of the interradial loculi of the polyp above and beyond the lip of the calyx. The mesenteries of the loculi are continued into the edge-zone and support the oral surface of the polypal body wall. Naturally this continuation of the soft parts of the polyp into interpolypal areas is almost inevitable when the radial structures rise up prominently from the wall-thickening as "confluent" septo-costæ. On the other hand, if the wall is contemporaneously developed with the septa, or developed before the septa, as it is in some *Madreporas*, there is far less chance of the mesenteries of the polypal loculi being continued above and beyond the wall. Then it is—in the absence of distinct interradial canals outside the polyp, and of mesenterial support for the oral body wall—that an irregular *cœnosarcal* system of canals develops, and a light skeletal framework supports the aboral body-wall of the polyp and pushes it

upon costal spines or teeth against the oral body-wall, thus supporting it also (*cf.* fig. 56, p. 209). We find, therefore, that one of the most characteristic features in the anatomy of the colonies of *Turbinaria*, *Madrepora*, as well as colonies of *Stylophora*, *Pocillopora*, *Seriatopora*, is the *absence of an edge-zone* round the individual polyps.*

If we compare the Astræidæ and the Turbinolidæ in respect of an edge-zone, we find that the Astræidæ, like the Fungidæ and their allies, *always* have an edge-zone round the individual polyps of colonies, except in such colonies where the adjacent polyps are in direct communication with one another above a common calicinal wall (ex. *Goniastræa*), whereas the Turbinolidæ have primarily no edge-zone. Only after a polyp has attained its maximum of height does an edge-zone begin to develop in certain genera. Then also the radial structures grow upwards freely from the wall, and septo-costal lines of structure divide a *limited edge-zone* into narrow intercostal loculi, corresponding with the interseptal loculi of the polyp. I have frequently pointed out that the relations of the septa and wall in the skeleton of the Turbinolidæ are identical with those of *Madrepora*, *Turbinaria*, and *Porites*. They are also identical with those in *Stylophora*, *Pocillopora*, and *Seriatopora*. On the other hand, the relations of the septa and wall in the skeleton of the Astræidæ (ident. Astræinæ, E. H., *vide antea*, chap. iii.) are the same as those in the Fungidæ, Lophoseridæ, and Eupsammidæ.

The Oculinidæ show extremely variable relations of the septa and wall, and I have not yet had time to make a special study of this group. The majority of the Oculinid genera seem to develop septa and wall contemporaneously at first and then the septa outgrow the wall. At the same time the polypal edge-zone extends in its proportions. The genus *Lophohelia*, examined by FOWLER (Q. J. M. S.) is a very good example. It shows, as described above for the Turbinolidæ, how *first the primary* septa and *then the smaller* cycles gradually grow higher than the wall—the centres of calcification, originally continuous in septa and wall, becoming in

* FOWLER has shown the following genera to be *without* an edge-zone, and has pointed out that all possess a *well-developed cœnenchyme*:—*Madrepora*, *Turbinaria*, *Stylophora*, *Seriatopora*, *Pocillopora*, *Heteropsammia multilobata*. Other genera which have been proved to possess an edge-zone are *Astroides*, *Rhodopsammia*, *Dendrophyllia*, *Fungia*, *Cladocora*, *Caryophyllia*. FOWLER inclines to think the possession of the edge-zone the more primitive condition, while its absence and the development of cœnenchyme is a secondary condition. The "edge-zone," as at present understood, is in my opinion itself a "secondary" condition (*cf.* p. 262) and arises in independent types. It may well be, however, that in the Eupsammidæ, the presence of a pseudotheca and of a well-developed edge-zone is the primitive condition, and that retrogression of the edge-zone may bring about the appearance of cœnenchyme characteristic of certain forms (*Heteropsammia*). This is possible, but the anatomy and skeletal structure of *Heteropsammia* is not yet known in detail. In all the typical cœnenchymatous forms just quoted, there is no foundation for supposing retrogression of an edge-zone (*cf.* pp. 265, 312). On the other hand, the cœnenchyme (= "peritheca," E. H.) of *Galaxea* is very possibly a retrograde form of the primitive edge-zone of Stylinids.

consequence interrupted. *Galaxea* shows similar variations (*cf.* p. 121). The septa in such types have the tendency also to be toothed at their upper edges, correlative with their freer upgrowth and exsertness above the wall.

The skeletal relations which I have observed in *Galaxea* led me to unite that genus with the Stylinidæ, a family which from its earliest origin has shown considerable resemblance to the Oculinidæ.

The fossil group of colony-forming genera allied with *Stylina* show also variable relations of septa and wall. Very often they seem to be more akin to the Astræidæ. Yet the microscopic structure of the septa, the character of the basal structures, and the presence of an epithecal deposit round each individual polyp in several genera, indicate also a near relationship with *Galaxea* and with the less branching of the Oculinid types. For the complete proof of these relations a detailed examination of various types of living Oculinids is needed (ref. "Stylinid" type, fig. 35).

We arrive at general systematic results by the careful study of the growth-relations observed in different parts of one polyp, or one colony, as the case may be. Throughout my description of the foregoing types I have frequently emphasized the correlation of the detailed microscopic structure in the various skeletal parts with the *relative time* of their development. Thus, differences in the microscopic structure go hand-in-hand with the differences in the relative time of development of the radial, tangential, and basal structures.

The most highly differentiated radial structures are those of the Astræidæ and Fungidæ. Each septal and costal ridge in those types is a firmly-knit group of trabeculæ arranged with reference to an ideal axis in the ridge. The whole series of septal and costal ridges are again definitely arranged in a fan-shaped group with reference to an ideal axis in the radial structure.

The firmness thus attained by the radial structures is correlated with the absence of tangentially placed thecal structures. The septa grow up from the embryonic "basal plate" *without any thecal support between them.* This is true of the Astræidæ, Fungidæ, Lophoseridæ, and Eupsammidæ. The septa themselves develop in most cases a "pseudothecal" thickening, which forms a lateral connection between them. In others, interseptal pieces are also introduced in the calyx, either in fragmentary fashion (synapticulæ) or continuously (the synapticular bars of *Fungia*). *In other cases no pseudothecal thickening is apparent, and the calyx may be said to be entirely without a theca.* At the same time the retreating lappet of the polypal disc lays down outside the calyx a fragile *epitheca*, which completely encircles the septa and costæ, and has no structural connection with them. This epitheca is formed always, whether a pseudotheca is present or not. Its structure is more brittle than the calicinal skeletal structures, and there never are in it "centres" of deposit, for the simple reason that the part of the polypal wall which deposits it is never pouched up in any way.

Montlivaltia, for example, is an Astræid genus and *Microsolena* is a Fungid (Tham-

nastræid) genus with an epitheca and no pseudotheca. Both these are examples of simple corals. *Thecosmilia*, *Cladophyllia*, and other branching Astræid colonies have an epitheca round each branch, and seldom develop a distinct pseudotheca. In massive Astræid colonies the epitheca envelops the whole colony, and is not present around each individval polyp. Usually the individual polyps have pseudothecæ; again, among the typical *Pseudoastræinæ*, no pseudothecal wall is developed between adjacent calyces.

Among the Stylinidæ genera occur in which the calyces have each a pseudotheca and an epitheca. The latter is common to adjoining calyces. The pseudotheca and epitheca go in these cases usually under the name of an "inner" and an "outer" wall respectively (*vide* below, p. 262). It is noteworthy that throughout all those families in which a "pseudotheca" occurs, the pseudotheca occupies a position, as it were, *within* the calyx. To one side of it are septa, to the other costæ, in the usual acceptation of these terms. As, however, the septa and costæ are continuous, I have used the more general term "radial structure," and the pseudothecal ring of thickening may occur at any part of the radial structures—near the periphery, ex. *Mussa*; near the middle, ex. *Heliastræa*; or at the very periphery, ex. *Goniastræa*. In the last case, the epitheca of the whole colony closely invests the pseudothecæ of the calyces which happen to be at the outer rim of the colony. In all other cases the pseudothecæ are free structures, not coalescent with an epitheca, and practically within the calyces.

In the living polyps the part of the polyp which extends beyond the pseudotheca is called the edge-zone of the polyp ("Randplatte").

These remarks may be said to exhaust the possible relations existing between septa, "wall" (= pseudotheca), and epitheca in the above-named families—Astræidæ, Fungidæ, Lophoseridæ, and Eupsammidæ. The fundamental feature in all of them is that the embryonic basal-plate does not develop farther. The ectodermal folds in the embryo are solely radial folds, and, as they grow upward, septa are developed within them. No tangential folds rise up simultaneously. The first connection between septa is made when the first floor of dissepiments, or the first series of synapticular bridges is laid down in the interseptal loculi by the basal parts of the polypal wall.

A marked contrast is presented by the families Turbinolidæ, Madreporidæ, Poritidæ, Pocilloporidæ, Oculinidæ. The mature calyx in them always possesses a theca. It will be remembered that "*theca*," as distinct from "*pseudotheca*," indicates a peripheral wall in which tangentially-placed lamellæ occur. These are deposited quite independently of the septa, in special wall-folds of the polypal flesh. The wall-folds form and grow upward, simultaneously with the septal folds. Thus the centres of calcification are continuous in wall and septal folds. The septal structure is the same as the thecal structure, except that it is placed radially in the calyx, and the calyx is placed tangentially. One may even see on the lateral surfaces of the septa, fine, fragile, transverse folds, which exactly correspond to the "epithecal" folds

outside the theca. From the very nature of its growth, the "epitheca" in Turbinolidæ is not separable from the theca, it is in other words the outermost part of the theca. Its place is taken by the cœnenchyme between adjacent calyces of the colonial families, Madreporidæ, Poritidæ, etc. (see below, p. 267).

The concentric folds of epitheca forming the outer surface of the Turbinolid theca, are structurally the same as the concentric skeletal rings around the naked septa of *Montlivaltia*, *Microsolena*, etc. Hence it is desirable to retain the term epitheca for both, although in these Astræids and Fungids the "rings" in question are *not* placed "upon a theca" but on the outer edges of the crowded, numerous septa.

It is readily seen that where a theca is developed simultaneously with the septa, there is no need for the building up of a pseudotheca. And a free pseudotheca is never present in these thecate families. Still, the continued deposit of growth-laminæ on the inner surfaces of the theca and on the lateral surfaces of the septa is sometimes so great that it fills up the interseptal loculi near the periphery, and lateral surfaces of the septa come into contact.

We may say then that the characteristic condition in all these families is *the presence of a theca in structural union with the septa and of an epitheca as superficial rings on the outer surface of the theca.* Variations, of generic value merely, may occur in the relative development of septa, theca, epitheca. The septa have a tendency near the lip of the calyx to grow more rapidly than the theca, and the theca in its turn to grow up without much in the way of epithecal rings. This tendency on the part of septa and theca is correlated with the development in the mature polyp of an edge-zone in those particular genera. Otherwise an edge-zone is absent in those families.

Before going further, I shall show diagrammatically the main points in which I agree or disagree with the classificatory system of EDWARDS and HAIME. The classification given by those authors is as follows :—

Madreporaria aporosa. ED. and H. (*Loc. cit.*, 'Corall.,' II., p. 7)

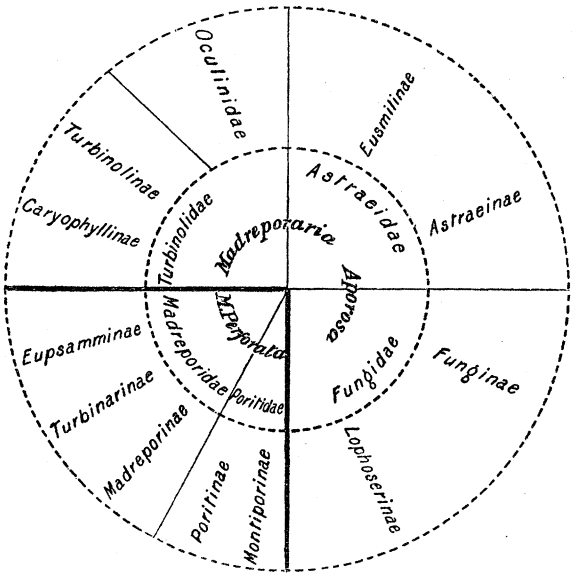
- Turbinolidæ.
- Dasmidæ, Oculinidæ, Stylophorinæ, Echinoporinæ } See foot-note, p. 223.
- Astræidæ
- Merulinaceæ (foot-note, p. 186).
- Fungidæ

Madreporaria perforata. ED. and H. (*Loc. cit.*, 'Corall.,' III., p. 90)

- Eupsamminæ, Madreporinæ, Turbinarinæ } Madreporidæ. E. H.
- Poritinæ. E. H. (= Poritidæ Dana).
- Montiporinæ (included by KLUNZINGER in Madreporidæ).

The Seriatoporidæ, E. H., originally grouped by EDWARDS and HAIME under "*M. tabulata*," have since been removed to *M. aporosa*.

The chief Madreporarian families enumerated by EDWARDS and HAIME under these two main sub-divisions are represented in the following diagram :—

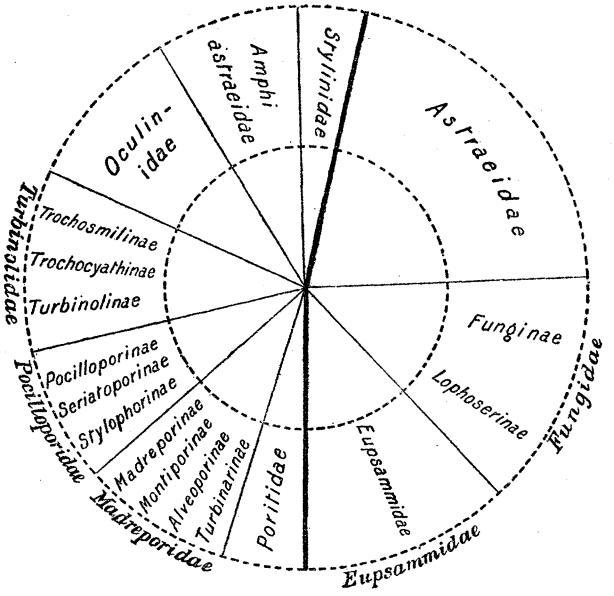


This we may take as the basis of classification in Madreporaria, although in the course of time several important alterations have been made. I have represented it in circular form for readiness in comparison with my own general results.

In the next diagram I follow KLUNZINGER in placing the sub-family Poritinæ, E. H., in the rank of a family, in accordance with DANA'S classification. My reasons are founded on the characteristic microscopic structure of the skeletal parts. Again the genera grouped by PRATZ as Pseudoastræinæ regulares are recognized as a special sub-family Thamnastræinæ under the Fungidæ DANA. And I propose to remove the sub-family Eupsamminæ, E. H., entirely from the Madreporidæ, E. H., and place it as an independent family next the Lophoserinæ, E. H.

I have considerably altered the sub-families Eusmilinæ, Turbinolinæ, Caryophyllinæ of EDWARDS and HAIME for reasons into which I shall enter more fully in the second part of this paper. The fissiparous Eusmilinids (type: *Euphyllia*, p. 161) are placed under the new family of Amphiastræidæ (*cf.* p. 334); the Trochosmilia group are included under the Turbinolidæ, and the Stylina group are erected into a separate family.

In the accompanying circular diagram I have entered the Madreporarian families which are represented in *Recent* time.



It will be seen that I do not accept the main sub-divisions of Recent Madreporaria made by EDWARDS and HAIME, viz., the *M. perforata* and *Aporosa*. My reasons have been already stated. The simplest polyps are those belonging to the Turbinolidæ; in the Pocilloporidæ, Madreporidæ, and Poritidæ the polyps remain simple, the calycinal structures of the two first-named agreeing with the Turbinolidæ in microscopic details. The extrapolypal flesh lays down a cœnenchyme of various form. The Amphiastræidæ and Oculinidæ show a greater complexity in the microscopic details of the calycinal skeletal structures, and the form of the polyp is distinctly intermediate between the typical Turbinolid and the typical Astræid. The Astræidæ are distinguished by strongly-marked regularity in their processes of growth. The septa are built up step for step; one floor of dissepiments is laid down after another until the whole corallum presents one of the most striking examples among the invertebrata of a perfectly-constructed shell.

The Fungidæ and Eupsammidæ can only be properly studied when the details of their structures are compared, part for part, with those of the Astræidæ. They agree with the latter in the general plan of structure in septa and wall; their distinctive feature is in the frequent synapticular union of septa in the middle of the calyx, *i.e.*, above the horizon of the floor of the polyp. This introduces irregularity in the arrangement of the soft parts of the polyp, and the uniformity so remarkable throughout the Astræids is entirely wanting in those two related families.

I shall conclude Part I. by giving a table, in which the classificatory features of the main Madreporarian families can be readily compared with one another. But, before doing so, it will be necessary to recapitulate the chief features of structure in the Madreporarian skeleton, and the meaning of certain terms which I have introduced or made use of throughout the first part of this paper.

Summary of Skeleton Formation.

The Madreporarian Skeleton is a complicated shell wholly built up of successive calcareous laminæ or lamellæ. These laminæ are virtually growth laminæ, the equivalent of so-called "Anwachsstreifen" in the molluscan and other shells.

The Calcareous Laminæ of Madreporaria are composed of coalescent calicoblasts which gradually lose their cell-wall and organic contents as calcification proceeds.

The Calicoblasts are ectodermal cells in which, by a process of chemical change, lime is secreted and at once laid down within the cell in the form of a more or less connected group of aragonite fibres. An organic remnant of the cell may be left, especially at the part of the cell remote from the polyp and next the skeleton.

Alternate bands appear in each lamina, a narrow band, dark by transmitted light, representing the proximal organic ends of calicoblasts, a broader lighter crystalline band representing the fibrous deposit within adjacent cells. The breaking down of cell-walls and cellular tissue leaves often an irregular intermixture of disintegrating carbonized products in the laminæ.

At the upper edges of all invaginations of the polypal wall, septal and mural, growth and cell-multiplication takes place very rapidly. There the calicoblasts are rapidly calcified and shed off from the living ectoderm. In those calicoblasts a relatively large amount of cell material is present in unchanged condition. It may disintegrate quickly or slowly, and gives rise to various appearances in microscopic sections. The upper edges of the septal invaginations necessarily correspond to the median plane of the septum, and the presence originally of a larger amount of organic material at this part causes it often to have a somewhat different appearance from the rest of the septum.

One of the most frequent appearances is that of a "dark line" in the middle of the septum. This line is in many cases a fissure filled up by carbonized *débris*, in other cases it is the first-formed laminæ in which the large mixture of organic cell-material has given rise by disintegration to impure, mixed products. The actual fibrous deposit within the calicoblasts is also in some genera denser in the early deposited growth-laminæ than in those laid down at later periods of growth, and this fact alone causes a greater opacity at that part of a thin section.

Again, the growth-laminæ laid down at the edge are sometimes very smooth, and those of later growth-periods are less uniform, the cells being active only at certain areas of the lateral surfaces of deposit. This local activity of the calicoblast cells of the side-flaps produces granulations on the septal surfaces. Sometimes the early growth-laminæ are not smooth. That is, their calicoblast cells form active groups of deposit, and granulations are marked out at the first laying-down of the septum. These differences are of minor importance. The chief point is that organic cells—calicoblasts—are converted into small groups of fibres, and that as the cell-walls

break down, the small groups of fibres coalesce and form a calcareous layer which may be compared with a layer of living cells.

Following the stages in the building-up of an Astræid septal segment :—

(1.) It is laid down at the upper edge of an invagination of the aboral body-wall of the polyp. During one growth-period some five or six laminæ are laid down by both of the invaginated flaps, and the septal segment has a thickness of 10 or 12 calcareous laminæ.

(2.) A second period of growth finds the same septal segment no longer at the edge of the invagination, but moved as it were one tier below the edge. Deposit goes on less actively, granulations become more marked. The calicoblasts are, in fact, developed more fully at some parts of the invaginated flaps than at others, and the lamina bulges out at those parts.

(3.) A third period follows in which local activity is still more pronounced, a fourth and fifth period follows, and then, as a rule, the soft body-wall is withdrawn from the particular segment owing to the upward growth of the polyp. The primary septa in an Astræid usually has a large number of calcareous laminæ, from 25 to 35 on either side of the median plane of the polyp. The septa of the smaller cycles have few laminæ, from 5 to 15 on an average. Clearly the activity of the calicoblast deposit varies immensely, being such as to allow, say, five times as many laminæ to be deposited on the primary septa than on the septa of the smallest cycle in an Astræid calyx.

Owing to the method of growth, the successive growth-lamellæ are parallel with the surfaces of the septum when seen in transverse section, but when seen in tangential longitudinal section, they form an acute angle with the surface, the laminæ of the two halves meeting at a point in the median plane of the septum.

These investigations disprove the distinction which has hitherto been made by palæontologists between a "primary septum" and "stereoplasm." The structure of the primary septum has, indeed, never been described satisfactorily, although the term has been in general use as signifying the "dark line" in the median plane. The stereoplasm has been spoken of sometimes as fibrous, sometimes as structureless. While certain authors have limited its application of an "Ausfüllungsmasse," or secondary compacting tissue, which was said to be lamellar. I find no need for all these terms, since the first lamina laid down at any part of the aboral wall is exactly like the last in essential structure. And the elemental unit of structure is a calcified calicoblastic cell shed off from the living ectoderm of the polyp.

I have brought forward proofs from typical genera representing the recent families of Madreporaria that the lamina has this structure. In many specimens the actual outlines of the cells could still be clearly traced in the growth-laminæ, since they retain their organic nature after the cell contents have been entirely changed. The changes which render the fibrous deposit in the cells of successive laminæ

apparently continuous are purely of crystallographical nature. The subsequent orientation of the fibres is dependent on the original form of the deposit. For example, where the laminæ bulge out into a granulate eminence, the fibres form a fascicle or bundle radiating from the centre of the hemispherical eminence.

Nomenclature of Skeletal Parts.

The chief skeletal parts may be classified as follows :—

(1.) The *Radial structures*—septa, costæ, pali.
(2.) The *Tangential structures*—theca, pseudotheca, epitheca.
(3.) The *Basal structures*—tabulæ, dissepiments, solid laminar deposit, synapticulæ, columella.
(4.) The *Extrathecal structures*—rugæ, rootlets, cœnenchyme.

The Radial Structures.

In some cases different parts of the same radial structure may be distinguished as palus (*cf. Goniastræa*), septum, costa. The palus is then an elongated septal tooth growing obliquely upwards from the inner edge of the septum. The septum is the part of the radial lamella within the calyx, while the costa is that part of the lamella external to the wall of the calyx (*cf.* figs. 74*a*, *b*). Both palus and costa may take origin independently of the septum, alternating in position with two neighbouring septa (*cf.* fig. 55). In all cases, the radial structures are laid down within radial folds of the aboral body-wall of the polyp.

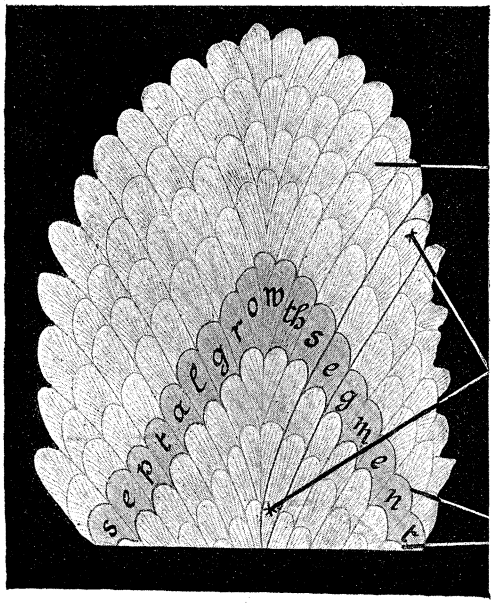
If the radial folds are *smooth*, a flat-shaped radial structure is formed with two uniform halves laid down by the opposite flaps of the fold (fig. 68*b*).

If the radial folds are *pleated*, a ridged radial structure is formed, and a more or less complicated system of septal trabeculæ is developed (figs. 68*c*–68*f*).

The Growth-Period ; Surface Growth-Curves.

The Madreporarian skeletal structures are not added to throughout the whole existence of the polyp, but growth takes place from time to time at definite periods. The interruptions in the laying down of the deposit are, as a rule, very easily distinguished in the skeleton. Any single period at which the calicoblast deposit is actively formed may be called for convenience a *growth-period* (*ante*, pp. 121–124), and the part added to a skeletal structure during one period, a *growth-segment* (fig. 67). The thinner lines or curves between successive growth-segments are fitly termed *growth-lines or curves* (*cf.* fig. 3 with fig. 67).

Fig. 67.



Radial structure (equiv. whole *septum* of primitive types) marked out in types with exsert septa, *e.g.*, Astræids, into so-called "septal" and "costal" wings to left and right of the *area of divergence*, at which the trabeculæ take their origin and diverge. The trabecula (*tr.*) signified in the figure, is composed of seven *trabecular parts* (*tr.p.*), and represents, therefore, seven successive gowth-periods. The trabecular parts between two *growth-curves* (*g.c.*) form a *septal growth-segment*, and represent *one growth-period.*

The Septal Growth-Segment in its relation to the "trabecular part" and the "fascicle."

A septal growth-segment is the part of a septum which is added along its upper edge during a single growth-period of the polyp. In fig. 67 one complete growth-segment is marked out from the others by means of darker shading and thicker limiting-lines between it and the segments formed just before and after it. A single trabecula is also denoted in the figure, in order to demonstrate how it is here made up of a row of the individual parts belonging to successive growth-segments. Each such part may be fitly called a *trabecular part.* I have elsewhere shown the "trabecular part" to be a composite of "*fascicles*," and thus we arrive at the elementary "group" or "fascicle" of calcareous fibres which I have discovered to be *the unit of skeletal structure* throughout the Madreporaria (*cf.* pp. 118 and 124).

In other words, an isolated needle or fibre does not exist *per se* in the Madreporarian skeleton as it does in related groups of the Cœlenterata; on the contrary, the calcareous fibres are formed primarily in *bunches* of various size and form; each bunch is a clear structural *unit*, distinguishable from its neighbours, sometimes bound to them only during the life of the polyp by the fleshy substance, more often bound to them in the actual skeleton side by side—in part or wholly. ***Contemporaneously-formed bunches radially placed***

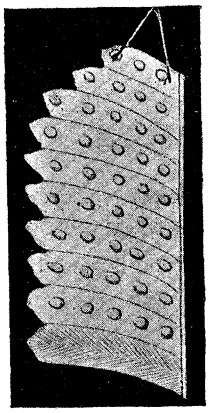
within the calyx of the coral skeleton build up a single growth-segment of the septum. **These bunches may form one or more "trabecular parts"; if the latter, they may be attached or unattached.**

Septal segments may be classed in two varieties, which I propose to call the *monaxial* and the *polyaxial* types.

The Monaxial Septal Segment; Septal Spine.

Here the *septal growth-segment is represented by one trabecula* of a compact septum, or by an *isolated "septal spine,"* directed horizontally, sometimes at a low angle

Fig. 68A.



Diagrammatic drawing of a compact septum composed of monaxial septal segments.
Tr. = trabecula from wall to centre of calyx. The lowest trabecula is shown in section; those above are drawn with their surface granulæ.

inwards, from the periphery towards the centre of the calyx (fig. 68A). The calcareous fibres laid down during the growth-period are aggregated around one axis of calcification. The figure represents a compact septum with smooth upper edge, the inner row of teeth being apices of the successive trabeculæ. The lowest trabecula in the figure is represented in thin section to show the continuous axis of calcification; those above are represented in surface view bearing the granulations. Examples of "septal spines," with precisely the same structure and relative position as these "septal trabeculæ," are found chiefly within the groups of Madreporidæ and Pocilloporidæ among recent corals.

The Polyaxial Septal Segment.

Far more frequently the *septal growth-segment is represented by a large number of trabecular parts at various angles,* belonging to as many trabeculæ attached more or less completely side by side. Such a segment is indicated in fig. 67, and it is manifest that here the calcareous fibres aggregate around numerous axes of calcification in the

median plane of the septum. According to the completeness of the lateral attachment of trabecular parts, the *polyaxial septal segment* is compact or porous (*cf.* figs. 67 and 69). A row of *erect* "septal spines" in a radial line (ex. the ancient *Cystiphyllum* or Triassic specimens of *Stylophyllum*), projecting upwards from the base into the lumen of the calyx, is, in my opinion, simply one of the primitive forms of a polyaxial septal segment.

The Compact Septum.—The compact septum is composed either of a succession of *monaxial* septal segments (ex. *Turbinaria*), or of a succession of *polyaxial* septal segments (ex. *Galaxea*), each of which is in and for itself compact (fig. 68), and is united at every point with its predecessor and successor.

The Porous Septum.—The porous septum is always composed of a succession of *polyaxial* septal segments, each of which is in and for itself porous. In many cases where the septal fold of polypal flesh is deep, the originally porous septal segment may be gradually thickened and compacted. This takes place during the several growth-periods which ensue between the first formation of the segment at the edge of the septum and the ultimate complete withdrawal of the polypal flesh from the lateral surfaces of the same segment as the polyp grows upward.

Porous septa occur only in the families of Fungidæ (*cf.* fig. 69), Eupsammidæ Poritidæ. In all of these families synapticular union of the septal surfaces is present in addition to the deposition of dissepiments in interseptal loculi. In some subdivisions belonging to these families the septa are from the first compact; and it is, therefore, necessary in identifying the generic features to make vertical sections parallel with the septal surface. Such sections betray at once whether any individual septal segment was originally porous and subsequently had the apertures filled up by secondary deposit (ex. *Thamnastræa*), or was originally a compact segment (ex. *Siderastræa*). The porosity of the septum is a feature which is certainly of frequent occurrence in the families named, but is in nowise constant. KLUNZINGER, and others, have shown that in many genera the septa of the first cycles are compact and the smaller septa porous. It is to other skeletal features, such as the synapticular, and most of all, the microscopic structures of the septa, that we must look for a satisfactory means of classifying the genera within these families.

The systematic importance of the septal porosity is its correlation in these families with the *canaliculate nature* of the interseptal loculi. At the same time synapticulæ are formed in other families in which the septa are wholly and primitively compact. Thus, neither the one feature nor the other justifies the erection of a special group for these families. By virtue both of the general habit of the corallum and of the microscopic structure of the skeletal part the Poritidæ are probably more closely related with the Madreporidæ than with the Eupsammidæ. Again, the Fungidæ are, on the one hand, related with the Astræidæ, on the other with the Eupsammidæ.

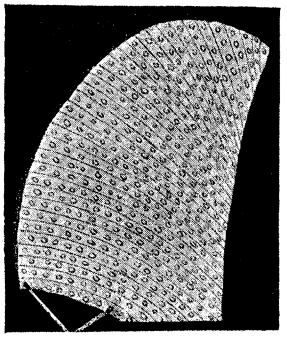
Macroscopic Appearances on the Septal Surfaces and their Relation to the Microscopic Structure.

The surfaces of septa may be either marked with fine lines or *striæ*, or they may be strongly *ridged*. Granulations are merely a secondary feature of these septal markings. *Perfectly* smooth septa do not exist to my knowledge. Examination with a hand-lens will demonstrate in all those cases of so-called "smooth" septa, the presence of extremely fine "striæ," like these in *Galaxea*, fully discussed in the first chapter of this work.

Striated Septa.

The striæ on the one surface and on the other of any striated septum are usually placed exactly opposite to one another, but they may also alternate with one another in position. Each pair of striæ on the opposite surfaces culminates in a common apex

Fig. 68B.



tr.

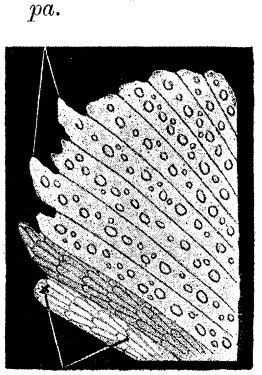
Type of septum in a Turbinolid coral; the striæ on the surface correspond to "simple" trabeculæ, whose elliptical axes give rise to a "median dark line" in transverse sections.

at the edge of the septum. This apex is, in many cases, visible to a careful observer as an extremely fine "serra," or tooth; in other cases again, magnifying power must be used to demonstrate the distinct apices of "striæ." As a matter of fact, a great number of genera, in which serræ are readily visible, have been described by former authors as *smooth-edged*, *e.g.*, several in the sub-division of Eusmilinæ, E.H. It is only the precise microscopy of such genera which can permit of their proper description and classification. Now, after the microscopic research of this paper, one may compare a Turbinolid type (fig. 68B) and any Eusmilinid or Stylinid type (*cf.* fig. 35). Comparison will show the fundamental similarity in their microscopic structure, and the contrast they present to the various types of *ridged* septa below.

I need scarcely repeat again how each pair of striæ on the opposite septal surfaces is the external expression of a "trabecula" in which "fascicles" of fibres are gathered round successive opaque-looking "centres of calcification" in the median

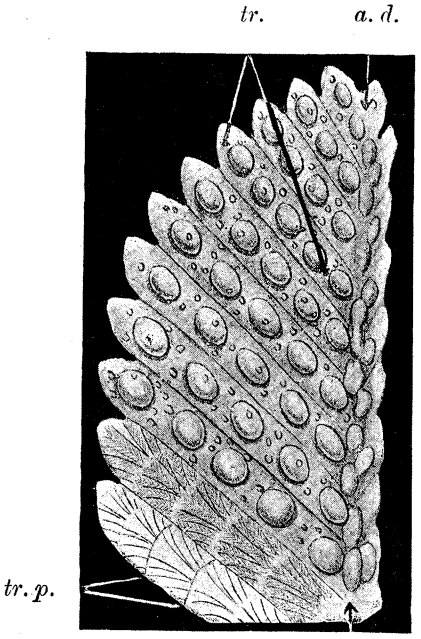
Types of Astræid Septa.

Fig. 68C.



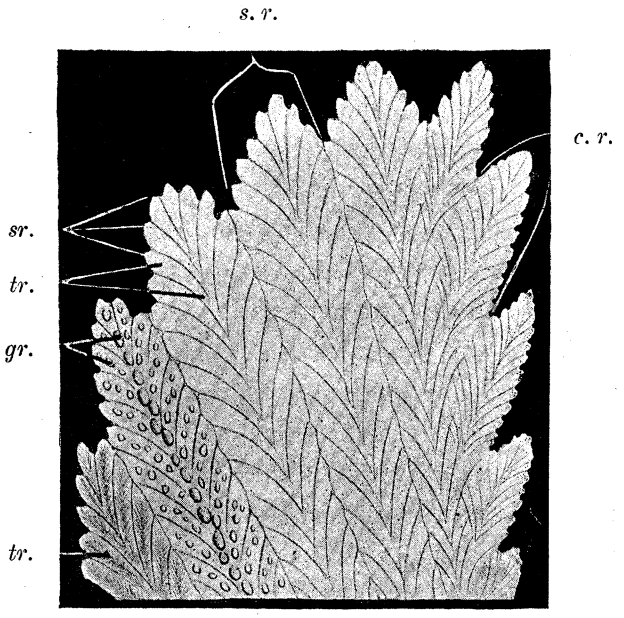
Septum with fine granulations. The trabecula (*tr.*) shows four successive fan-groups of fascicles = four "trabecular parts." Any trabecula may be elongated as a palus (*pa.*), or to form part of a "spongiose" columella. (The two lowest trabeculæ are drawn in section to elucidate the microscopic structure.)

Fig. 68D.



Septum with regularly placed, large granulations marking successive "trabecular parts" (*tr. p.*) on the septal ridges. At the "area of divergence" (*a. d.*) the granulations coalesce and help to form the pseudotheca between septum and costa.

Fig. 68E.



Septum with broad ridges studded with granulations (*gr.*); *s. r.*, septal ridge; *c. r.*, costal ridge; *s.r.*, serræ at the tips of the trabeculæ (*tr.*).

septal plane. Each "centre" is, in reality, lens-shaped and the trabecular radius extremely short. Hence, in transverse sections across a septum, the "centres" of adjoining trabeculæ, which are met variously in the line of section, become fairly continuous with one another, to all appearance, and give rise to a well-marked "dark line" along the middle of the section.

Ridged Septa.

The septal ridges are sometimes broad and flat, as in the *Mussa* type (fig. 68E). They are composed of fan-shaped systems of fairly uniform-sized striæ, easily observed on the surface. The ridges on opposite surfaces of the septum culminate in spiniform teeth. The teeth may be themselves finely serrated, corresponding to the striated structure of the ridge. Granulations of very various size are scattered over the surfaces of the ridge.

Sometimes the ridges are narrow and highly bulged, as in the *Heliastræa* type (fig. 68D). In this case there is usually one large trabecula in the middle of the ridge, and smaller trabeculæ form lateral union of the larger trabeculæ in the septal plane. The fan-shaped systems of trabeculæ are not readily observable as striæ on the surface, but are demonstrable in all microscopic sections. The smaller trabeculæ have lens-shaped centres of calcification and bilaterally placed fibres; the larger have the fibres radially arranged around two or more centres of calcification, closely grouped, and corresponding to the trabecular axis (*cf.* fig. 24B).

The marginal apices of those ridges are conical smooth-edged teeth. The surfaces of the ridge are granulate. Coalescence of small granules takes place, and one large granulation marks each growth-segment of a ridge. Rows of granulations are thus produced, following the course of the ridges. Fig. 68C represents a similar, but finer type of septum, characteristic of Faviaceæ and certain meandroid Astræids.

When one imagines a circular group of simple trabeculæ forming one compound trabecula, and the latter coming only at intervals into contact with its neighbours, the characteristic "trabeculate" septum of PRATZ is obtained (fig. 69). Thus we pass from a compact *Astræid* type to a porous *Fungid* type. In all these cases of ridged septa, the "centres of calcification" are small, and the trabecular radius is relatively long, so that in transverse sections the appearance of the "dark line" in the middle of the septum is neither so continuous nor so well marked as in the case of *striated* septa.

Superficially, the trabeculæ of a septal type belonging to the *Fungidæ* (as above defined) are marked by their extreme uniformity. Fig. 68F presents a compact Lophoserid type, practically the same as the *Fungia* type; fig. 69, on the other hand, a porous Thamnastræan (Pseudoastræid) type. These two figures display again the broad, flat variety of ridge and the narrow, highly bulged variety (*antea*, figs. 68E and

68D). One large granulation on the surface denotes each successive growth-part or growth-segment added at the apex of the trabecula during a single growth-period.

Microscopically the arrangement of the fibres is perfectly radial in each trabecula. At the same time, distinct fascicles of fibres can be traced passing from the individual centres of calcification outward to the surface, and giving rise there to small granulations. These then coalesce during growth and form the one large granulation corresponding to a trabecular growth-part.

The large trabecula with *radial symmetry of fibres* is a particular case, where several pairs of striæ may be said to be arranged *circularly around a common axis*

Fig. 68F.

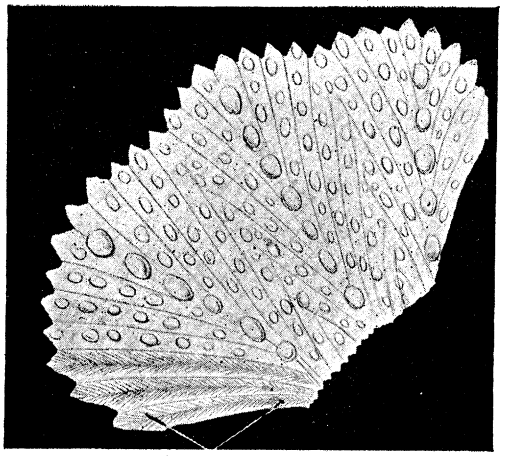
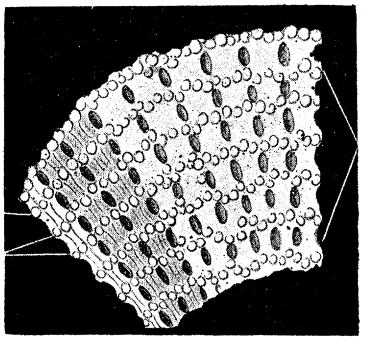


Fig. 69.



Types of Fungid Septa.

Septum compact, composed of three main "fans" of trabeculæ (*tr.*) shown in section at the lower part of figure. Synapticulate granulations mark trabecular growth-parts.

Septum porous; adapted from a drawing by PRATZ ('Palæontographica,' *loc. cit.*, Taf. 14); *tr.* trabecula; *tr. p.*, a trabecular growth-part; *gr.*, synapticulate granulations coalescing in parallel lines between the pores.

instead of in plane series. One can frequently distinguish on the surface of the trabeculæ fine striæ exactly like those on the surfaces of a striated septum (ex. *Galaxea*), or on the surfaces of a striated septal ridge (ex. *Mussa*). The *large, radially symmetrical trabecula* is indeed nothing more than a rounded ridge, and there are all transitional stages between the broad, flat ridge of *Mussa*, with its long, elliptical outline and the squarish or circular ridges of *Cyclolites*, *Microsolena*, etc.

The individual trabeculæ of a trabeculate septum culminate at the septal edge in teeth of various form, most commonly rounded and irregularly knobbed. Any individual trabecula is made up of successive trabecular growth-segments or *trabecular parts*. These "parts" may firmly adhere to one another lengthways, when they

form compact trabecula, or they may be not very closely attached to one another, when the individual trabecula is in and for itself *porous*, as in Eupsammids.

Again the trabecular parts of any one septal growth-segment may be laid down at the edge of the septum as a compact row (ex. *Siderastræa*), or as a porous row (ex. *Microsolena*). In the family of Eupsammidæ, the pores in the radial structures are of extreme irregularity, for the reason that they occur originally both in the individual trabeculæ and in the septal segment.

Granulations.

Great variety obtains in the actual form of granulations. Many of the septa which have hitherto been described as having smooth surfaces are in reality studded all over with minute pin-points of granulations, whose microscopic structure may, according to my investigations, tally with much larger and more prominent-looking granulations.

On the other hand, I have found that *all the large granulations have not one and the same microscopic structure.* In short, the word "granulation," as at present used in Madreporarian literature, has received no exact definition. It is merely a general, descriptive term used for any kind of hump on the *septal* surfaces. Whatever the form of the hump—hemispherical or irregular, smooth or knobbed, tooth-like or conical—the name applied is always the same. One or two noteworthy attempts have been made to make some systematic use of the occurrence of these granulations (I refer to EDWARDS and HAIME and to MILASCHEWITZ), but these attempts have confined themselves to the *position* of the granulations on the surfaces, in short, to the occurrence and external arrangement of *prominent* granulations, and have overlooked all cases where the granulations were not of sufficient size to obtrude themselves on the observer's notice.

I should define a granulation as a *protuberance on any part of the skeletal surface, caused by the emergence at that part of one or more fascicles of fibres.* Such a definition would include the so-called echinulæ on various types of "cœnenchyme," and the adornments on the wall and costæ of many Turbinolids, as well as the "granulations" on the septa. The fundamental fact in the definition is the relation of the granulation in all its forms to *fascicles of fibres*—and, therefore, to one or more *definite centres of active calcification*, already fixed at the laying-down of the very first growth-lamella at that part of the skeleton.

It will be remembered that the "growth-lamella" is simply the term I have applied to the completely calcified layer of "calicoblast" cells. Hence we may describe the building-up of granulations in terms of the calicoblast. A group of actively-dividing calicoblasts, at any part of the ectodermal layer of the polyp or cœnosarc, will give rise ultimately to a corresponding group of calcified cells, whose fibrous elements arrange themselves with respect to a definite centre or centres of calcification. Each new calicoblastic layer behaves in the same way until a thick shelly growth has accumulated over the original centre or centres of active calci-

fication. This growth forms the protuberance known as a *granulation.* If there be but one centre of calcification in the group only one fibrous fascicle is formed, and the granulation looks simple and has symmetrical proportions. If there be two or more centres of calcification, as in the trabeculæ in the middle of the septal ridges of *Heliastræa, Mussa, Fungia,* etc., several small fascicles are formed and grow so closely crowded together that a large knotty-looking or irregularly-shaped granulation is the result.

Once more I repeat the important observation that the same microscopic structure holds good for *all* protuberances on the skeletal surfaces of Madreporaria, and I therefore recommend the use of a single term, preferably "granulation," for all cases. The typical appearance of a "granulation," as seen in surface section, is shown in fig. 33. This figure yields also unmistakeable evidence of the fundamental *lamellar* structure of the Madreporarian skeleton.

Full-grown coral skeletons often show much larger granulations at the uppermost part of the calcareous framework than lower down. This is simply due to the fact that growth in thickness of the septa, costæ, etc., is continued after the coral has reached the full height which happens to be characteristic for that particular species. During this continued growth in thickness the "granulations" are the parts of the skeleton most added to, and they assume a variety of shapes. They very often lose at the same time their primitively clear arrangement in rows along the course of "*trabeculæ,*" since they keep spreading sideways, crossways, or lengthways, and become confused with neighbouring granulations. It is in this condition that the granulations are apt to become "pseudosynapticular," *i.e.,* to form calcareous bonds between adjoining septal, costal, or indeed cœnenchymal parts of the skeleton.

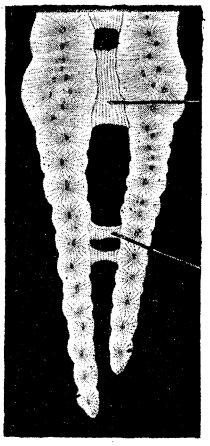
Again, "pseudosynapticulæ" (*vide* fig. 71) was a term applied to the appearance of uniting bars in a few particular cases studied by PRATZ. The very general occurrence of such bars is demonstrated by my observations (*antea Heliastræa*), and is discussed below (p. 246). We simply have a general law of the correlation of parts to deal with. Where the coral is one which grows to a considerable height under its normal conditions of life, the ectodermal layer expends its building energy on adding to the height and not to the thickening of the skeletal parts. And the large number of our common Astræids are tallish corals. But where the coral is one of low-growing habit, as the most of the Fungids are, it is predestined as it were to the development of pseudosynapticular granulations. The occurrence of "true synapticulæ" in the Fungid group may be considered, I believe, only a specialized mode of interlocking skeletal parts which have a "pseudosynapticular" habit. Hence I have not allowed this to influence my system of classification in any great degree, but hold that the Astræidæ and Fungidæ are very nearly related to one another, more nearly than either family with any other members of the Madreporaria. From the Astræidæ, however, I have removed the Stylinid and Eusmilinid groups on several grounds. From what has been said it will be seen that the systematic

use of granulations according to their *superficial* appearance is for the most part misleading. It must be combined with an exact *microscopic* study of the *trabecular* relation of the granulations. My meaning will be at once understood by referring to some of the foregoing figures (*cf.* figs. 68, 69).

Basal Structures.

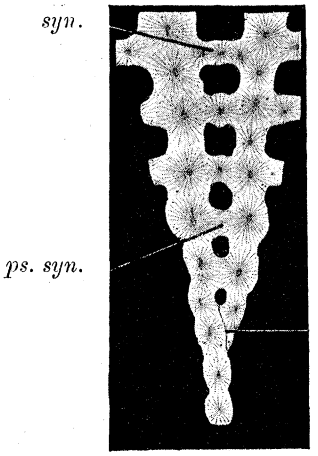
Solid Laminar Deposit.—Smooth horizontal laminæ or growth-lamellæ may be successively apposed on one another without interruption. In this way a solid laminar deposit occupies the base of the calyx, added to during each growth-period, but leaving no free space between the group of laminæ deposited in two successive growth-periods. Solid basal deposit is typical chiefly of low small corals, ex. Turbinolidæ, as well as branching colonies in which the individual calyces are very short, ex. Oculinidæ.

Fig. 70.



Dissepiments belonging to different "floors" between two septa, and met obliquely in a transverse section.

Fig. 71.



True synapticulæ, "*syn.*," pseudosynapticulæ, "*ps. syn.*," and synapticular coalescence of septa, "*co.*," seen in transverse section (p. 240 and *cf.* p. 176).

Tabulæ.—A tabula represents a horizontal group of growth-lamellæ deposited in the calyx at the close of an active growth-period. The base thus formed spans the calyx completely in its central part. The tabula may be smoothed or arched (*cf.* fig. 12). Tabulæ occur in most Palæozoic corals, and in certain of the Pocilloporidæ, Stylinidæ, Oculinidæ, and Turbinolidæ. In a word, the great majority of ancient types of Madreporaria which we know possessed tabulæ, but, as time went on, tabulæ became almost a sign manual of "old fashion," and has now become limited to these recent families which I, in my systematic table, have derived from the ancient Zaphrentoids.

Dissepiments are small tabulæ present in the interseptal loculi, but not in the

lumen of the calyx. Whereas a tabulate floor is understood to have only one group of growth-lamellæ, a dissepimental floor is made up of many groups of growth-lamellæ, usually highly arched and resting at their rims upon one another. The floor of the interseptal loculus assumes therefore an uneven appearance, and if the dissepiments are very small and delicate, it may be described as vesicular. In most cases the floor is wholly compact, leaving no part of the interseptal loculus unoccupied by calcareous tissue. Transverse sections (as in fig. 70) however do not pass through the plane of the dissepimental floor, but meet usually the upper parts of successive floors.

The development of regular dissepimental floors at the intervals of growth-periods is particularly characteristic of the Astræidæ (*antea*, p. 157).

Columella.

Columellar Style.—The so-called "true columella" is styliform or fasciculate in character, and is laid down in an arched or pouched central part of the aboral body-wall of the polyp (*cf.* figs. 35 and 56). I have, in the second part of this paper, traced back the origin of the true columella to direct modification of the tabulæ in the central part of Palæozoic corals. In this case the columella is a purely basal structure.

But the longer septa often invaded the central tabulate area of Palæozoic corals, and shared therefore in subsequent modifications which that area underwent. Curious examples of a partly septate, partly tabulate columella, are common among carboniferous genera, more especially the Clisiophyllinæ. In them, small septal spines are caught up as it were by the bent, vesicular tabulæ. And possibly in this we have a primitive form of the irregular "trabeculate" or "spongiose" pseudocolumella in many younger genera.

Pseudocolumella.—A pseudocolumella may be defined as an irregular skeletal tissue composed of the inner or central ends of the septal trabeculæ, bound together by intermediate calcareous deposit of various character, sometimes vesiculate, sometimes bar-like. A pseudocolumella is of extremely frequent occurrence in the families of Astræidæ, Fungidæ, and Eupsammidæ (*cf.* figs. 1B, 23, 45).

The Lamellar Columella.—The most primitive form of a lamellar columella is the elongation of the main septum into the middle area of the calyx in many Zaphrentid corals. Occasionally, union of main and counter septum occurs with the formation of a complete mid-line across the calyx. In many Jurassic corals one still finds a "main septum" continued as a columella (*cf.* Part II., p. 292); in others again, a lamellar columella is present in the middle of the calyx, which cannot be observed to be actually in continuity with any of the primary septa. Yet there can be little doubt that the free, axial lamellar columella present in certain Trochosmiliaceæ, etc., is due to retrogression of a main septum. This origin is farther indicated by its microscopic

structure, which is identical with that of a septum. The lamellar columella has usually been spoken of as a "true columella," like the styliform columella, but its origin and structure is in reality "septal," like that of the pseudocolumella.

Synapticulæ.—The name of "synapticulæ" was introduced by EDWARDS and HAIME. These authors wrote: "A certain number of the septal granulations sometimes meet those on the adjacent septal surface; thus transverse prolongations of the septa result in the form of interseptal bars which we have called synapticulæ" ('Corall.,' I., p. 35). "The presence of these solid bars characterise the family of the Fungidæ, and have not as yet been observed in any other group of the class of corals. It is in the genus *Fungia* that the synapticulæ are most highly developed," etc. ('Corall.,' I., p. 66).

PRATZ distinguished later two kinds of synapticulæ, according to their fine microscopic structure. He found that the solid interseptal bars were not always "prolongations of the septa," but that they might be in part or wholly independent structures. Synapticular bars formed by the fusion of granulations on the adjacent surfaces of two septa, were called by PRATZ "pseudosynapticulæ." While synapticular bars, whose microscopic structure showed new centres of calcification for the calcareous fibres, were regarded by him as "true synapticulæ." Macroscopically, it is scarcely possible even for a practised eye to see any distinction, yet microscopic study proves that PRATZ was right. In most of the Fungidæ, both kinds of synapticulæ are present.

Fig. 71, shown above, side by side with fig. 70 on p. 224, displays the occurrence of "*true synapticulæ*" at the peripheral part of a calyx, where the interseptal loculi are wide, and of "*pseudosynapticulæ*" about the middle of the calyx where the interseptal loculus is narrower, while still nearer the centre the end of a shorter septum is shown to be coalescent with the lateral surface of a longer septum. This figure may be confirmed by reference to figures of *Siderastræa* given above. It is made somewhat diagrammatic here, in order to bring out (1) the "centre of calcification" in a true synapticula, (2) the absence of any such centre in a pseudosynapticula, and (3) the gradual passage to the actual coalescence of septa centrally. The genus *Fungia* itself also shows similar variety in septal union according to the width of the loculus. In *Lophoseris* again, the septa are very closely placed throughout their whole length, and the interseptal loculi are easily bridged by pseudosynapticulæ. "True synapticulæ" are formed only when the *interseptal loculus is fairly wide*, and the granulations are not prominent enough to meet each other. Then part of the body-wall is compelled, as it were, to form a new interseptal invagination between the granulations, and to lay down fibrous laminæ around a new interseptal centre of calcification. At the same time the body-wall draws itself up locally, the unsupported interseptal parts on either side of any synapticula hanging freely downward between it and its neighbours. Thus the body-wall in the interradial loculus has an *interrupted synapticular series of basal supports* instead of a continuous, if uneven, dissepimental

floor. I have already pointed out that the openness of the synapticular floor is specially adapted to low-growing forms of Madreporaria (*antea*, p. 237). Previous illustrations (*e.g.*, fig. 37) have demonstrated their essential structural relation to the septal trabeculæ and to the growth-segment of a septum. Their distribution in a calyx in consequence entirely corresponds with the course of the main trabeculæ in the septa.

The distinction made by PRATZ, of true and false synapticulæ, is of use in classifying Fungid genera. An important Mesozoic and Tertiary group of Fungids, the Thamnastræinæ (= Pseudoastræinæ Regulares, PRATZ, p. 107) possess *only* pseudo-synapticulæ, whereas all the recent Fungids (Funginæ) possess both true synapticulæ and pseudosynapticulæ. The Lophoserinæ have mostly pseudosynapticulæ, the Eupsammidæ mostly true synapticulæ.

In all three families, the synapticulæ may be defined as interradial calicinal structures, which afford a partial support for the aboral body-wall of the polyp in interseptal and intercostal loculi. They replace dissepiments to a large extent in these families, a few synapticulate genera being entirely without dissepiments.

Typically, the synapticulæ are merely transverse rods between septa, one tier of "rods" being formed at each growth-period.

Carinæ.—"Carina," the name which has been given to vertical bars marking the surfaces of septal ridges in *Heliophyllum*, and one or two other Palæozoic genera. The carina, in this case, represents the coalescence of the granulations *on any one ridge* of a septal surface.

In many Triassic and Jurassic genera, horizontal bars occur running across the septal ridges. These bars represent the coalescence of the granulations at the same horizon of growth in the neighbouring ridges of a septum. The name of "carinæ" may be very well applied also to these horizontal bars.

The carinæ on the adjacent surfaces of two septa meet occasionally in the interseptal loculus. The same specimen may show adjacent septal carinæ in parts coalescent, in parts not touching (*cf.* PRATZ, *loc. cit.*, "Horizontalleisten").

The genus *Fungia* may be regarded as presenting an example of *horizontal carinæ* running transversely across the septal ridges, which are always coalescent with one another across the interseptal loculus. Coalescence of carinæ takes place just in the same way as the coalescence of a pair of granulations. In short, one may have synapticular carinæ just as one may have synapticular granulations. Again, the carinæ may sometimes be united by the intercalation of new centres of calcification in the interseptal loculus. The figures given of *Fungia* above (chap. iv.), show that the carinæ of *Fungia* are united in both ways.

Carinæ may be defined as bars running either lengthways, *i.e.*, parallel with, or transversely across the ridges of the septal surfaces. They are formed by vertical or lateral coalescence of the septal granulations. They may meet across an interseptal loculus, either as pseudosynapticulæ or true synapticulæ, or both combined. When

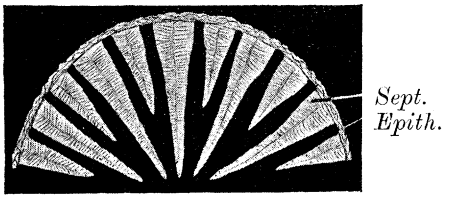
such interseptal coalescence of adjacent carinæ takes place, the latter may be called *synapticulate carinæ.*

Although synapticulæ are characteristic of the calyces of the Fungidæ and Eupsammidæ, I have observed the occurrence of synapticulæ in Astrældæ. Fig. 27 above shows interseptal coalescence of granulations, *i.e.*, "*pseudosynapticulæ*," in *Heliastræa.*

Tangential Structures—Epitheca, Theca, Pseudotheca.

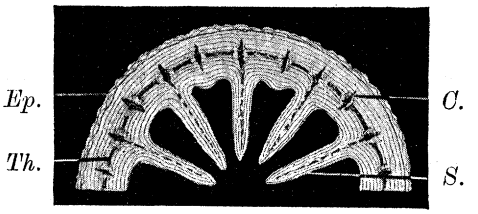
Epitheca.—Whereas an Epitheca is a primitive structure in Madreporaria, thecal structures are of secondary origin. The epitheca is an external basal structure, laid down at the angle of the aboral wall, where it bends towards the oral or peristomal

Fig. 72.



Transverse section showing the relation of Epitheca to Septa, where neither Theca nor Pseudotheca is present. The interseptal loculi are filled by basal supports, omitted for clearness in the figure (tabulæ, dissepiments, or synapticulæ), which coalesce directly with the epitheca at their external edges.

Fig. 73.



Transverse section showing the structural relation of "S." = Septa, "C." = Costa, "Th." = Theca, and "Ep." = Epitheca in a typical Turbinolid.

region of the polyp (figs. 22, 36). It is the continuation upwards or outwards of the embryonic "basal plate," and may be well-developed or remain rudimentary.

Fig. 72 represents part of a calyx in which the septa are directly surrounded by an epitheca, no theca being present. This case may be observed in *Montlivaltia, Microsolena*, etc., also in several Palæozoic genera.

Theca.—Tangential folds of the aboral wall of the polyp may rise at the peripheral part of the polyp, simultaneously with the septal folds. A theca is then developed within these tangential folds. A "dark line" or "centre of calcification" in the theca corresponds to the edge of the tangential fold just as that in the septum corresponds to the edge of the septal fold.

When septal and tangential folds keep pace with one another in growth, their centres of calcification are continuous (fig. 73). In many genera the septa grow more rapidly than the theca, and then the thecal centres of calcification appear between septa (*antea*, figs. 4 and 5).

In *solitary* thecate corals (*e.g.*, Turbinolidæ), the epitheca encircles the theca, and is coalescent with it. In *colonial* thecate corals the epitheca may encircle the theca of

each polyp (Amphiastræidæ); more frequently it is limited to the base of the whole colony. In the latter case, the parts of the aboral wall around the thecæ of adjacent polyps form cœnenchyme (ex., Oculinidæ, Madreporidæ, Pocilloporidæ, Poritidæ).

When the cœnenchyme is of compact structure, the theca is also compact, *e.g.*, Oculinidæ, Pocilloporidæ); when the cœnenchyme is porous, the canals in its meshes are rendered continuous with interseptal loculi in the calyx by means o "pores" in the theca (*e.g.*, Madreporidæ, Poritidæ).

Pores are not altogether unknown in the theca of Turbinolids. They are present in the genus *Trematotrochus*, WOODS, in the same position as the intercostal dimples of the Turbinolidæ, *i.e.*, in the same position as the pores in the thecæ of *Turbinaria*, *Porites*, and *Madrepora* (figs. 55, 64). Two rows of pores occur between adjacent septa on either side of a small thecal costa, which is placed midway between the same septa. I take this thecal costa to be the same as an "epithecal costa" in many of the Palæozoic genera.

Pores also occur in the thecæ of Turbinolid genera which have rootlets (ex., *Rhizotrochus*). Similarly in certain Palæozoic genera which characteristically retain the rootlets. The thecal pores are, in those simple types, always a means of communication between the interseptal loculi and the canals of the rootlets, and are, in my opinion, the exact homologue of the thecal pores in cœnenchymatous colonial types which have a porous cœnenchyme.

Note on the Porous Theca.—ORTMANN has, in his systematic arrangement of the Madreporaria, treated the solid parts of the porous theca in Madreporidæ and Poritidæ as the homologue of the synapticulæ in Fungidæ and Eupsammidæ. (I use these titles of families in the sense in which I have already defined them in foregoing pages.) He classifies all these families as "*Athecalia*," ORTMANN, and places them in contradistinction to the "*Euthecalia*" (HEIDER, ORTMANN), represented chiefly by the Turbinolidæ, Pocilloporidæ, *Galaxea*, *Euphyllia*, etc., and the "*Pseudothecalia*" (HEIDER, ORTMANN), represented by the Astræidæ (*vide* below, pp. 310–314). I entirely disagree with the main sub-groups erected by ORTMANN. Reference to my figure of *Madrepora* (fig. 60, p. 214) will be sufficient to prove that the theca of *Madrepora* corresponds in structure precisely with ORTMANN'S own definition of an *Eutheca*, differing only in the fact that it is porous. To call the solid parts of the *Madrepora* theca "synapticulæ," is to deviate wholly from the original application of the term by EDWARDS and HAIME (*antea*, p. 167), in so far as *no part of them is made up of septal granulations*. The *synapticula* would, in this case, have to be defined as a *thecal bar*, having its own centres of calcification set at *right angles to*, or very obliquely to, the centres of calcification in the septum. *These thecal bars are, moreover, always built up exactly opposite each other, and at one definite radial distance from the centre of the calyx.* The homologue of such uniting bars is found in the theca (= *Eutheca* of HEIDER and ORTMANN) of Turbinolidæ, and not in the occasional irregular rings of synapticulæ and pseudosynapticulæ in the calyces of *Siderastræa*,

Lophoseris, etc. (of figs. 42B, 46). Hence I would apply to the wall in *Madrepora*, *Turbinaria*, and *Porites* exclusively the name of a *porous theca*, thereby indicating (1) the fact that a tangential thecal ring of calcification is present, even if it is not continuously developed during upward growth of the polyp; (2) its structural homology with the usually *compact theca* of Turbinolidæ, Pocilloporidæ, and Oculinidæ. The same relations obtain in all these cases between the theca and the septa, whether the theca be porous or compact.

The interrupted development of a skeletal structure is nothing unusual. An analogy may be, for instance, made with the septa of *Madrepora*. Some are continuously developed, and appear as a compact septal plate; others, in the same calyx, are interruptedly developed, and appear as a vertical uncompacted series of septal spines. Yet the structure of the septal spine is precisely the same as that of successive growth-parts in the flat septal plate. Thus, we must seek for the structural homologue of the "porous wall" of *Madrepora*, without paying any respect to its interrupted development, and need not feel surprised to find it in a *compact* form of theca.

Extrathecal Structures, or Structures external to the "true" Theca.

The extrathecal structures which I shall enumerate are forms of cœnenchymal and epithecal deposit. The epitheca may be present as occasional rings round the theca, or round the exposed edges of septa. In many Turbinolidæ the deposit of calcareous matter on the outside of the thecal centres of calcification becomes very great, and may be either compact or may show hollow spaces. The thin epithecal rings in some genera are probably the homologue of this thick concentric extrathecal deposit in others. The latter simulates "cœnenchyme," but is an entirely irregular structure, and its calcareous composition seems to me to be utterly distinct from that of all interpolypal cœnenchyme in coral *colonial* life.

The following are the chief forms of extrathecal structures:—

a. *Occasional epithecal rings*, not forming a connected pellicle.
b. *Pellicular epitheca*, solid or vesicular in structure.
c. *Ornamentations*—bosses, echinulations, crests, ridges. Such ornamentations may be solid, and are then of secondary origin. More frequently they are hollow, and represent original concavities and irregularities of the body-wall, or the scars of buds and embryonic rootlets. The costæ on the "rugose epitheca" of many Palæozoic genera alternate in position with the septa; they find their counterpart in the extra costæ introduced in the wall of Turbinolidæ and of many cœnenchymatous types.
d. *Rootlets*—definite, hollow, calcareous tubes at the lower part of a theca, by which the young polyp attaches itself, and which may or may not be retained during its free existence later.

e. *Cœnenchyme*—(1) *compact*: a system of calcareous superficial channels between adjacent thecæ in a colony; (2) *porous*: a complicated system of intra-skeletal and superficial channels between adjacent thecæ in a colony. The skeletal channels open into the calyces by means of pores in the thecæ.

Pseudotheca.—This term is a very useful one, which has been applied by HEIDER

Fig. 74A.

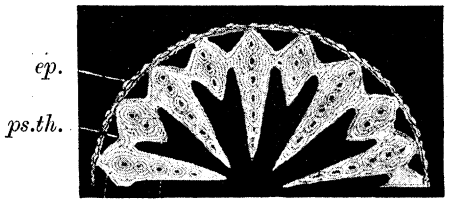
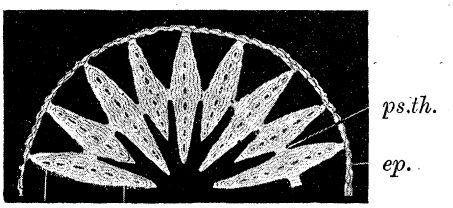


Fig. 74B.



Transverse sections showing the structural relations between "*s.*" = septum, "*c.*" = costa, "*ps.th*" = pseudotheca, and "*ep.*" = epitheca. The pseudotheca is shown rather nearer the centre of the calyx in fig. 74B than in fig. 74A; all grades occur between a position of the pseudotheca very near the centre and very remote from it, until it may be almost coalescent with the epitheca; the costa is respectively longer or shorter.

and by ORTMANN to the ring of septal thickening which may arise at any part of the calyx in the Astræidæ. Those authors have defined it as a compact "false wall," formed entirely by the lateral coalescence of septal surfaces at a definite zone in the calyx. During the course of my microscopic investigations I have found that one must slightly modify this definition, since in many cases the laying down of the basal structures materially helps the compacting of the false wall (*cf. Heliastræa* and *Mussa*). Even then it may not infrequently be that tiny apertures are left unfilled.

According to the position in the calyx at which this thickening takes place there will be a narrower or broader costal area around the inner part of the calyx (see figs. 74A and 74B). As the epitheca is external to the costal area, the appearance of "two walls" may be produced. In colonial Astræids, however, budding goes on in the inner or outer zone of the calyx, and the epitheca surrounds all the polyps of a colony in common.

The *pseudotheca* distinguishes itself structurally from the *theca* by being formed within radial, *i.e.*, septal, folds of the calyx.

It will readily be seen that the synapticular rings in *Siderastræa*, *Lophoseris*, etc., may be regarded as the *homologue of the pseudotheca, although not of the true theca.*

If the pseudotheca forms very near the periphery, the epitheca may be coalescent with it (ex. *Goniastræa* at the edge calyces of a colony, and frequently *Mussa*). Usually, however, there is a fairly-developed costal or edge zone between pseudotheca and epitheca.

NOTE.

Before closing Part I., I wish to refer again to the series of figures, 2, 22, 35, 36, 56, which are longitudinal sections of various coral types, treated diagrammatically.

They show the investiture of the hard skeletal parts (printed black) by the soft polypal flesh (printed red). In one portion of each figure, the polypal flesh is represented covering the septum and costa; in another portion, it is seen clothing the basal structures in an "interradial loculus" between adjacent septo-costæ (*cf.* pp. 107, 108). The edge-zone ("Randplatte") of polypal flesh is specially indicated, and its relation to the epithecal deposit. In *Mussa* and *Fungia*, representative types of my proposed sub-division, Septocorallia (p. 322), the prominence and shape of the *septal* wing of the "radial structure" determines the particular curvature of the edge-zone along the *costal* wing. *Stylina*, *Galaxea*, and *Turbinaria* all belong to my group of Cœnenchymata (p. 320), and may be said to represent three very distinct grades of cœnenchymatous corals. (1.) The fossil Stylinids, to judge from their skeletons, supported an edge-zone upon the broad costal wings of the radial structures and the intercostal vesicular tissue. But the costæ of adjacent calyces frequently did not quite meet, and cœnenchymatous deposit filled the gap. (2.) The living *Galaxea* has an edge-zone supported on the narrow costal wings of radial structures, but a very considerable gap between adjacent calyces is filled up by cœnenchymatous deposit supporting a "common cœnosarc." (3.) In *Turbinaria*, a "common cœnosarc" entirely covers the space between adjacent calyces. The rings of the cœnenchyme nearest the calyces show the same structural relations with the "radial structures" as are to be found between the primitive wall (eutheca) and the radial structures in many non-cœnenchymatous corals. Hence I look upon the "cœnenchyme" of perforate corals simply as a particular form of deposit laid down by the wall area of the polypal flesh. Correlatively I regard "cœnosarc" as of *mural* origin in contradistinction to the "edge-zone" which I have traced to an *intracalycinal* origin (p. 262). Both are adaptations of special parts of the polypal flesh; and neither, so far as I see, has any right to be considered more primitive than the other. (*exc.* foot-note p. 226).

List of Abbreviations used in lettering the Figures.

This "list" will be found at the end of Part II. on p. 345.

To face page p. 252

Radial structures (septa, costæ, pali).			
Centres of Calcification, with especial reference to the arrangement of the microscopic calcareous fibres and the appearance of a so-called "dark line."	Compactness or porosity.		Direction of the or trabecular the radial str
	Successive growth-parts in individual trabeculæ.	Contemporaneously-formed growth-parts of adjacent trabeculæ (the septal segment).	
Several centres of calcification are gathered in groups corresponding to the individual trabecular ridges. Each group is clearly distinguishable in transverse section from neighbouring groups, and as the trabeculæ meet the septal edge at a high angle, no appearance of a continuous "dark line" in the median plane of the septum is presented. The calcareous fibres pass upwards and outwards from the axes of the trabeculæ to the surface of the septum. Fascicles of longer fibres emerge as septal granulations.	The individual trabeculæ consist of a continuous, *compact*, vertical series of trabecular growth-parts.	A *compact* tier of trabecular growth-parts is formed at the edge of the radial structures during each successive growth-period.	The trabeculæ c diverge obliq wards, in *reg* like form, to r left, from one areas of diver the radial st
		The tier of trabecular growth-parts at the edges of septa and costæ are *often not compacted* within one period of growth. Apertures may remain unfilled between the neighbouring growth-parts or they may be subsequently filled up.	
The first-formed fibrous deposit is more horizontal in position than the latter. The groups of "centres" are again present, but always in close contiguity with one another, and in a straight median row, so as to give the effect of a continuous median line of calcification.	The individual trabeculæ are *not primitively compact*; the series of growth-parts are not joined up end to end, successive parts may sometimes alternate in position.		The trabeculæ di irregular fa figures in th structure.
Characteristic wheel-like arrangement of *fascicles of fibres directed horizontally outwards* from one common axis or centre in each trabecula. No appearance of a "dark line" in the median septal plane.	Successive growth-parts are always directly above each other in position, but *pores are sometimes* left in the trabecula, opposite synapticulæ.	*Usually porous.* The individual trabeculæ are very distinct, and their parts at the edge completely enveloped in polypal flesh during any one period of deposit.	The trabeculæ rected almos cally upward or less paral one another.
Strongly-marked "dark line" in the median plane of the septum, owing to the almost horizontal position of the trabecula or spine. The fibres pass obliquely upwards and outwards.	*Compact septa.* The individual trabeculæ are compacted (*Turbinaria* and *Madrepora*, (pp. 213, 214) or remain free from one another as septal spines.	*Compact.* Since the trabecula or spine is *horizontal* with the growing septal edge, *one growth-part represents the whole septal segment.*	The trabeculæ rected almos zontally inwa the theca tow centre of th and outwards the cœnenchy
The fibres vary, horizontal or oblique. Strongly-marked "dark line" here, owing usually to the very close setting (in serial line) of the centres of calcification.	The individual trabeculæ consist of a continuous, *compact*, vertical series of trabecular growth-parts.	*Compact.* The trabeculæ are extremely narrow and adjoining growth-parts in any one septal segment are intimately	The trabecula greatly in d At the very septum an divergence is present, afterv *trabeculæ grou*

TABLE of Classificatory Features.

on of the trabeculæ abecular ridges in radial structure.	FAMILIES.	Relation of the *radial structures* (septa and costæ) to the wall.	*Interradial and axio-polypal basal supports*:—(Tabulæ, dissepiments, synapticulæ, pseudo-synapticulæ, lateral septal coalescence, terminal septal coalescence, columella.
beculæ or ridges ge obliquely up- s, in *regular* fan- form, to right and from one or more of divergence in radial structure.	ASTRÆIDÆ.		*Dissepiments.* Rare occurrence of pseudo-synapticulæ Terminal septal coalescence produces very often a pseudo-columella.
	FUNGIDÆ: THAMNASTRÆINÆ.	*The radial structures pass through the pseudotheca* and the interradial loculi correspond in the adjacent polyps of colony-building forms.	*Pseudo-synapticulæ* in vertical series. Dissepiments also present. Occasional occurrence of a pseudo-columella.
	FUNGIDÆ: FUNGINÆ. LOPHOSERINÆ.	All costæ are represented by septa within the calyx.	*Synapticulæ* (both true, and pseudo-synapticulæ) in vertical series. Dissepiments also present except in the genus *Fungia*, where the synapticulæ form continuous bars. Lateral septal coalescence characteristic; terminal septal coalescence also present.
beculæ diverge in ular fan-shaped es in the radial ture.	EUPSAMMIDÆ.	*The radial structures pass through the pseudotheca*, but the interradial loculi do not always correspond in adjacent polyps of colonies. All costæ are represented by septa within the calyx.	*Idem*, but the synapticulæ are not placed in regular vertical series, they are mostly limited to the wall area and form an irregular network.
abeculæ are di- d almost verti- upwards, more ss parallel with nother.	PORITIDÆ.		*Synapticulæ* (only true synapticulæ) in vertical series. *Dissepiments* also present. *Columella* frequent. *Lateral coalescence of septal pairs* to form pali.
abeculæ are di- d almost hori- lly inwards from aeca towards the e of the calyx, utwards towards œnenchyme.	MADREPORIDÆ: MADREPORINÆ. TURBINARINÆ.	*The radial structures may or may not pass through the theca*; the interradial loculi never correspond in adjacent polyps of colonies. Alternate costæ occur in the wall which are not represented by septa within the calyx.	*Extremely variable nature of basal deposit*, representing an irregular combination of tabulate and synapticulate structures; *it is almost absent in the calyces, richly developed in the cœnenchyme*. A main septum is often continued as columella.
trabeculæ vary ly in direction. ne very *base* of a m an area of gence is usually nt, afterwards *the culæ grow inwards*	TURBINOLIDÆ.		*Interradial deposit almost absent*; represented at the base of the calyces by a solid tabulate deposit. Lateral septal coalescence may occur. *Columella* usually present either as an independent structure or connected

	Wall. (1) Compact or porous. (2) The "centres of calcification," their relation to septal "centres."	
ɔal *sup-* ınts, ɔulæ, al septal		
ɔticulæ oduces .		The theca is compact.
series. ısional ella.	Outer (true) theca very rarely present; a pseudotheca is formed by a thickening of the lateral surfaces of the septa at the peripheral area, together with a modification of the interseptal basal supports.	The theca is seldom compact throughout, it is usually partly porous, partly compact.
seudo- . ; in the ɔticulæ haracscence		
placed ey are ea and		The theca is irregularly porous.
ıiculæ) *ıirs* to		The theca is regularly porous; in form zigzagged.
basal egular synap- *absent* *in the* s often	Outer (true) theca is the only one present. It has its own centres of calcareous deposit, independent of those in the radial structures. The thecal deposit usually seen to bend tangentially round and form continuity between adjacent septa.	The theca is regularly porous; in form perfectly circular.
ut; re- alyces Lateral *Colu-* as an nected		The theca is compact, either zigzagged or circular in shape.

Strongly-marked "dark line" here, owing usually to the very close setting (in serial line) of the centres of calcification.	consist of a continuous, *compact*, vertical series of trabecular growth-parts.	tremely narrow and adjoining growth-parts in any one septal segment are intimately compacted.	septum an divergence is present, afterv *trabeculæ grou from the wall* Madreporidæ.

m an area of gence is usually nt, afterwards *the culæ grow inwards the wall as* in the reporidæ.	TURBINOLIDÆ.		by a solid tabulate deposit. Lateral septal coalescence may occur. *Columella* usually present either as an independent structure or connected with a main septum or with pali.

Lateral *Colu-* as an nected bali.		pact, either zig-zagged or circular in shape.

PART II.—PHYLOGENY OF MADREPORARIA BASED UPON SKELETAL STRUCTURE.

CHAPTER IX.—EVOLUTIONARY CHANGES.

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1. Koch's Description of the "Septal Spine" of a Palæozoic Genus.

The term "stereoplasm," as first used by Lindström, was applied to a "structureless" calcareous deposit on both sides of a narrow stripe, much darker in appearance, in the middle of the septum. This narrow stripe or inner septum of Lindström is not however the same as was meant by von Koch when he introduced the term "Primärstreif"; farther, the identification by Frech of Lindström's and Koch's nomenclature has been the cause of considerable confusion.

Koch's description of a *longitudinal* section of the septal spine of *Pholidophyllum*, Loveni, is possibly the most exact which is to befound in the literature (*cit. ant.*, ‡ p. 89). It reads as follows:—

"The central mass appears in quite thin sections to be composed of small crystals, showing no particular arrangement; in this mass one can observe small dark spots and points crowded together in greater or less number, and glancing brightly in some positions of the microscope. . . . . The second, *clearer* zone, consists also of small crystals, between which spots and points occur, and, indeed, more numerously and generally larger than those in the middle area; but the crystals appear radially arranged; this is most plainly seen near the periphery, where they become rather larger. . . . . That mass which unites the individual spines together and forms the "*wall*" is composed of crystals, the same as the crystals in the spines themselves, but they are arranged in rows which run nearly parallel, and in somewhat thicker

sections appear separated from one another by strong, dark lines. These lines seem to run concentrically when seen in transverse sections of the spines, but in longitudinal sections they are parallel with the vertical axis of each individual spine and pass into the similar lines of neighbouring spines with a slightly crooked course."

My reason for quoting the entire description is twofold: (1) because of its agreement with a longitudinal section of a septal spine of the recent coral *Madrepora spicifera*, DANA (*antea*, fig. 61), and to which I shall presently return; (2) because it is important to understand clearly the nomenclature used in the literature of the day.

KOCH makes no mention of the word "stereoplasm" neither here, nor when, a few pages farther on, he describes the transverse section of *Cyathophyllum*, sp. The latter is, he says, composed of a *darker median area* like the central mass in the *Pholidophyllum* spine, and two *clearer lateral areas* on opposite sides of the median line in which the crystals are arranged radially. The median area in *Cyathophyllum* takes the *form* of a narrow band which he calls "Primärstreif"; to the lateral areas he gives no special name.

I shall now represent in tabular form the comparison made by KOCH between *Cyathophyllum*, sp. and *Caryophyllia cyathus* on the one hand, and *Pholidophyllum* on the other. I add a third column, which will show how KOCH's description of *Pholidophyllum* may be compared with mine of *Madrepora*.

I.—KOCH. *Cyathophyllum*, sp. (Palᵉ·). *Caryophyllia cyathus* (Rec.).	*Septum*. KOCH's distinctions.	II.—KOCH. *Pholidophyllum Loveni* (Palᵉ·).	III.—AUT. *Madrepora spicifera* (Rec.).
Septum, long in radial direction, and compact.		Septum = a vertical *interrupted* series of short "septal spines."	
a. Dark "Primärstreif" as a continuous median band	= Central area	= Dark, central mass, circular in section	*Idem* (called "core" or "axis" of calcification in my paper, regardless of its appearance, light or dark, homogeneous or crystalline, filled or empty !).
b. Lighter-looking, radiating crystals forming lateral bands	= Clearer zone	= Lighter-looking, radially arranged crystals, around the central mass	*Idem* (called above, "primary growth-segment," or first-formed deposit of similarly-oriented calcareous fibres.)
c. Absent	"Wall mass"	= Crystals arranged in rows parallel with the axis of growth; uniting the spines at their basal parts, corresponding with their points of origin at the periphery of the calyx	*Idem* (described above as larger fibres, *irregularly* swathed round the primary growth-segments, in the course of the withdrawal or dying-off of the soft parts at any particular horizon of polypal growth).

KOCH'S *"Septal Spine" in* Pholidophyllum *ident. Author's "Septal Spine" in* Madrepora *and, generally, Author's Growth-segment in the Madreporarian Septum.*

When KOCH suggests that the septum of *Cyathophyllum* and *Caryophyllia* is structurally similar to the septal spine of *Pholidophyllum*, he expressly states that the suggestion is based on the agreement in appearance of "*a*" and "*b*" in the respective columns.

I have given actual evidence in the cases of *Madrepora* and *Turbinaria*, that *a series of horizontal septal spines, may, when in contact at the successive horizons of deposit, make up a compact "Turbinolid"-looking septum.* In the genus *Madrepora* itself, the "principal septum" is often just a closely-set series of "spines," and thus approaches the condition of the septa in *Turbinaria*, as well as in *Turbinolia, Caryophyllia*, etc. Whereas the less-developed septa have their spines originally placed at wide intervals, and only get compacted at their basal parts, just as KOCH has described for *Pholidophyllum.*

Summarizing my results, there are certain Madreporarian genera in which the septal growth-segments are laid down, at first in the form of *free, separate spines*, and the spines are subsequently compacted either in part or wholly. The greater number of such genera is to be found amongst *Perforata*, in the former signification of this group. During the process of compacting, the fibres may be deposited in the same direction as those in the free spines, or they may slope more in one direction and another entirely according to the local axis of growth during this secondary deposit. Some of the Fungid genera show a different orientation of fibres according to the period of deposit. Again, the Eupsamminæ, E.H., show an even greater difference in the orientation of the fibres nearer or farther from the median plane, so that an inner band of fibrous deposit may be distinguished from an outer. Both bands are composed of radiating fibres, but those of the outer band very obliquely inclined, while those of the inner form a very small angle with the horizontal. The Poritinæ, on the other hand, have the fibres of the secondary deposit oriented in exact continuation of those of the primary; moreover, the fascicles are placed horizontally, *i.e.*, at right angles always to the upward axis of growth. The Madreporinæ show the most marked difference in the orientation of the primary and subsequent layers of deposit. The primary fibrous deposit is horizontal and regular, the subsequent deposit follows no definite system.

The whole foundation for the term of stereoplasm rests, I believe, on those differences in the orientation of the calcareous fibres, differences which are observable only within some of the Madreporarian groups. Among recent corals, these differences are only well-marked in the Turbinolidæ, Madreporidæ, and Eupsamminæ, the Lophoserinæ also showing indications of it now and then. In short, difference of orientation is a feature in many cases correlated with the laying down of the septal spines in isolated pockets at the edge of the main septal invagination, in other cases

correlated with rapidity of growth and the quick formation of a mere scaffolding of "septal spines" instead of continuous septal structures; in still others it is a result of *slow* growth, which allows crystalline changes of disintegration to go on very considerably during intervals of growth.

"*Primary Streak*" (KOCH) = "*Primary Septum*" (FRECH),
"*Crystalline Deposit*" (KOCH) = "*Stereoplasm*" (FRECH, *non* LINDSTRÖM).

Summarizing my statements above, I may say that the primary streak ("Primärstreif") of v. KOCH signifies the median dark band, and wherever it is present it is the *only truly structureless part* of the skeleton. Any crystals which may appear in it are due to later infiltration of water. The *fibrous deposit* may be from first to last, *i.e.*, from median plane to surface, similarly oriented and similarly constituted, in which case there is no appearance of "stereoplasm." On the other hand, some difference in the actual constitution of the layers of deposit may give rise subsequently to differences in the crystallographical properties of the fibres, in which case one *may* speak of "primary" bands opposed to "stereoplasm." In KOCH's description of *Pholidophyllum* the "wall mass" may be looked upon as stereoplasm, but in his description of *Cyathophyllum* there is no such mass, and nothing therefore to represent stereoplasm.

Yet FRECH has drawn the following comparison between KOCH and LINDSTRÖM:—

"According to LINDSTRÖM's description, a structureless calcareous deposit, which he calls *Stereoplasm*, occupies the sides of the septa in certain '*Tetracoralla*' genera (*Cyathophyllum*, *Pycnophyllum*, *Cyathaxonia*, *Zaphrentis*) in such a manner that the septa are distinguished from the surrounding mass only as thin, shadow-like ('Schattenähnliche') streaks. Transverse sections of *Cyathophyllum mitratum*, a species cited by LINDSTRÖM as an example, entirely corroborated this description, and agree, on the other hand, with KOCH's figures (of *Cyathophyllum*, sp., referred to in column 1 above, p. 254). Accordingly, we may call the calcareous deposit at the side of the 'Primärstreif' in KOCH's figure also 'Stereoplasm.' Extending the sense still farther, I feel justified in also calling the above-described compacting mass (Ausfüllungsmasse) 'stereoplasm' which unites the septal spines. This mass appears similarly structureless and has the same significance as the stereoplasm, namely, to strengthen later the septa previously laid down"* (*loc. cit.*, pp. 931–932).

Those two conceptions of "stereoplasm" are not identical; the first of them applies the "stereoplasm" to the middle zone of KOCH ("*b*" in comparative columns above), while the second is word for word that which KOCH indicated in describing the "wall" or outer concentric mass of *Pholidophyllum*. After the explanation I have just given of the actual difference in orientation of the fibres, it is easy to interpret the limit between KOCH's *middle* and *outer* zones, and also to identify the "middle" zone with the inner layers of lighter crystalline deposit so often depicted in sections of various Palæozoic genera. These are indeed the same layers

* FRECH, "Ueber das Kalk Gerüst der Tetrakorallen," "Zeitschrift d. D.G.G."

which gave LINDSTRÖM and others the idea of a primary septum being *double*, and *flanked* on both sides with lamellar "stereoplasm."

But confusion began when a "dark streak" in the middle of the septum was said to be the same as the apparently "double" primary septum. Then the question came to be, was the primary septum single or double? And all kinds of appearances in fossil septa were raised to the dignity of "primary streaks."

FRECH now professes to simplify the matter by calling KOCH's axial "dark band" *the* "primary septum," and *all* the rest "stereoplasm." The actual differences of KOCH's middle and outer zone go for nothing.

This first misconception on the part of FRECH led to another some years later.* Whereas, in 1885, FRECH used the various expressions *spine*, *trabecula*, "*isolirte Pfeiler*" = the whole "septal spine" (KOCH) of *Pholidophyllum*, in 1890, he used the same three terms in a new sense, namely, for the isolated "dark points" in the "Primärstreif" (KOCH) of an Astræid septum. And the "Primärstreif" of KOCH was called "*primary septum*," an entirely new use of KOCH's term, never intended by KOCH himself, so far as he had given expression in published work. Thus, only the "dark points" in transverse sections of the Astræid septum are recognized by FRECH as the "primary septum" (single or double) of previous authors, and *the whole of the calcareous fibrous deposit* of the septum becomes, in his eyes, "stereoplasm." It stands to reason that LINDSTRÖM would never have thought of inventing a new term, viz., "stereoplasm," for the *whole calcareous structure which has been called a septum* since the earliest days of Madreporarian literature. Yet that is the end which in 1890–91 is arrived at by FRECH (*cf.* pp. 99, 100 above).

If now, the "primary septum" of FRECH is analysed, we find throughout his work no indication of its structure. The "dark points" are regarded as cross-sections of "trabeculæ" or "spines," but this use of "trabecula" is not that of PRATZ, who was the first to describe the microscopy of trabecular structure. We learn from FRECH that each "primary spine" in the "primary septum" may be seen microscopically as a number of points, or as shorter or longer rods, variously placed—again, that it may appear light or dark; all of which are true observations, but give no ground whatever for transferring the term "septum" to this structureless, mysterious central portion, and leaving all the calcareous substance to be called "stereoplasm"! Again, HEIDER describes these central portions as "sometimes filled, sometimes empty," and HINDE states that they are occupied as a rule by deposit which he

* Compare—

A. 1885, p. 929, footnote 6, and p. 931, footnote 1, where the terms "primary spine" and "trabecula" are used as the equivalent of both the "dark, central area" and the "light fibrous deposit" in KOCH's original sense of the septal spine of *Pholidophyllum*.

B. "Trias Korallen," Palæontograph., 1890–91, p. 22, where the same terms are used as the equivalent of the dark central area only: "Der aus Primärdornen bestehende Primärstreif' (I. *a* in comparative columns above).

believes to have been introduced later, and therefore, to afford little clue with regard to the original condition.

I have already given my own explanation of the *dark* points, and spots, and lines, and rods, whether those of the "Primärstreif" (Koch) or those in the fibrous deposit.

My conclusion is that they are due to the subsequent disintegration of organic cell-material, under conditions of preservation favourable for the slow conversion of any organic parts of the calicoblasts left in the skeleton into graphite, or, generally speaking, coaly compound. In rapidly growing corals it would seem that a considerable mass of organic cell-material remains uncalcified within the "pockets" which are invaginated at the apical edge of the septum. And these pockets seem to have been on the whole larger and more irregular in Palæozoic than in recent forms, enclosed uncalcified portions being in consequence greater. Yet we have seen how in the recent genus, *Madrepora*, large "cores" of organic uncalcified substance are present. The black appearance of these cores too, is often as bright and glancing as that described by Koch for the Palæozoic genus *Pholidophyllum*. Probably the exact nature of the subsequent changes undergone by enclosed organic matter is influenced by the rapidity or completeness with which the cellular fragments are enclosed in the skeleton.

Whatever the state of preservation, or the exact nature of the chemical changes, the so-called "primary septum" (if we could succeed in separating it out at the growing surface of a living coral) would be, in its *original* condition, always organic and cellular. In its *carbonized* condition we seem to observe dark, ramifying stems or detached rods in the middle of a Madreporarian septum. These merely represent the original axes around which the calicoblasts became converted into calcareous skeleton.

The lines may branch from an "area of divergence" in some cases, in others they may be irregular, in others non-branching and parallel. These axial lines are specially pronounced at the lowest part, which is likewise the youngest of most septa. I have observed in the case of some Turbinolidæ, that the dark lines develop in the septum of the mature coral almost parallel with one another (inwards and all but horizontal), but in the embryonic calyx, they are arranged at first in a fan-like, divergent form, much as in Astræidæ.* It is to the mature coral that we must look for the characteristic setting of the trabecular axes in the septa. The process of calcification would seem also to be more vigorous in the mature than in the quite young polyp.

* This observation is important, as it indicates that probably in the embryonic stages and early development of the skeletal parts, the relations of the septal folds are much the same both in Astræidæ and Turbinolidæ, a peripheral "area of divergence" being present in both. Possibly the thick wall and *special wall-fold* of Turbinolidæ is only an adaptation to the free-living, simple habit of the typical Turbinolid polyp; all the more may we expect a variation such as "cœnenchyme" when reef-life is especially assumed by an allied genus.

2. *Similarity in Microscopic Structure of the Septa in Palæozoic and Recent Madreporaria.*

The Table of Classification (Part I., p. 252) which I have given above is, I believe, fair evidence of the value which microscopic structure can have when applied to systematic affinities. And I am convinced that the application of the same main principles as I have there used, to Palæozoic genera, would introduce uniformity in the classification of *Madreporaria rugosa* (E. and H.). These main principles may be set down under the headings, I. *Radial Structures*, II. *Theca or Wall*, III. *Interradial Structures* (tabulæ, dissepiments, synapticulæ).

Under the heading of Radial Structures, the chief sub-divisions are yielded by the direction in which the *centres*, or better, *axes of calcification* (= central portions of the "septal spines" in KOCH's *Pholidophyllum*) are developed in the radial structure. Every variety is present amongst recent corals, from a horizontal position to a vertical, and the same is true of Palæozoic corals. I shall confirm this statement by mentioning a few figures (of Palæozoic septa), easy of reference, and naturally I select figures of sections made longitudinally, and, where possible, in radial direction through the septum. Seldom, however, does any longitudinal section show more than a dark axis and a lighter "structureless" surrounding substance.

Several figures given by FRECH* of Devonian corals are important. A longitudina section of *Cyathophyllum heterophylloides*, FRECH (*loc. cit.*, Plate 1, fig. 2*c*, p. 30), shows dark lines curving inwards and upwards. The lines are "mostly broken up into rows of connected points. Each row of points is laterally flanked by a clearer stereoplasm zone.". . . . . *Phillipsastræa pentagona Goldf.* sp. *var. micrommata*, F. ROEM, shows more marked dark lines (*loc. cit.*, Plate 3, fig. 13*a*) in correlation with the presence of prominent striæ ("Verticalleisten," "Carinæ") on the septal surface. *Haplothecia filata Schloth*, sp., Plate 4, fig. 7A, is like *Phillipsastræa*; *Hallia prolifera*, A. ROEM, sp. (*loc. cit.*, Plate 7, fig. 5*b*) again shows the same general direction of the dark axes of calcification, but this same figure has for me a particular interest, as the dark lines diverge at the *base* of the septum in fan-like shape just as in the septum of *Galaxea*. Yet, later, all the "lines" bend at a very low angle inwards, just as in Turbinolids. And thus an example is afforded in the Palæozoic genera of the observation which I have stated above on p. 258. Moreover, the figure shows at the same part the separate short lines or "rods" into which the long, curving, dark line breaks up. This is an evidence that the short, "dark line" was in Palæozoic as it is in recent genera, a *separate axis of calcification corresponding to a single growth-part* of any particular trabecula of the septum.

Still another section may be cited from the same author, *Endophyllum torosum* ("Zeitschr.," 1885, Plate 41, fig. 6, 6*a*). The interest of this section is in the entire

* "Die Korallenfauna des Oberdevons in Deutschland," "Zeitschrift d. D.G.G.," 9, 1885, p. 21.

individuality of the "dark lines," representing, in my estimation, the axes of isolated trabecular parts. Thus interpreted, the Palæozoic genus *Endophyllum* would present an antetype of the arrangement of trabecular growth-parts in the Eupsammidæ. It is, in fact, a type in which the septal spines tend to a serial arrangement, although they show in certain regions the irregularity of the *Cystiphyllid* septal spines.

All those figures given by Professor FRECH show no signs of structure other than the presence of darker rods in the midst of a lighter-toned substance. Calcareous fibres are nowhere figured. At the same time Professor FRECH is perfectly justified in drawing the following conclusion ("Zeitschr.," 1885, p. 934):—"In *Phillipsastræa*, *Haplothecia*, *Cyathophyllum*, and many others, the septa appear to be built up essentially on the same plan as the living corals with, however, the variation, that originally a greater number of septal spines (= "dark rods," in figures) are independently laid down and afterwards bound together by differently-formed Stereoplasm."

Dr. R. SCHÄFER showed the *minute fibrous structure of Phillipsastræa* (on *Phillipsastræa*, "Geol. Mag.," Sept., 1889, Plate 12, figs. 8, 9) and the similarity of the arrangement of the fibres seen in longitudinal sections of the septa with that which PRATZ had demonstrated in the Jurassic genera belonging to the Thamnastræinæ.

The same author has told me that his examination of the Palæozoic genus *Heliophyllum* seemed fairly conclusive that the "carinæ" were the homologues of the synapticular bars in the Mesozoic Fungidæ. In Dr. SCHÄFER'S opinion, the genus *Phillipsastræa* showed a microscopic structure essentially like the Thamnastræa. The habit of the corallum and the connection of the calicinal discs he regarded as an antetype of the "*astræiform*" colony, common to the Astræids and Thamnastræids as early as Triassic time. Professor NICHOLSON'S figure ("Manual of Palæontology, p. 247, fig. 127) may be again referred to, since it shows the *fibrous structure* in *Zaphrentis* and *Streptelasma* septa side by side with the septa of Caryophyllia, and still farther confirms KOCH'S comparison of Caryophyllia with Palæozoic types. In those cases the dark lines seem, so far as the transverse sections allow a conclusion, to be very obliquely directed inwards. It is very certain that in a large number of Palæozoic genera the spines are directed horizontally inwards as in *Pholidophyllum*, and thus the idea gained ground, rather awkwardly expressed sometimes, that the septum was a "*two-leaved 'structure' taking origin in a fold from the wall.*"

These examples suffice to exemplify the structure of the Palæozoic "Rugosa." To judge from the few detailed figures of longitudinal thin sections and the far greater number of good transverse sections, their structure was *even in microscopic features* identical with that presented in recent Madreporaria.

In so far as septa are concerned, I recognized in the Table of Classification five leading types, viz. (1) Astræid; (2) Eupsammid; (3) Turbinolid; (4) Madreporid; (5) Poritid. The facts which I gather from sections of Palæozoic* septa lead

* In speaking of Palæozoic genera, I shall follow NICHOLSON in his distinction of Cyathophyllidæ, Cystiphyllidæ, and Zaphrentidæ.

me to recognize in the majority of species referred to the genus *Cyathophyllum*, the antetypes of the *Astræidæ*. Amongst allied Cyathophyllid genera, antetypes are yielded of the Mesozoic representatives of the Fungidæ, whilst the Zaphrentids seem to me more directly the structural forerunners of the Turbinolidæ, and the colony-building forms most nearly related to them, the Oculinidæ.

The Cystiphyllids may be looked upon as the group of Palæozoic genera most estranged from recent Madreporaria. They show typically at each growth-period an utterly new set of invaginations, without serial connection with the foregoing. *The whole tendency in the history of the Madreporarian septum is towards symmetry and regularity in this respect.* Within Palæozoic time this change had made itself markedly felt, to the almost entire extinction of the Cystiphyllids. During Mesozoic time certain Triassic genera, like *Stylophyllum*, or Jurassic genera, like *Haplaræa*, include species showing transitional stages from a loose, detached condition of the septal spines to the more serial and compact arrangement characterising the trabecula (*cf.* below, p. 301). Lastly, in Eupsammids, we possess analogous cases at the present day of the more primitive disconnected mode of septum formation. I am not of the opinion that *Eupsammia* should be for this reason derived from the Cystiphyllids, but rather believe the actual Palæozoic ancestry of the Eupsammidæ to have been more immediate allies of the Cyathophyllids than are the majority of Cystiphyllids; whereas the genus *Cystiphyllum* itself is no very remote ally of the Cyathophyllidæ, the genus *Calceola* and *its* allies seem to me entirely isolated in their character, even among Palæozoic corals.

As a distinct case of atavism in respect of skeletal radial structures, the *cœnenchyme* of *Turbinaria* may be mentioned; its likeness to the irregular succession of spines in the Cystiphyllids will be granted at once, although the calicinal features show clearly the inherent family differences.

From the above comparison it appears that the building-up of the trabecular growth-part by minute calcified calicoblasts, which I have described in the skeletal structures of recent Madreporaria, may be safely extended to the skeleton of Palæozoic types. Conversely the "septal spine" of *Pholidophyllum* presents no chance identity with that of the recent *Madrepora*. It may be looked upon as an example of the "Rugose" growth-part, similar in plan to the "growth-part" of the recent *Madrepora*. At the same time, it affords a striking testimony of the want of change in the history of the fundamental relations between the Madreporarian polyp and its skeleton.

3. The "Cœnenchyme" of "Perforates" (see Note on p. 226).

The figures, to which I have referred in discussing the septa of Palæozoic types, serve also to show that the theca is composed of thickened portions of the septa. Nicholson points out that the "theca," in the case of Zaphrentids, is probably of epithecal nature.

Comparing now *Cyathophyllum* with a recent Astræid, the homologies of parts at once allow the broad outer peripheral disc beyond the inner tabulate area of *Cyathophyllum* to be recognized as the representative of the "costal" area beyond the so-called theca of Astræids. We are familiar with the fact that the aboral polypal body-wall extends over this costal area of an Astræid and, doubling on itself, becomes then the oval, or peristomal, body-wall, which is continued as the stomodæal wall. The extracalycinal, or costal portion of the Astræid skeleton, corresponds with the "Randplatte," or edge-zone (*vide antea*, fig. 2), of the polypal flesh, and it will be remembered that the mesenteries, in Astræids, are continued from the visceral chamber into the edge-zone.

Looking back in the history of Astræid and Fungid evolution, it becomes all but self-apparent that the origin of the polyp's "edge-zone" is to be found in that part of the primitive Cyathophyllid polyp which clothed the "peripheral disc," *i.e.*, the dissepimental zone of the skeleton around the inner tabulate area. Moreover, we find that the *epitheca* bears exactly the same relation to the septa in both Astræid and Cyathophyllid. It is deposited in Astræids usually, a little *below* the actual surface-level of the calyx; in Cyathophyllids, it is practically *at* the surface of the calyx, on a level with the edges of the septa. We know that in living Astræids the position of the epitheca relatively to the soft parts of the polyp is always the same, viz., at the farthest extremity of the extrathecal canals. The polypal flesh tucks downwards over the skeletal rim and doubles again upwards, the epitheca being formed below the *doubled angle* of the tucked fold as it is carried upward during growth. The relative position of the skeletal parts in Cyathophyllids would indicate likewise that the epitheca had been formed by the angle of the polypal fold, but that the said fold did not tuck downwards to any distance below the septal edges; it apparently wrinkled itself concentrically around them, and thus gave rise to a rough, irregular "rugose" epitheca. The inner, or real "*wall*" lining of this rugose epitheca might be solid through and through, or there might remain free spaces amid the irregular corrugations. The main consideration is that the epitheca, in all primitive Cyathophyllids, *kept pace in growth* with the septa, and since the septal deposit was usually very thick at the periphery, there was a strong septal and epithecal bulwark around the calyx whose various skeletal elements were all grouped together under the general, descriptive term of a "wall" or "theca."

But, in some cases, the septa atrophied more or less towards the epitheca, and their thickest portion was somewhere *within* the calyx, generally at the boundary between the tabulæ and the dissepiments. Here an "inner wall" was formed. Further, in *Phillipsastræa*, *Acervularia*, and several of the later Palæozoic species of *Cyathophyllum*, this inner wall became more marked, and the outer epithecal wall dwindled, until eventually it became scarcely developed between adjacent polyps of a colony. In other words, the transition to the typical Astræiform colony had already been marked out in many Palæozoic types of the Cyathophyllidæ. Calices adjoined

directly at the peripheries of their dissepimental zones, the outer epithecate walls became abortive, except at the outside area of the whole colony, and the inner walls, composed mainly of septal thickening, became correlatively more important and elaborate.

On the other hand, Palæozoic types, such as *Zaphrentis*, *Amplexus*, and allied genera, in which the dissepimental zone was either absent or extremely narrow, showed no tendency to the degradation of the primitive epithecate wall. Even when the formation of a new inner wall became indicated in certain colonial forms, *e.g.*, the Amphiastræidæ, with few exceptions the septa still remained in connection with the outer wall, and epithecal rings were still formed round all the individual polyps. Modification seemed rather to concentrate itself upon the *basal* skeletal tissue. In certain lines of evolution the dissepiments became spongy in texture, or even porous, and were incorporated with the wall-lining of the epithecal rings to form a light cœnenchymal framework. This I take to be the origin of the particular form of colony characteristic of recent *Madreporas*, *Turbinarias*, the *Oculinids*, etc. In all of these the epithecal rings develop apparently only where a polyp is exposed at the periphery of the irregular, or ramifying colony. I may further point out how the tendency for the epitheca to be less developed *within* the colony in these groups, while the cœnenchymatous elements became more so, may be fitly compared with the specialization of the inner, or wall lining of the epitheca in Turbinolidæ. In these simple corals the inner folds of the epitheca continue to grow upwards at the same rate as the septa and costæ, while the outer folds become, at any rate, in many well-known types, subject to irregular, or partial development. These innermost folds give rise to the so-called "true theca," which has, like the cœnenchyme, special centres of calcification; the outer folds deposit epithecal material, which varies in its structure, shows no special centres of calcification, and is not always purely calcareous.

It also occurs very frequently in the Turbinolidæ that the epitheca bears some kind of armature for the better protection of the solitary growing polyp—spines, knobs, ridges, crests, &c.; not seldom, root-like processes are given off like those characteristic of the rugose epitheca of Palæozoic corals. In the living Turbinolid, these "rootlets" are canals in open communication with the visceral chamber of the polyp. This is an important fact when we compare it with the cœnenchymatous canals of the Madreporidæ, &c. In my opinion, the cœnenchymatous canals, and the root-like processes, are homologous structures originated by the inner wall lining of the epitheca, the particular modification depending upon the habit of the polyp—solitary or colonial.

I shall now cite a few examples of the occurrence of root-like processes, taken from DUNCAN'S account of recent Turbinolidæ. "In *Rhizotrochus affinis* the epitheca comes *up to the very margin*, is striated and coarse, yet is inseparable from the wall, and, indeed, not to be distinguished from it. The radicles are large and are offshoots of the epitheca." ("Madreporaria," *loc. cit.*, p. 14.) *R. fragilis*: "The corallum has an exquisitely fine pellicular epitheca ornamented with curves and vandykes, which is

not to be distinguished from a wall. There is no theca in the ordinary sense. The rootlets are small, and their cavities are continuous with those of the interseptal loculi" (*loc. cit.*, p. 15).

Stenocyathus, POURTALÉS. "The *costal tubercles are hollow and communicate with the visceral cavity.* There is some doubt about the epitheca, some specimens having it according to LINDSTRÖM" (*loc. cit.*, p. 25).

Pleurocyathus, MOSELEY. *Corallum*, "entirely covered by a thin, plicated, coloured, bark-like epitheca, which rises *higher than the margin of the calicle*" (*loc. cit.*, p. 27).

Desmophyllum, EHRENB. "In some instances the base extends as a film of hard matter on the supporting body and in others there are rootlets. Costæ visible near the calice, irregular, often as crests, nodules or ridges here and there on the wall" (*loc. cit.*, p. 11). Also "MOSELEY notices that his great *Desmophyllum ingens* is covered with an abundant dense epitheca, and some forms of *Desmophyllum crista galli Ehr.* sp. have it and others have not. *But the epitheca is not separable from the wall.*"

Schizocyathus, POURTALÉS. In *Schizocyathus fissilis*, LINDSTRÖM states, "that the wall proper between the septa consists entirely of the *same sort of thin epitheca which surrounds the whole outside of the coral*,* or, in other words, there exists no wall as a separate formation distinct from the epitheca," (*loc. cit.*, p. 12).

It is unnecessary to give more quotations. It will already be sufficiently clear that the recent Turbinolidæ have retained, in many cases unaltered, the *epithecal* wall of Zaphrentidæ. A deposit from the interseptal portion of the body-wall may thicken the epithecal deposit internally, but such thickening has no immediate relation to what takes place outside the polyp at the thick wrinkled rim of the calyx.

Whereas in all Astræids the body-wall of the polyp laps *over* the edges of wall and septa, and forms an edge-zone ("Randplatte"), in many mature free Turbinolidæ the body-wall is pushed out *between the septa* into the hollows of a wall, or into rootlets! And in this habit, handed down from untold generations, we have a reason for the non-existence of an edge-zone of soft tissue in these types. It is, besides, the morphological equivalent of what takes place in the formation of the so-called "porous wall" and "cœnenchyme" of Madreporinæ and Turbinarinæ. The difference is, that in the solitary coral the out-pushings led, primarily, to the surface of fixture, while in the colonial coral the out-pushings of neighbouring corallites (getting more or less involved with basal tissue) formed a cœnosarc, or became directly attached to each other as confluent rootlets (*cf.* below, p. 277). While this is no evidence that the Madreporinæ and Turbinarinæ are directly descended from Zaphrentidæ, it is in favour of their having a very much closer relationship with Turbinolidæ and Zaphrentidæ than has hitherto been imagined, and at least of having a collateral ancestral type.

Hence, arguing simply from the homologies of parts which I have traced in the

* The italics are mine in all cases.

ancestral and recent types, I arrive at the conclusion: (1) that there *never was* an edge-zone (in the present acceptation of the term "Randplatte") in a large number of Madreporarian corals, among others, *Turbinaria*, *Alveopora*, *Montipora*, *Madrepora*, *Pocillopora*, *Stylophora*, *Scriatopora*, and many of the simple Turbinolidæ; (2) that the wall itself, *i.e.*, the "true theca," is in the free living, simple Turbinolidæ a modified form of the purely calcareous inner layers of "rugose epitheca" as seen in more primitive types. And just as in Zaphrentids, these inner layers are sometimes incorporated with a narrow "dissepimental" and "costal" area. While, in the colonial types the "cœnenchyme" is either a modified form of the same primitive skeletal elements, or a particular development of the canaliculate or other outgrowths from the periphery of the polyp. In the latter case, the homologies of parts still show the connection between the spined processes, outgrowths, and channelled rootlets of the Turbinolid wall and epitheca on the one hand, and the spined or tuberculate adornments and channelled passages in many forms of cœnenchymate colonies on the other.

I have refrained from giving expression to this view in the first part of my paper, since it may not be regarded by some as fully proved until we have more anatomical research on recent Turbinolidæ.*

Bourne and Fowler have suggested that the "edge-zone" in some of the perforate types may be in a retrograde condition. This may be the case in some Eupsammids, but fossil evidence is, it seems to me, in favour of the cœnenchyme in the Madreporidæ, &c., being a distended form of wall from the first; there is no fossil evidence to show that it may have developed as an extended visceral chamber.

It is worth repeating here the familiar fact that costæ are present in these types which have *no necessary relation to the septa of the peristome.* Moreover, the discontinuity of the septa and costæ (even when placed opposite each other) is one of the most characteristic features of cœnenchymes in the "perforates." Generally speaking, it may be said that the distribution of costæ on cœnenchyme depends on the particular position of the folds of cœnosarcal flesh around the polyps, and differs considerably in different members of one and the same colony. Except at the innermost wall-rim these folds are not influenced by the polypal system of septa and mesenterial loculi; thus any multiple relation between the number of septa and costæ is usually lost at no very great distance from the polypal rim. It will be remembered that the costæ marking the epitheca of *Madreporaria Rugosa* are likewise independent of the septa in their position and number, and apparently depended on the particular position of the folds, varying at different periods of growth. These relations are quite distinct from the strict symmetry of number and position which controls the septo-costæ characteristic of typical "edge-zones."

* The actual incorporation of dissepimental tissue in the wall has also been made out by Dr. Reis in several simple corals of Cretaceous and old-Tertiary age, although he did not apply his observation to any further cases of homology. I may quote the genus *Hydrophyllia*. (Reis, *citat.* p. 293.)

There are, however, other non-perforate cœnenchymatous types, such as *Lophohelia*, in which an edge-zone of varying length has been proved to be present. (*Vide* FOWLER, "Madreporaria," 'Q.J.M.S.,' cix., pp. 4 and 7.)

Observation of several allied fossil types shows that in most of the Oculinidæ a septo-costate skeletal area, corresponding presumably to an edge-zone of polypal tissue, lengthened itself out in proportion as the septa, and the inner calyx generally, outran the periphery in rapidity of growth. At the same time, the influence of the mesenterial loculi (and of course the septal symmetry) would become extended more and more to the folds of the body-wall enclosing theca and epitheca. In these cases I consider the history of the "edge-zone" not one of retrogression but of progression, signalizing the higher individuality and specialization of the polypal units within a colony which was originally solely coenenchymate.

The best developed "edge-zones" are, however, beyond doubt found in the Astræinæ and Fungidæ, and are inherited from the broad outer disc of Cyathophyllids with its septal continuations and dissepiments. In the living Astræids and Fungids all the corallites of a colony are practically united by their calicinal edge-zones.

To sum up the views expressed above, I give a general tabular form of the skeletal relations in some of the leading family types. I place, as the heading of the three parallel columns, terms which were first given by German zoologists to "plates" of the soft tissue clothing different parts of the periphery of the polyp, beside each name I give the skeletal tissues, which, in my opinion, represent these particular "plates" of the soft body-wall distinguished in zoology.

	"Innenplatte."	"Randplatte."	"Aussenplatte."
	Pseudotheca.	Septo-costate area.	True theca ± coenenchyme; epitheca.
Cyathophyllidæ (Palæozoic)	Often present as an *inner* septal thickening at the periphery of the so-called "tabulate area" forming a pseudotheca within the calyx	Edge-zone well represented in the fossil skeleton by the presence of a broad outer disc with septa and dissepiments	Outer wall of septal and thecal thickening present as the lining of a concentric rugose usually well-developed epitheca
Astræinæ; Fungidæ (*pro parte*); recent types	Always present as a septal thickening and always within the calyx	Edge-zone *typically present*, as an outer disc — represented in the skeleton by both radial and basal elements	Outer wall very seldom present; the epitheca retrograde on individual polyps; limited as a rule to the periphery of colonies and often little developed beyond embryonic stages
Zaphrentidæ (Palæozoic)	Often present as a septal thickening against the theca—no inner pseudotheca	Edge-zone seldom indicated in the fossil skeleton—a narrow disc of dissepiments is present in some genera, but nearly, or wholly identified with the wall	Strong thecal lining and epitheca present; may be drawn out as spines, muro-costæ, rootlets, &c.
Turbinolidæ (*pro parte*); recent types	Septal thickening occurs as part of the theca, never *within* the calyx. No inner pseudotheca	Edge-zone *absent or very narrow* — the corresponding skeletal parts are embodied in wall-thickening	Strong theca always present with muro-costæ in contact with the epitheca as far up as the latter develops, above that, free. Theca and epitheca may bear various protective outgrowths as in Zaphrentidæ. In colonial allies (Amphiastræidæ) the epitheca ascends round each corallite
M. Perforata E.H. excl. Eupsammidæ (*pro parte*); recent types	,, ,,	,, ,,	Theca always present. The cœnenchyme is a grooved or channelled structure incorporating mural and muro-costal elements and clothed with epithecal tissue

Bourne (Anat. of *Mussa* and *Euphyllia*, *loc. cit.*, p. 48) has stated his agreement with Koch regarding the *epithecal* nature of the "wall" of *Flabellum* from anatomical grounds. I limit, however, the actual epithecal tissue to the somewhat organic, external coat of coral. The chief fact is that the *wall* of *Flabellum* comprising septal, muro-costal, and mural calcification, is solid and is *everywhere in contact* with this epithecal coat.

So far as I know it has not hitherto been suggested that a simple solid-walled Turbinolid, such as *Flabellum, without* an edge-zone, gives the clue to the absence of the edge-zone in the *M. perforata* (*excl.* Eups.). The walls of the *M. perforata, excl.* Eups., it is true are channelled, and the wall pores open into vesicular and muro-costal coenenchyme, but the structural homologies of the parts are perfect, and the essential relations of the epitheca. This would perhaps not have occurred to me if I had not been first struck by the *identity*, in groups apparently widely apart, of the *microscopic structure of the septa and of the wall* as well as the similarity in the internal plan of the calyx. For example, the columella of *Turbinaria mesenterinæ* is entirely unparalleled in Astræinæ and Fungidæ, yet it has plenty of likeness to that of various Turbinolid genera. Then take the basal structures, in several cœnenchymatous allies of the old "perforate" group, *e.g.*, Oculinids, Pocilloporids, etc.—they compare very closely with Turbinolid endothecal deposit. The pre-eminence again of one long septum or the occurrence of a lamellar (septal) columella is also common in all these groups.

4. The Tabulate Area of Palæozoic Madreporaria gave place to the Columellar Area of Neozoic and Recent Types.

The most striking difference between Palæozoic and recent Madreporaria is associated neither with septa nor theca, but with the basal structures. In Palæozoic forms, at the highest period of their development in Silurian and Devonian time, the basal structures were smooth throughout the calyx, in other words they were tabulate or dissepimental. Yet a certain exception must be made in the case of many Cyathophylloid genera which showed a tendency to the formation of an irregular columellar structure in the central depression of the calyx. The explanation of this tendency is very simple. The typical Cyathophylloid calyx is shallow, and the septa mere narrow "ribs" marked out on the basal structures, very different from the prominent exsert septa of the typical Astræid. When we think how insignificant in height the septal invagination of the Cyathophylloid must have been and remained, we can readily understand that at its inner end it gave rise to no confused wrinklings, but rather smoothed itself out as it bent from the dissepimental into the tabulate area of the calyx. In genera, however, where there was a relatively more rapid growth at the outer than at the inner end of the septum, the septal folds tended necessarily during each successive growth-period to be higher, that is deeper, at that outer part. This was the first beginning of the changes which led to the *exsert* Astræid *septum*, with its well-marked "area of divergence" of septal and costal trabeculæ, and its tendency to thicken laterally and form a pseudo-theca.

In accordance with the sloping downwards of the septal fold from the heightened septum, another change was induced in the Cyathophylloid form, namely, the gradual usurpation of the tabulate central area by the now deeper, longer, septal folds, and the

transformation of that area into a *columellar* area. There is practically no difference between the confused meshwork of septal ends in the centre of the calyx of certain Cyathophylloid genera and the so-called "spongiose columella" of an Astræid genus such as *Rhabdophyllia*. Yet this change, which brought with it the disappearance of tabulæ, was being accomplished by Cyathophylloids of Devonian age, and the Clisiophyllids of carboniferous time show marked change in the same direction.

The Zaphrentids, on the other hand, held more persistently to their tabulate base, as might have been expected from the narrowness or entire absence of a dissepimental zone, and the more turbinate shape of the calyx.

It is easy to trace how some of the modifications undergone by the "Zaphrentid" tabulæ went directly to the building up of a columella. The convexly-arched shape of the tabulæ in the genus *Zaphrentis* is indicative even in that genus of a tendency of the aboral body-wall to be pouched upwards. Still more positive evidence of the modification of the tabulæ to form a complicated columella is given by the Clisiophyllids. The description given by WAAGEN of the columella in 'Lonsdaleia Indica' is particularly suggestive. He writes: "It is remarkable that in longitudinal sections there can barely be any tabulæ observed outside of the columella." ('Salt Range Fossils,' p. 898, "Cœlenterata in Productus-Limestone.")

Not infrequently the tabulæ seem to have been laid down so closely that they formed an almost solid calcareous deposit. The Cyathaxonidæ, E.H., is a family including Palæozoic genera and one Triassic genus; it is of special interest in the study of basal structures. The essential feature is a prominent columella; a second feature which may be regarded as correlated, is the scanty development or absence of basal structures. *Lindströmia*, the oldest of the genera (Ordov. to Carb.), has well-developed septa *reaching to the columella*; the septa are smooth on their surfaces and at their edges; they have "pinnate" arrangement with regard to four principal septa, and a slight fossula is present. The chief fact which at present calls our attention is that "stereoplasm" fills the lower part of the visceral chamber, while in the upper part dissepiments or tabulæ are scantily developed (*cf.* NICHOLSON, 'Manual,' *loc. cit.*, p. 298). FRECH says the endothecal deposit is sometimes entirely stereoplasmic. ('Trias. Korallen Paleont.,' *loc. cit.*, p. 81.) In certain recent Oculinids in *Seriatopora*, and in a few Turbinolids (all of which I hold to be related to the ancient Zaphrentidæ), the basal structures are at times individual laminæ, *i.e.*, tabulæ or thin dissepiments, and in the same coral may take the form of solid deposit, so-called "stereoplasm." We need not then place much importance on the difference in the basal structures of *Lindströmia*, and of the genus of the Cyathaxonidæ next to it in age—*Cyathaxonia*. The latter has similar septal and columellar features, but no tabulæ or dissepiments.

A Triassic genus, *Gigantostylis*, has been referred to this family by FRECH (*loc. cit.*, pp. 82, 83); in it the septa are rudimentary; a very slight deposit of stereoplasm round the base of the columella is present, as in *Cyathaxonia*, and the columella is

extremely large. Its structure is finely laminated, the laminæ becoming more and more convexly arched from below upwards. This structure is worthy of note, since it marks a difference between these Cyathaxonidæ and certain other genera, which appear in most respects allied. Such a genus is the Silurian *Duncanella* (*cf.* NICHOLSON'S figure, *loc. cit.*, p. 267), which ROEMER had included in the Cyathaxonidæ. It has been described as having no columella by some authors, by others as having a pseudocolumella. To judge from NICHOLSON'S longitudinal section, it has a distinct fascicular columella made up of a number of pali. The septa, besides, agree in structure with those of most Turbinolidæ, but the same structural lines are not continued into the columella. I take *Duncanella* to be an ancestral type of many genera included in the Caryophyllaceæ, E.H. No fossula is present in it, and it has radial symmetry.

The common feature in all these forms is the entire usurpation of the axial area, which is tabulate in the related family Zaphrentidæ, by a large columella. The Palæozoic forms have septa reaching the columella, the Triassic form has a circular trench around the columella not invaded by any skeletal structure. At the same time it has retained only indications of the tetrameral symmetry possessed by *Lindströmia* and *Cyathaxonia*, and *has no fossula.*

I may here remark that the Jurassic genus *Lingulosmilia* (KOBY), to which FRECH refers, has less connection with this family than with some other Jurassic genera, ex. *Amphiastræa.*

Opinions may differ regarding the best systematic treatment of such a family as the Cyathaxonidæ. FRECH has placed *Gigantostylis* as an independent sub-family of the Cyathaxonidæ under the *Madreporaria rugosa*, E.H. (= Pterocorallia, FRECH). NICHOLSON, again, has removed *Cyathaxonia* from *M. rugosa* to the Turbinolidæ, but has left *Lindströmia*, at any rate, provisionally, under *M. rugosa*, in the family Zaphrentidæ. He gives as his main reason the pinnate arrangement of the septa, in which it "agrees with the typical Rugosa." The tetrameral symmetry of *Cyathaxonia* and the presence of a fossula are not regarded by NICHOLSON as a sufficient basis for separating it from the Turbinolidæ.

Speaking generally, I incline to Professor NICHOLSON'S position in the matter. As regards *Lindströmia*, however, I would make an exception, where the characters of the corallum so entirely agree with later forms, and the pinnate arrangement is still recalled by tetrameral symmetry. I would include it among the Turbinolidæ. It is otherwise with a genus like *Zaphrentis*, between which and any Mesozoic genus there are no links preserved to us, of *simple* corals, showing intermediate stages between the loss of the pinnate development of the septa and the gradual advance towards radial arrangement within the polyp. Such a genus must be held apart from Mesozoic types (*cf.* "Turbinolidæ," p. 332).

The Cyathaxonidæ therefore and the genus *Duncanella* give indications which cannot be mistaken of the significance of the elaborate paliform or fasciculate Colu-

mella which is seen in so many recent Turbinolidæ, and is correlated in that family with the almost entire absence of "endothecal" basal structures. I do not mean by this that all Turbinolids with such columellas are descended from Cyathaxonidæ; simply that their ancestry may be directly traced to the *Zaphrentoidea*, and especially to types having a large axial area free from septal structures. The *flat* central body-cavity, supported on the *tabulate* base of some primitive Zaphrentid genera, gave place to the much *deeper* body-cavity—suspended over a *central* pillar, and often twined round it—presented by more advanced descendants among the Turbinolidæ. I look upon the Turbinolid columella then, as in many cases, a modified "*basal*" (tabulate) structure.

On the other hand, a number of Turbinolids have a *lamellar* columella. Those find antetypes in such carboniferous Zaphrentoid genera as *Lophophyllum*, in which the *counter-septum* is prolonged far into the middle of the calyx. Sometimes the principal septum was thus prolonged in Palæozoic genera. In either case the fundamental point is, that the columella of certain recent Turbinolids can be traced with security to a *radial, i.e.*, septal structure modified from primitive Palæozoic types. Amongst these Turbinolids I include now several genera previously classified by EDWARDS and HAIME amongst the Eusmilinæ (fam., Astræidæ, E.H.).

Where it was a septum which became marked out as a columellar support, the axial line of symmetry remains longer evident, and is indeed still present in many Turbinolid genera. An appearance of bi-lateral symmetry is thereby frequently shown by the skeleton, whether the soft parts partake in it or not. I may also mention the cristiform "main septum" in species of *Enallohelia*, *Turbinaria*, *Madrepora*, *Pocillopora*, etc., which has assumed a collumellar function.

It may seem a small thing in itself to follow out the evolutionary history, so to speak, in the columella in Madreporaria. And to bring together evidence of its having taken origin as a modification in one case of tabulæ, in another of a principal septum, in another of a meshwork of septal ends and basal structures. In all cases we read a lesson with which zoologists have already made us familiar in many other chapters of animal life, viz., the economy practised in the workshop of evolution, how old structures become adapted to perform new functions. Where no adaptation takes place the tendency is for these old structures to retrograde or vanish. The fertility of resource in the adaptation is shown by the fact that both radial and basal structures could be transformed into a central columella. The new requirement on the part of the coral polyp was apparently always one and the same, and it was attained by the simple means of a central support in the visceral chamber. Before we consider what the new requirement was, it is important to note that the different skeletal modifications to produce a columella must have been in every case associated with a change of shape in the skeletal support of the polyp's visceral chamber. The latter, from being flat, or saucer shaped, assumed cup-like proportions, but was fitted over a central stalk, leaving thus a deepened circular trench in the middle of the chamber.

The examination of living polyps shows well enough the use of this trench around the columella, and how well this particular shape suits the looping-up of the mesenteries and the protection of the gonads. It is, therefore, no very far-fetched conclusion that the gradual appearance of the columella in fossil types of Madreporaria marked always a distinct step in the polyp's evolution, a step which was associated with the support and efficiency of the mesenteries and their filaments.

Passing now to Mesozoic and recent types, which have probable affinity with the Palæozoic Zaphrentoidea, I may mention certain "Eusmilinid" genera, more especially the *Stylina* group (*cf. Stylina, Pleurostylina, Cyathophora, Coccophyllum*, etc.), and the Trochosmiliaceæ, E.H. (*cf. Trochosmilia, Cœlosmilia, Stephanosmilia; Pleurosmilia, Axosmilia, Conosmilia*, etc.). In those examples some show a pillar-like columella indicating the invagination into an elongated pouch-like form of the aboral body-wall; others have no invagination and form either dissepiments or tabulæ; others combine a pillar-like columella with basal dissepiments; still others have a "lamellar" columella formed in a fold continuous with one, two, or more septal folds, or in the same radial direction, but deeply notched and giving rise to "pali"; still others show a winding round of the invaginated pouch or pouches during their upward growth, giving rise to a columella like that of *Conosmilia*; dissepiments may be richly or sparsely developed. *Caryophyllia, Turbinolia, Flabellum*, and many genera belonging to the Turbinolidæ show similar varieties of the columella; the aboral body-wall is, however, in the Turbinolids almost entirely dependent on the columella as a *basal* support in the upper part of the calyx, having few or no dissepiments or tabulæ. The calyces of Madreporidæ resemble Turbinolids; on the other hand, the Pocilloporidæ possess invariably tabulæ as basal support.

Although those recent types show an extraordinary variety in the particular character of their basal skeletal deposit, they agree on the whole *in keeping a central area more or less distinct from the radiating septa*, whether that area presents a lamellar, pillar-like, or coiling columella, or none at all. In the latter case, other skeletal characters always suffice to point out the relationship of the genus with more typical columellate forms.

On the other hand the Astræinæ and Fungidæ carry the radial structures into complete coalescence in the central area, and the columella has often been in consequence distinguished in typical genera belonging to those groups as a "pseudo-columella."

While I place no value on the presence or absence of a columella in nearly-related genera such as *Stylina* and *Cryptocœnia*, there is a broader systematic aspect of the columella when it is studied in distinct generic types. It is well known how much wider the generic title of Palæozoic forms is in its systematic significance than that of Neozoic and Recent. If a classificatory system were to be uniformly carried out, nearly all the Jurassic genera at present classified under Trochosmiliaceæ, E.H.,

might be included under a single generic title *Trochosmilia*, and the single genus would have about an equal rank with that accepted for any one Palæozoic genus such as *Zaphrentis*. This one example is enough to show that only when we gather together the closely-allied Neozoic genera into broader groups can we hope to trace the main lines of descent among Madreporarian corals which may be founded on outstanding features of such groups. Looked at in this light, I think it of importance systematically to note the sometimes tabulate, sometimes dissepimental nature of the basal structures in the Mesozoic and Tertiary group of Stylinaceæ, the frequent sparseness of dissepiments in the Trochosmiliaceæ E.H., also mainly a Mesozoic and Tertiary group, there being few Recent genera; again, the independence and varied form of the columella in those two groups when it is present. All those features show (1) that the Eusmilinæ, E.H., are, in the main, intermediate between Turbinolidæ and Astræinæ; (2) that their ancestry is to be sought, not in typical Cyathophylloidea, but rather in Palæozoic genera, intermediate between Cyathophylloidea and Zaphrentoidea. NICHOLSON, while distinguishing those two Palæozoic types, carefully shows how they merge in one another; *and so do their descendants*.

Summarizing (*cf.* also p. 318), the above considerations, I may say that I look upon the columella and pali of Turbinolids as the homologue of the tabulate area of Zaphrentids, the septa representing the originally short septa of Zaphrentids in the limited dissepimental area. Correlated with their shortness, is, I believe, the fact that they never developed in the mature condition a well-marked area of divergence, and that their axes of calcification are usually very obliquely placed, or point almost horizontally inwards to the central area.

Further, the "sunken calicles" characteristic of the cœnenchymate allies of the Turbinolidæ are also correlated with the smaller prominence of the septa and the direction of the axes of calcification. The primitive shape of the calyx of *Zaphrentis* and its Palæozoic relatives have been the main cause of the immense functional activity demanded of the mural and *epithecal rim* in their descendants (*vide antea*, p. 263). And it will be at once seen that similarly the broad dissepimental disc of *Cyathophyllum* and its Palæozoic allies has been perpetuated in the endotheca (whether dissepimental or synapticular) of the Astræinæ and Fungidæ, as well as in the importance of the edge-zone (Randplatte) in these same groups.

5. *Precocity of the Radial Symmetry in Cyathophylloids.*

The broad dissepimental zone in the Cyathophylloid calyx indicates that the polyp had a broadly expanded peristomal and extrathecal disc. This feature cannot have been other than favourable both for vegetative and sexual reproduction. In the vegetative form of budding, great rapidity could be attained, and a bunch of peristomal and extrathecal buds developed simultaneously. We may, indeed, trace back all the

wonderful variety in colonial "fissiparous" and "budding" Astræids to the primitive, expanded, oral surface of their Palæozoic ancestors.

Judging from the habits of many recent corals, the same surface probably served at certain seasons to give attachment to sexually-produced polyps during the early stages of their development, and was thus functional as a nursing organ. Both the ease with which vegetative budding was accomplished, and the protection afforded to young polyps must have encouraged the *sessile, colonial* habit, so characteristic of the descendants of Cyathophylloids.

Be this as it may, it will be readily granted that the broad disc of the Cyathophylloids was favourable for budding. It gave also greater strength to the skeleton, since the septa were longer and could be more highly differentiated. Correlatively also the mesenteries may be supposed to have had fuller development.

An interesting observation was made by FOWLER on the mesenteries in three living genera which depart little from the typical Palæozoic coral in their *calycinal* features: the genera *Seriatopora*, *Pocillopora*, and *Madrepora*. He found that of the twelve mesenteries, six were reproductive or strongly developed in *Madrepora*, which were rudimentary in *Seriatopora*. Of the remaining six in *Seriatopora*, two were reproductive-bearing, the others were well-developed but not reproductive. In *Pocillopora*, the same two as in *Seriatopora* were long and reproductive-bearing, in the other four a "mesenterial filament might also be detected" (FOWLER, "Madreporaria," Q.J.M.S., 1887, p. 13). FOWLER remarks, in suggesting an explanation, "the tendency observed in both *Seriatopora* and *M. Durvillei* towards the exclusive assumption of function on the part of six mesenteries and towards a correlated retrogression (?) on the part of the other six, has not attained to such a pitch in *Pocillop.* (and *M. aspera*) as in the other two forms."

Exactly that point in this explanation which the author himself marks with interrogation, seems to me in the highest degree doubtful. The skeleton of many Palæozoic forms shows only one fossula, others have two fossulæ opposite one another, and the natural inference is that each of these fossulæ were the pits for one large mesenterial filament. *Seriatopora* bears out faithfully the primitive condition of an opposite pair of fossulæ. In each of the fossula one large mesenterial filament with gonad is present. We have, therefore, good reason to believe that a similar pair of reproductive mesenteries were developed in bi-fossular ancestral types. Why then retrogression? Rather we may read the observation more simply and look upon *Seriatopora* as a more primitive genus than *Madrepora* and *Pocillopora*.

When this primitive condition is departed from, it is only natural that considerable variation should be shown with regard to the particular mesenteries which became specialized as reproductive or filament-bearing organs. *Pocillopora* adheres so far to the tradition, *Madrepora* has become utterly inconstant. At least one deduction may be drawn with fair safety, namely, that each of the twelve primitive mesenteries were *potential* gonad and filament-bearers.

If now we assume that any Palæozoic species got as far as *Pocillopora* in rendering a certain number of the mesenteries the bearers of small filaments, external conditions being favourable, they might act as valuable *aids* to reproduction and make themselves persistent in the type. This accomplished, the change from bilateral to radial symmetry may be said to have been initiated in the species. Inasmuch as the change helped towards perpetuation of the type, it may be looked upon as an *evolutionary change re-acting on the whole organization of the polyp*, and leading to better equipment of parts, muscular and digestive as well as reproductive.

For fuller development of the inner ends of the mesenteries demanded corresponding accommodation within the polyp and a certain modification of the form previously assumed by the aboral body-wall in the central part of the polyp. This might take place in various ways, such as the formation of *several* instead of only one or two basal "pits" (this I have observed in a Jurassic genus), the continuation of the septal invaginations into the centre of the calyx and a general *deepening of the interseptal loculi* (Astræids, Fungids, etc.), the formation of a styliform columella in the middle of the calycinal base, leaving a circular trench between it and the septa—*the said circular trench being homologous with a ring of pits or fossulæ* (Stylinidæ, *Cyathaxonia*, *Turbinolia*, etc.).

Whereas many Palæozoic coral species belonging to *Cyathophyllum*, *Acervularia*, *Phillipsastræa*, and other genera of the Cyathophylloidea were precocious in the matter of radial symmetry and its correlated features, there was considerable tardiness on the part of the Zaphrentoid genera. Only this can explain the fact *that in the Jurassic coral fauna of Europe a very large number of bilaterally symmetrical genera are present* whose calycinal structures have the characteristic features, macroscopic and microscopic, of *Zaphrentis* and allied genera. The main advance shown by these Jurassic genera is the loss of pinnate development of the septa, although the septa strictly retain in most cases a definite arrangement with regard to "main" and "alar" septa. A fossula is sometimes present, more often absent. Again colonial habit has largely been gained, each corallite, however, having a distinct rugose epitheca of its own which invaginates inward and upwards to give rise to septal structures. Enough has been said to show how essentially Palæozoic such genera seem, a number of them having been described by Koby* and grouped as members of the *Madreporaria rugosa*. I have had very interesting specimens amongst the Tithonian Stramberg fauna, and have had occasion to enter fully into morphological features in that paper. I have grouped them and the allied genera belonging to other geological ages as a new family, the Amphiastræidæ. In all the genera in question the septa have *retained apparently unaltered the essential septal structure of ancestral types among Zaphrentoid genera.*

* Koby, "Polypiers Jurassiques de la Suisse," 1880–89, Geneva 'Mém. de la Soc. Pal. Suisse,' vols. 7–16, *loc. cit.*, pp. 419–437 and pp. 571–2.

6. *The Change from Bilateral to Radial Symmetry was an Adaptation to the increase in number of the "Reproductive" Mesenteries.*

In the foregoing discussion I have assumed that for any reason whatever an additional number of the mesenteries became filament-bearing in different Palæozoic species, and have indicated how such a change would bring with it correlated changes in the invaginations of the aboral body-wall, and, therefore, in the subsequent symmetry shown by the calicinal skeleton.

The assumption is thoroughly justified by palæontology. It is admitted that the so-called typical "Rugose" coral has one, two, three, or four fossulæ, seldom so many as four, and usually one or two; farther, that these fossulæ represent specialized "reproductive" or gonad-bearing mesenteries.

On the other hand, many of the Recent Astræids have all their mesenteries thus specialized, the filaments and thickened reproductive part being suspended into the hollow of the visceral cavity. This I hold to be the main direction of evolution in the group of Madreporaria; all other changes—respecting bilateral or radial symmetry; tabulæ, dissepiments, synapticulæ; one wall or two walls; cœnenchyme or no cœnenchyme;—I look upon as subsidiary. Such modifications may or may not take place; at the most they are correlative features accompanying a leading change in the increase in number and higher specialization of the reproductive mesenteries.

It is useful to compare in a general way the form of the skeleton of Recent types with that of Palæozoic antetypes.

The Recent Astræid has a much deeper calyx than the Palæozoic Cyathophylloid; its septa are stronger, higher, and usually more firmly built. The ends are as a rule firmly interlocked in the axial columellar part of the calyx. We are now perfectly aware of the pleated *muscular* nature of the mesenteries, and their government of the peristomal disc; and we may take it that the greater strength and prominence of the septa in Astræids is evidence of higher differentiation of the mesenteries in respect of all their functions than was the case in the Cyathophylloids. Moreover the Astræid septum is much more completely corrugated, more ridged and furrowed, and more granulate than the septum of a typical Cyathophylloid. And one cannot doubt that the complication in the septal skeleton was called forth by a greater need for support in proportion as the mesenteries became more muscular and corrugated. The interlocking of the septal ends centrally is correlated with the continuation of the mesenterial invaginations from periphery to centre. The central columella of Astræids afford the mesenteries a means of firm attachment, one might almost say of improved leverage.

Again, as all the mesenteries of the first, second, and usually third cycles are long, they split up the body-space into a great number of loculi, and these mesenterial chambers are at once seen to be of advantage to the polyp for purposes of digestion and nutrition.

The *Zaphrentoidea* retained longer than the *Cyathophylloidea* their comparatively free axial area and shallow calyces (*cf. antea*, p. 271), and we find that amongst the groups, which I regard as their descendants, various methods have been hit upon for increasing the digestive space.* The usual method was the adaptation by means of cœnosarc to a colony-building existence, and the correlated development of the cœnenchymal canals or grooves between polyps. In the canals digestion and the circulation of the nutritive-fluid went on ; moreover, during the periods of vegetative increase, the buds sprang from these extra-polypal canals, seldom from the polyp. The canaliculate cœnosarc of cœnenchymatous colonies is, properly speaking, a modification of the loose, often wrinkled part of the polypal wall at the rim of the oral disc.

The development of cœnenchyme seems to have been invariably correlated with a very small size of the calyces and fewness of the mesenterial chambers, for example : *Seriatopora, Madrepora, Turbinaria.* In all these, the digestion and nutrition of the colony is mostly carried on outside the actual body-cavities of the polyps, in the canals of a spreading cœnosarc. Now, I must make a companion statement to that made above, p. 275, about the Jurassic Amphiastræidæ. *The great majority of living cœnenchymatous Madreporaria have calyces whose skeletal features have retained the primitive structural characters of Zaphrentids.*

The only exception to this occurs amongst the Eupsammidæ, a family whose calicinal features indicate their ancestral line to be *Cyathophylloid*, although certain genera occur which have cœnenchymatous colonies. The cœnosarc in cœnenchymatous Eupsammids has the same significance for the colony as has just been indicated.

Taking *Dendrophyllia* as a cœnenchymatous Eupsammid type, an active nutritive and digestive canalicular system is there directed along the main branch of the corallum. The canals run parallel with the upward growth of the corallum, and are connected by branch canals with the individual polyps. The polyps carry on the protective and predatory duties of the colony as well as the elaboration of the reproductive cells. While the cœnosarcal canals are a material aid to the rapid digestion and nutrition, and their ectoderm is actively engaged in depositing skeletal layers. These canals are a higher form of stolonal growths.

One may almost distinguish various grades among Madreporarian colonies. The possibility of developing rootlets may be accepted as a character of the class Madreporaria. To this inherent feature the first or simplest form of colony-building is due, viz :—

I.—*The Stolonal*, or lowest grade of a Madreporarian colony, in which stolons grow

* One of the most remarkable is *Euphyllia*, a fissiparous colony in which the stomodæum is continued downwards into a number of convoluted canals lined, like the stomodæum, with ectoderm. The ectoderm cells here perform the function of digestion otherwise exerted by the endoderm of the visceral chamber. BOURNE, who describes this, attributes the modification chiefly to the unusual vegetable-living habit of the polyp.

out from the body-wall of the polyp either near the base, as *creeping stolons*, or from the sides as *lateral stolons*. This grade of colony occurs occasionally in all recent Madreporarian families, but was particularly common in the Palæozoic types—more especially among Zaphrentoids and so-called "Tabulates."

II.—*The Cœnosarcal* grade where "stolons" grow out from the body-wall of the polyp *at the upper edge or lip* of the polypal cup. (*a.*) If the stolonal apertures are left open during farther upward growth, the cœnosarcal stolons form a meshwork of canals between the polyps of a colony and the "cœnenchyme" or skeletal deposit which they lay down is correspondingly *porous*. (*b.*) If the stolonal apertures are closed as successive periods of upward growth ensue, the cœnosarcal stolons run only on the surface of the colony and the "cœnenchyme" which they deposit is practically *compact*.

Those two varieties are of equal dignity, they are the expression of different adaptation to different external circumstances.

This grade of colony is permanent in the families of the Madreporidæ and Pocilloporidæ (*cf.* below pp. 336–338). It is one which is correlated with small, simply-built polyps *whose individuality is always retained but is little advanced*. The bilateral symmetry of the simple Zaphrentid corallum, the smooth character of the septa, the horizontal septal spines, and broad tabulate base, are features of such constant recurrence among the genera of the families Madreporidæ and Pocilloporidæ that their close relationship with the Zaphrentids cannot be doubted. At the same time the ancestral types of these two cœnenchymatous families may have branched off from the main stem of the Zaphrentoidea at a very early period in the phylogeny of Madreporaria.

The cœnenchymatous colony is almost a mimicry of dimorphism. The tentacular mouths and polypal cavities have definite functions—to capture the booty and fertilize the reproductive cells, while the cœnosarc is an extensive gastral organ. Looked at in this light, it is no great step from a recent Madreporid to a Palæozoic Heliolites and other genera of the so-called Tabulates. But I have not specially studied this aspect of the question. Be that as it may, the mimic dimorphism which prevails in these families stamps them at once as lower in the scale of colony-building animals, than are the Madreporarian colonies, in which each polyp carries on all the essential vital functions of its existence.

III.—The "*edge-zone*" grade in which the original oral discs of the individual polyps are well developed and form an area of greater or less extent between the actual tentacular rings of the polypal mouths. The remote angles of the edge-zones coalesce with one another. The polyps in such a colony are bound to advance in evolutionary features more than in the case of the polyps of "cœnosarcal" grade, since each individual polyp is a complete organism carrying on all the vital functions within itself. It is in such colonies that the number of mesenteries is increased, the muscles more highly differentiated and *radial symmetry* attained permanently.

This grade was reached very early by Cyathophylloids, more slowly by Zaphrentoids. It is a grade which was inherited in time by nearly all descendants of Palæozoic Cyathophylloids, the Astræinæ, and the Fungidæ. The early Eupsammidæ were mostly simple corals, they became only very slowly adapted to colony building habits and show at present every variety in their modes of adaptation.

The direct Mesozoic colony-building descendants of the Zaphrentoids are Amphiastræidæ (see p. 275). In Jurassic forms an edge-zone might be temporarily or permanently formed, but, as might be expected, it was very limited, and radial symmetry was not attained.

The same is in smaller measure true of the Oculinidæ, a large family of undoubted Zaphrentoid descent, in which the polyps are either radially or bilaterally symmetrical, and the colonies *waver between the cœnosarcal grade and the edge-zone grade.* They usually present an intermediate condition. There is in most Oculinids an overlapping edge-zone into which mesenteries are continued, but it passes into a common cœnosarc without mesenterial loculi.

It would demand too much space to enter into a full discussion of bilateral symmetry, as shown in recent Madreporaria, and I hope to give the subject special attention in a later paper. I may, however, indicate some other considerations in addition to those already mentioned.

7. *The old-fashioned Character of the Recent Genus, Seriatopora.**

The genus Seriatopora, which has amongst recent Madreporaria the smallest known number of reproductive mesenteries, agrees in skeletal respects with the bilateral ancestral type.

Two reproductive mesenteries are placed in *Seriatopora* on opposite sides of the polyp, symmetrically with regard to the mid-line or long axis of the elliptical calyx (see below, diagram E, p. 290). The two septa on either side of a reproductive mesentery are rudimentary. In all, twelve septa are present, and their relations at the porous theca are similar with those described under Turbinaria (see above, p. 207). The basal skeletal tissue is usually a compact calcareous deposit like that common in Turbinolidæ, but in the nearly related *Pocillopora* the calyx is *shallower*, and the basal tissue is in the form of *tabulæ*. The latter genus has also twelve mesenteries; two oppositely placed reproductive mesenteries are well developed, four other mesenteries give occasional indications of mesenterial filaments. The septa of *Pocillopora* though twelve in number are short spines jutting into the calyx, only one being prominent and long and forming an axial line in the calyx.

Madrepora has usually *six* mesenterial filaments, and six non-reproductive mesenteries. Septal spines are again present, with an axial line formed by one septum or the coalescence of two. The spines are sometimes more numerous than twelve; again

* Moseley, "Notes on *Seriatopora, Pocillopora*," etc., 'Quart. Journ. Micr. Sc.,' vol. 22. Fowler, "Madreporaria," 'Quart. Journ. Micr. Sc.,' vol. 27, August 1887.

in some species six of them are more prominent great irregularity prevails, but as is well known, bilateral symmetry of the calyx is fairly constant. The identity in their minute structure with the septal spines of the Silurian genus *Pholidophyllum* has already been pointed out. In all those cases the axis of calcification is directed vertically inwards or almost so, and wall and septa repeat entirely characteristic Palæozoic types.

The important feature in all these genera is that the bilateral symmetry is a distinct advantage still to the polyp, and on this account has apparently been retained. If we look upon the opposite "fossulæ" at the base of the body-chamber in *Seriatopora* as alar, we have in the case of the others still the same alar fossulæ, although a larger number of mesenterial filaments are accommodated in them. The midline of division is simply a strengthening calcareous rod sufficient for the small size of the calyx. On the other hand the calyx of *Turbinaria* is much larger, the same median rod is present, but it is surrounded by pali, and is actually grooved so as to permit of an uninterrupted fossular ring. Correlatively the number of reproductive mesenteries in *Turbinaria* is much greater than in *Madrepora*, FOWLER gives it from 17 to 22.

8. *The Fossula and the Pinnate Arrangement of the Septa.*

NICHOLSON points out (*loc. cit.*, p. 281) the frequency in certain Palæozoic genera of the elongation either of the "cardinal" (Hauptseptum) or "counter" septum (Gegenseptum) into the mid-line of the calyx in columellar fashion. The elongation was correlated with the rudimentary condition of the opposite "fossular" septum; in short the needed skeletal support was supplied by a septal or leaf-like invagination of the part of the aboral body-wall resting on the central tabulate area. And the invagination ceased at the special "pit" or "fossula" of the aboral body-wall left for the reception of the reproductive part of the specialized mesentery.

The position of the fossula, if single, might be in the dorsal or ventral portion of the dorso-ventral axis, or at one side in the transverse axis of the bisymmetric Palæozoic calyx. If paired, the pairs corresponded with *one* or *both* axes,—the dorso-ventral axis (= "sagittal axis" of HERTWIG) and the axis at right angles to it. If two pairs of fossulæ occurred, it can easily be realized that the "pits" in the skeletal floor of the calyx might become practically coalescent and form a hollow ring or trench. A case is described of a half-moon trench where two "alar" pits and one "cardinal" pit coalesced ("*Menophyllum*," vide NICHOLSON *loc. cit.*, p. 295).

The carboniferous genus *Menophyllum* may be compared, in the peculiar shape thus attained, with one or two genera which I have had occasion to examine in the Up. Jurassic, Tithonian fauna of Stramberg. The Jurassic genera (*ex. Amphiastræa*) show frequently a well-marked cardinal fossula with short septum. Young stages of the calyx show four septa, precisely arranged as in *Tetracoralla*. Then a pair

of long septa develop on either side of the short main septum, and together with the long "alar" septa and somewhat shorter "counter" septum, make five long septa and one rudimentary septum in that stage. In slightly more developed calyces another pair of long septa appear between the "alar" septa and those on either side of the cardinal septum—eight septa are thus present and remain the typical number of the first cycle in those genera, the whole calyx being entirely of Palæozoic character (*cf.* diagram, p. 291, "paired insertion of septa in Jurassic types.") The carboniferous genus *Pentaphyllum* has five long septa and one short cardinal septum. And it seems to me the general similarity which is shown with the carboniferous types by those of Jurassic age is no case of atavism, neither is it necessarily one of generic relationship. We probably see in all of them indications of transitional stages which various genera may have passed through at different periods during increase of their fossular area. The changes at the same time led to the loss of marked bilaterality, since the cardinal and counter septa owed their individuality to the ancestral single or paired reproductive mesenteries.

In other Jurassic genera (*Thecidiosmilia*, KOBY, *Lingulosmilia*, KOBY, *Opistophyllum*, *aut.*), and indeed in other species of *Amphiastræa*, the septa develop in pairs, but the main septum is long and all the septa between it and the two alar septa are longer than those on the anterior or counter septum side of the elliptical calyx.

The number of septa may be equal in the posterior and anterior parts of the calyx, but frequently there are more septa between the two alar septa anteriorly than posteriorly. Another peculiarity of some of the species of these Jurassic genera is the crowding together of the inner ends of the septa on the posterior side, and in such a manner that these septa *arrange themselves in a definite pinnate order of development with regard to the main septum.*

In several Stramberg genera I found by polishing the posterior epithecal surface, that the pinnate paired arrangement of the septa could be demonstrated in the better preserved specimens. The same young specimens of *Amphiastræa*, in which transverse sections proved the slow appearance of the septa in pairs according to KUNTH'S law, showed also the pinnate order superficially. But while full-grown specimens showed marked bilateral symmetry, I could find no sign of pinnate arrangement externally. The permanent number of primary septa in a calyx varies in different genera, 6, 8, 10, 12 are all common.

All those genera of which I now speak may be demonstrated by reason of their septal and "thecal" structure to be allied with the Zaphrentoids of Palæozoic time. In other words, Mesozoic corals, probably of Zaphrentoid descent, show pinnate arrangement of the septa in young stages of growth but not in mature calyces. It is well known that among Palæozoic corals pinnate arrangement of the septa is not universally present in mature calyces. KUNTH, FRECH, and other authors have been able to show that the pinnate arrangement is present in embryonic stages of certain species of *Cyathophyllum* although absent in the mature coral.

Again, the pinnate arrangement is not necessarily associated with bilaterality. The septa may be practically radial in the mature calyx, and yet pinnate insertion takes place (ex. *Palæocyclus, Streptelasma*, etc.). It is, however, necessarily associated with a *slow developmental history of the polyp*, where tangential expansion of the calyx takes place mainly at certain active areas—the posterior and two lateral areas.

The pinnate arrangement of the septa *within* the calyx is a feature dependent on the developmental relations between the radial lines of growth and the periphery of the calyx. The primitive developmental history may be thus expressed. New mesenteries and new septa appeared in paired fashion, the "*pair*" *being placed on either side of the main septum or on the abaxial sides of the two alar septa.* Contemporaneously with each new invagination, the body-wall distended peripherally, and thus effected a shifting round of the previously-formed invagination, so as to make room for the new invagination. If the septal invaginations were very short, a small amount of distension at the periphery of the body-wall would be sufficient to free the successive invaginations entirely from communication with one another, and the calyx would ultimately show radial structures free from one another at their inner ends (ex. *Omphyma*). Even if the invaginations were long and extended into the middle of the visceral cavity, the peripheral distension might go on rapidly enough to render the inner ends free. Very frequently, however, the invaginations were long, and the distension of the body-wall at the periphery went on too slowly to allow the successive invaginations to become free throughout their entire length. Then, inside the calyx, the septa might be seen diverging pinnately from main and alar septa.

Again, if distension were uniform in the axial-abaxial (postero-anterior) and in the lateral axes of the calyx, the latter might ultimately assume radial symmetry of its parts (*Streptelasma corniculum*). *On the other hand, if peripheral distension were not uniform*—say, it was more rapid at the "alar" regions of insertion than at the "main" region—then the periphery of the calyx necessarily tended to become elliptical, the long axis coinciding, in the case assumed, with an axial-abaxial line of bisymmetry in the calyx.

In a large number of the primitive Madreporaria, new invaginations were interpolated before complete development of the previous, and distension did not sufficiently free the successively-formed invaginations throughout their entire length. Hence the pinnate position of the septa in relation to the "main" and "alar" septa was retained during farther growth, and gave rise to their "divergence" within the calyx, in accordance with KUNTH'S laws.

Already, in early Palæozoic time, the pinnate insertion of septa at fixed regions of the polyp (calyx) had been often departed from. *Cyathophyllum heterophylloides*, FRECH (Devonian) shows feebly-marked pinnate insertion of the septa at the periphery in the embryonal end of the calyx, and irregular radial position of the septa in the upward continuation of the calyx. It is, moreover, only one of several examples which could be quoted from Palæozoic genera. And such examples prove that

already, in Palæozoic time, a tendency displayed itself towards the peripheral expansion of the calyx at early stages of development *round the whole periphery,* instead of at the primitive fixed localities. With peripheral expansion of the embryonal body-wall *at any place* is associated the insertion of new radial septal invaginations of the body-wall at that part.

The same tendency which appeared in mid-Palæozoic time in certain corals seems to have made itself felt throughout different groups at different time-periods, since the embryonal ends of many Jurassic corals (Amphiastræidæ) show still the pinnate insertion of septa otherwise characteristic of Palæozoic types. Meantime, those families (Astræinæ, Pseudoastræinæ) which are probably directly descended from *Cyathophylloidea,* show, in Jurassic time, no sign of pinnate insertion of septa even in the embryonic calyx. And in many of them a distinct cyclical arrangement of septa indicates a simultaneous development of the primary septa at a number of localities in the periphery.

A glance at the "Jurassic" circle in the "Phylogenetic Table" below (Part II., p. 331), will show that the genera belonging to the sub-families Astræinæ, Thamnastræinæ, and Lophoserinæ were at that period in reality cyclical, or at least radial, types; whereas those belonging to the Oculinidæ and Amphiastræidæ were, in the majority of species, altogether backward in the attainment of radial symmetry. In the Amphiastræidæ several cases of embryonic pinnate arrangement of septa have been demonstrated.

It is at least striking that the families—backward in this respect—were also backward in another, namely, the rapidity in colonial types of vegetative budding within the "theca." Each bud was still completely developed as an independent member of the colony, and had its own theca and epitheca (often erroneously called "theca"). In addition to the epitheca of the individual, there was the general epitheca of the colony. It seldom happened that a series of buds were surrounded by a common epitheca and themselves had no individual epitheca. In these more primitive families the aboral body-wall of the polyp went through, at the giving-off of each bud, the complete process of peripheral expansion, accompanied by the appearance of new invaginations in a radial direction, whereas in the case of the Astræinæ and Lophoserinæ, etc., the aboral body-wall of the polyp curtailed the process. Radial invaginations formed very rapidly, and grew up independently of any wall-ring of tissue. The proliferation of polypal "mouths" went on with much greater rapidity, and massive astræiform colonies were built up of fissiparous and meandroid habit. In these colonies no epithecal rings or "true wall" surrounded the individual calyces; all calyces were enclosed within a common basal epitheca. In branching colonies, naturally, an epitheca surrounded each branch.

I conclude, therefore, that the pinnate development of the septa was, generally speaking, thrust backwards in the life-history of the Madreporarian polyp, sooner in some groups than in others, sooner in some genera and in some species than others,

until what was a typical feature in the majority of Palæozoic corals became an extremely exceptional feature as time went on, was limited, in fact, to embryonic stages and then seemed to vanish. Yet not quite. For the primary mesenteries develop in the recent Madreporarian polyp in pairs according to an order of development exactly corresponding to that observed in the radial skeletal parts of Palæozoic Madreporaria. Comparative series are given in Diagrams A, B, and F, G, showing the stages in the development of the mesenteries in the Recent Astroides, and their correspondence with the primitive order of insertion of septa, still shown in certain Jurassic genera.

A similar general result has been deduced by ORTMANN ("Beobachtungen an Steinkorallen von der Südküste Ceylons," SPENGEL, 'Zoolog. Jahrbücher,' vol. 4, p. 569. Jena, 1889). ORTMANN draws attention to the gradual incoming of the change from bilateral to radial symmetry among Madreporaria. He points out that the tendency of corals to build colonies reacted against the upholding of the primitive bilateral symmetry. BOURNE also emphasises this factor in bringing about the change from bilateral to radial symmetry.

The main arguments considered by ORTMANN are thus stated :—(1) "Between the Palæozoic, Tetracoralla, and the Hexacoralla of Secondary, Tertiary, and Recent time there is no essential difference." (2) "Bilateral corals are chiefly such as are of simple-living habit" (*i.e.*, not colony-building). (3) "From Palæozoic time, when the bilateral corals occur in the greatest number, until Recent time, bilaterally symmetrical corals have become less and less frequent." (4) "The bilaterality of the Hexacoralla has been thrown back to the earliest embryonic stages." ORTMANN very justly places great importance on this last consideration, and draws from it and from the others the only possible conclusion: "We must, therefore, take it for granted that the so-called Hexacoralla are directly descended from the Tetracoralla."

It is impossible to base a classification of Madreporaria on septal symmetry. Will one include amongst *M. rugosa*, E.H. (= *Tetracoralla*, HÆCKEL), the genus *Cyathophyllum*; it will be also necessary to include a number of Jurassic genera, in which young calices show paired insertion of septa with reference to posterior and lateral parts of the calyx! Between these genera and many others with marked bilateral symmetry of their septa, there are all grades of transition. Again, certain genera belonging to the same family may have bilateral symmetry, others radial symmetry. Even within the same recent genus, *e.g.*, *Madrepora*, certain species might, with a considerable show of right, be referred to the *Tetracoralla*, and others to the *Hexacoralla*.

There are, therefore, abundant cases in Mesozoic, Tertiary, and recent Madreporaria of marked bilateral symmetry of septa retained in the mature calyces. In point of this feature, such types stand nearer a primitive "Rugose" type, in which pinnate insertion and bilateral symmetry of the septa were associated, than do certain Palæozoic types, in which the symmetry of the septa is radial in the mature calyx, and no pinnate insertion is observed.

In fact, if the feature of pinnate insertion were to be strictly adhered to as a great classificatory principle, many genera, Palæozoic equally with Mesozoic genera, would have to be split up in an utterly artificial fashion, certain species referred to the one group, and closely-related species to the other. I therefore entirely disagree with the main orders of Madreporaria erected by EDWARDS and HAIME—*M. rugosa, M. aporosa, M. perforata.*

The "Rugose" Epitheca is present in *M. aporosa* in all simple forms, always as a common base around complete colonies, and even in certain colonies around each individual corallite.

The *tabulæ* of *M. rugosa* are not peculiar to that order; they are still frequent in Mesozoic genera, classified in various families, and can be demonstrated in a large number of cases to have gradually given place to conical structures, viz., pali and columella. The latter change had taken place in Palæozoic time in some cases, in others it was of later date.

Bilateral symmetry is also not peculiar to Palæozoic genera, which, indeed, are often radially symmetrical. Thus there remains only the pinnate insertion of the septa, and this is not a constant generic feature in certain Rugose genera.

The conservatism in favour of upholding an Order, *M. rugosa*, is a palæontologist's prejudice. He wants, for convenience, a general title under which the Palæozoic genera can be classified, and so long as it does not make much disturbance in the conceptions of Palæozoic genera, he is not unwilling to admit a few Mesozoic genera under the same title. But he finds it impossible to recognize systematically that the paired development of the mesenteries in the embryo of recent types, and their pinnate insertion with respect to the embryonic "main" and "alar" invaginations of the body-wall, is exactly the same feature as was shown by Palæozoic septa.

Nevertheless the fact is there, and the embryonic development of *Astroides repeats in rapid stages the phylogenetic history of its race.* Few more beautiful examples can be afforded of this general evolutionary truth.

Pinnate insertions of the radial invaginations in which septa were deposited may therefore be regarded as a primitive character in the Madreporaria, which, as time went on, gave place to cyclical insertion of the septal invaginations. It was a change attained at quite different periods in nearly related genera.

Systematically, I would erect no order, no family, sub-family, or genus on this ground alone. But when *pinnate insertion in the mature calyces* of certain Palæozoic genera is correlated with a number of other systematic features, which give a general character to the corallum differing from that of any subsequent form, there is reason to erect a distinct genus, or sub-family of Palæozic age, as the case may be. The *main* sub-divisions must not rest on the geological age, neither should they rest on features which can be demonstrated to be highly subject to phylogenetic changes of the most varied kind. They must, if possible, rest on features which have remained

constant for certain types throughout the history of the group. Such features are presented by the fine structure of the calcareous skeleton.

It is well known that AGASSIZ thought the "Rugosa" were probably not Madreporarian corals at all. Most palæontologists of the present day show in their work not only a recognition of the right of the "Rugosa" to be called "Madreporaria," but also have placed a goodly number of Palæozoic genera not among "Rugosa" but among *Hexacoralla* (NICHOLSON, ZITTEL, and others).

A backward step has, on the other hand, been made by FRECH,* who classifies the Triassic corals under the Orders "Pterocorallia," FRECH (= *Rugosa*, E.H., = *Tetracoralla*, HÆCKEL), and "*Madreporaria*" (= *Hexacoralla*, HÆCKEL). He has lately been followed by VOLZ,† who similarly draws a sharp line of division between "Rugosa" and "Madreporaria."

9. *Correlation in the position of "Directive Mesenteries" with that of the fossulæ (axial, abaxial, alar) in Palæozoic Madreporaria.*

LACAZE DUTHIERS' account of the developmental stages of certain recent "*Hexacoralla*" types has been since frequently confirmed. From it the number twelve would seem to have become fixed as the fundamental cyclical number for mesenteries and septa. It is shown in diagrams A and B how the various stages proceed; pairs of mesenteries appear in a definite position around the oral region, and, when six pairs have formed, the first cycle of twelve septa begins to take origin in the entocœlic and ectocœlic chambers.

The axial and abaxial pairs of mesenteries are called "directive" mesenteries, because in Actinians and in most Madreporaria their pleats of musculature are placed on the faces of the mesenteries away from each other, while in all the other pairs of mesenteries they are placed on adjacent faces (see diagrams C and D). Thus a middle line, the "sagittal" line of HERTWIG, can be drawn through the polyp between these axial and abaxial pairs, and the arrangement of the two halves is the same on either side of this mid-line. Both in Actinians and in Madreporaria the presence of a sagittal line demonstrates the bilateral symmetry of the polyp. In several colonial forms of Madreporaria no mesenteries are marked out as directive, the polyps of the colony being then radially symmetrical. This change is a retrograde one, correlated with rapid vegetative increase in the colony and the loss of individuality on the part of the single polyps.

LACAZE DUTHIERS described the appearance of the early pairs of mesenteries as taking place at intervals of unequal duration. The first two pairs appear soon after one another, then there is a longer pause before the third pair appears. The

* FRECH, "Die Korallenfauna der Trias," 'Palæontog.,' 1890, p. 80.

† W. VOLZ, "Die Korallenfauna der St. Cassianer Schichten, Vorläufige Mittheilung," 1894.

fourth succeeds the third rapidly, then a second longer pause ensues, and the fifth and sixth then appear almost simultaneously. The general facts which LACAZE DUTHIERS observed in the development of the mesenteries are, as has already been

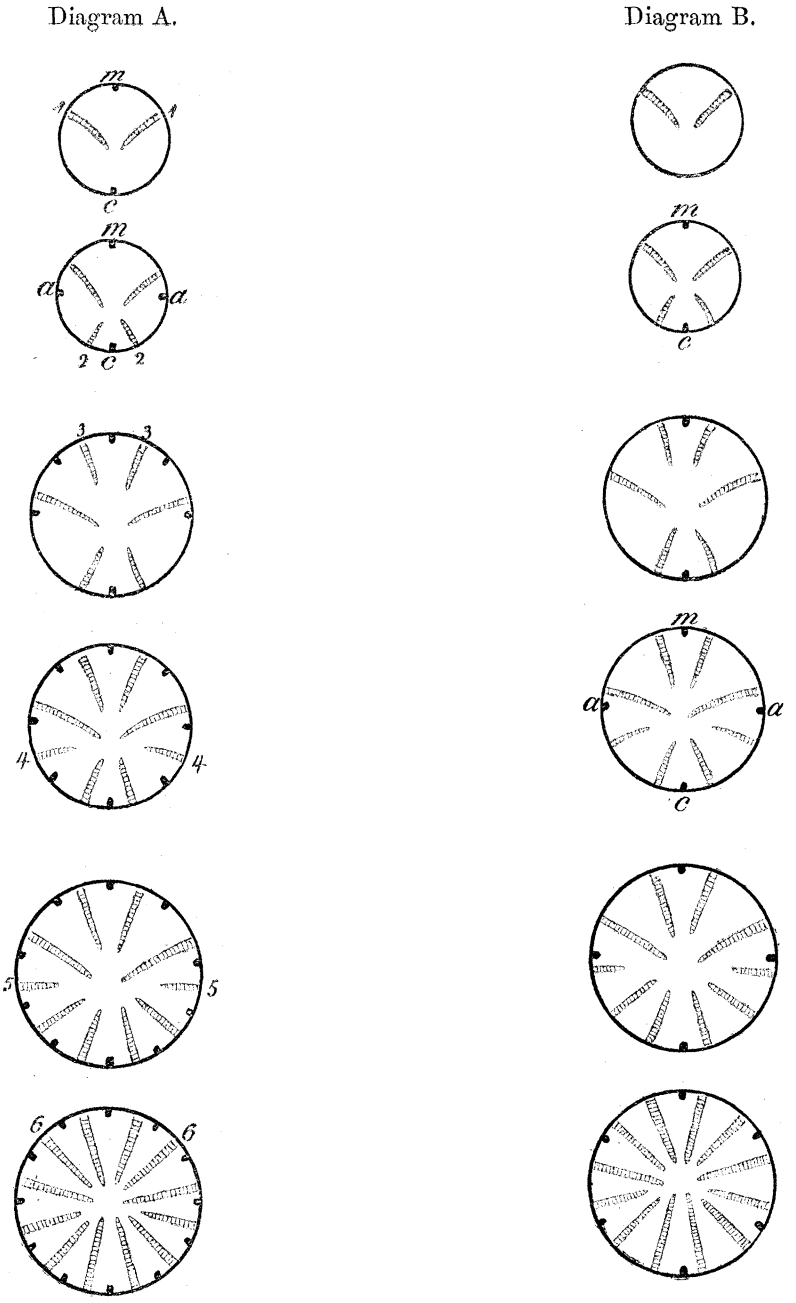


Diagram A.—Insertion of a pair of septa after each pair of mesenteries (hypothetic) would result in the *ectocœlic and entocœlic* position of septa (*primary cycle* 12).

Diagram B.—Insertion of a pair of septa after every two pairs of mesenteries ("pause" of LACAZE DUTHIERS) would result in the *entocœlic position only* of the septa (primary cycle 6). *m.* main septum; *c.* counterseptum; *a.* alar septa; (mesenteries after LACAZE DUTHIERS).

frequently pointed out, in complete agreement with the fundamental facts in the *pinnate insertion of septa* in primitive Madreporaria.

The three "pauses" in embryonic development, occurring after the appearance of each two pairs of the first twelve mesenteries, have been presumed by one or two authors to represent the interval during which septal invaginations formed. I have indicated in diagram A above, that there may have been, primitively, types in which septa appeared after each single pair of mesenteries. This would give a *raison d'être* for the occurrence of septa in every ectocœle and entocœle of a polyp. Whereas the other possibility,—insertion of one pair of septa after two pairs of mesenteries—would tally with cases of *entocœlic septa only* in a polyp. Of the

Diagram C.

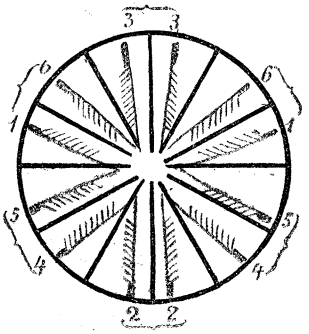


Diagram D.

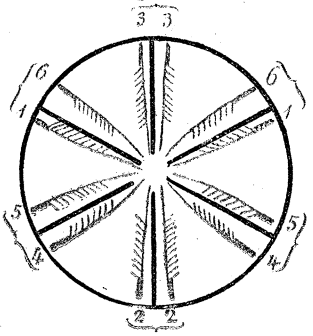


Diagram C shows 12 septa occupying the 6 ectocœles and the 6 entocœles formed by the mesenteries (*cf.* diagram A). Diagram D shows 6 septa occupying the 6 entocœles of the mesenteries (*cf.* diagram B). Note also that the *developmental* "pairs" of mesenteries indicated by the numerals coincide only in the cases of the 2nd and 3rd "pairs" (the "directive mesenteries") with the *muscular* "pairs."

two, there seems most ground for accepting the types with both ectocœlic and entocœlic septa as the more primitive. On such a basis the *dodecameral* cyclical symmetry would be explained as in reality a companion primitive form with tetrameral symmetry; while hexameral septal symmetry would seem to be associated already with signs of "hastening" of developmental stages. It is certainly the case that the incoming of radial septal symmetry in Madreporaria was more often marked by the number 12 in the primary cycle than by the number 6.

In using the word "pair" either of the mesenteries or of the septa, I refer to "pairs" as they develop. There is, however, a possibility of confusing such a "developmental pair" with a secondary use of the word which has become fairly general, namely, the pairs of mesenteries whose muscles work in connection with one another.

The accompanying figures illustrate the double use of the word "pair" as applied to the mesenteries. Lacaze Duthiers' use of the word includes not only the sense of *place* in the polyp, but also the sense of contemporaneity of development, each "pair of mesenteries" being simultaneously invaginated. In speaking of the "pairs

of mesenteries" in a mature polyp, only the sense of "place" is implied, and a "pair" may be composed of two mesenteries which were not simultaneously invaginated, but which are afterwards brought into connection by their musculature (*cf.* diagrams C and D). For example, FOWLER defined the "entocœle" as the cœlenteric space between the adjacent faces of two mesenteries belonging to one "pair of mesenteries." The term "pair" is applied here only in the sense of place and musculature (ex. pairs 1 and 6, 4 and 5, in diagrams C and D).

By comparing the "entocœles" in a mature polyp with the arrangement of the *embyronic* mesenterial pairs, it becomes evident that *only the axial and abaxial entocœles are contained within a "pair" of mesenteries in the sense of* LACAZE DUTHIERS. *In other words, the "directive" mesenteries enclosing the axial and abaxial entocœles are paired in development, all other entocœles are enclosed by mesenteries belonging to different developmental "pairs" in the embryo.*

I have shown this in diagrams A and B, founded on LACAZE DUTHIERS' results. The numerals give the order in the appearance of the mesenteries in the embryo, and it will be seen that only the second and third "pairs of mesenteries" in the embryo remain next one another so as to form a "pair" in the mature polyp.

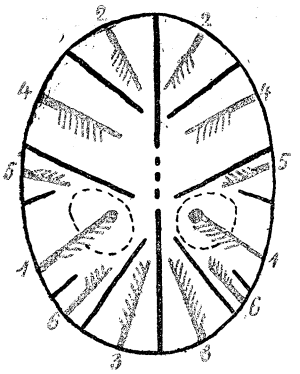
Leaving out of consideration the pairs of mesenteries connected by their musculature in the mature polyp, it will be seen in diagrams C and D that the muscles are placed on opposite faces of the mesenteries numbered "2" and "2," "3" and "3," in the diagram, and *also on opposite faces of the mesenteries "1" and "5,"* on either side of the median lateral line. These two mesenteries are originally in the position of the transverse line of symmetry in the polyp. It is true that "5" comes into muscular connection afterwards with "4," and "1" with "6," and thus it appears ultimately as if only the axial and abaxial "pairs" of mesenteries had the muscles on opposite faces. Embryonic stages, however, show that "directive" mesenteries were primitively present in both the original lines of bisymmetry in the polyp: axial and abaxial, *i.e.*, *dorso-ventral*, and also the line at right angles to it. In the latter line lay the "alar" fossulæ and "alar" septa of Palæozoic corals.

If we were to transfer this diagram of the principal twelve mesenteries in the recent coral to any typical calyx, introducing the fundamental features in respect of septa and fossulæ of a Palæozoic coral (say *Omphyma*), these very simple considerations become clear, and, with them, the sense and bearing of "directive mesenteries" in Actinian and Madreporarian polyps. *The mesenteries with the muscles on opposite faces were—to judge from their position relatively to the fossulæ—destined to be the specially modified gonad-bearing mesenteries; were, in fact, functionally active in reproduction, in addition to the usual function of the mesenteries in supporting the body-wall.* The presence of "directive mesenteries" is therefore hereditary, and has its origin in a time when one, two, or at most four mesenteries or pairs of mesenteries were specialized for reproduction. Now these mesenteries cannot be of any very special use, and we need not feel surprise to find they have become inconstant in Madreporaria.

In most Recent Madreporaria the greater number or all of the mesenteries are reproductive; the primitive significance of the alar pair has long been lost, and even that of the axial and abaxial pairs is no longer always retained (ex. *Lophohelia*, *Mussa*, *Euphyllia*).

In many Jurassic genera there is evidence that the alar regions were specially modified, and not the axial and abaxial. In the Recent genus *Seriatopora* (diagram E) it is distinctly the alar pair which are reproductive-bearing; that

Diagram E.



Plan of the septa and mesenterial "pits" in *Seriatopora* (after MOSELEY). The pair of mesenteries numbered 1, are specialized for reproduction, and occupy the lateral (alar) "pits" or "fossulæ" (*cf.* pp. 279, 280).

is, the *first-developed pair* of mesenteries in the embryo are apparently those which are specially modified as gonad-bearers in *Seriatopora*. Doubtless it was indifferent whether the alar or dorso-ventral line of symmetry was retained in a calyx, and either or both were marked out for a longer period in some genera than in others. The elliptical shape of many Madreporarian calyces still indicates one such line of symmetry.

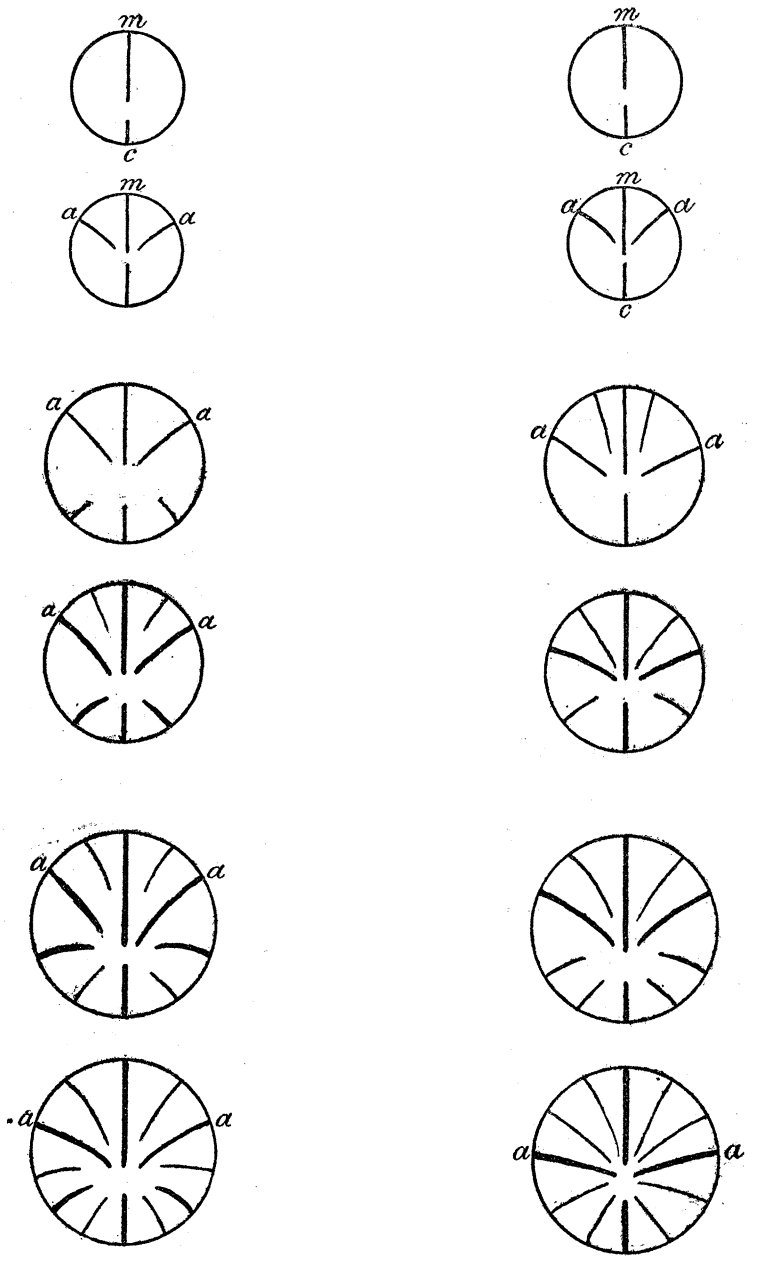
HEIDER'S description of the mesenteries in *Madracis pharensis* is especially worthy of attention, both for the question of bilateral symmetry and that of the musculature. I quote it in full:—

> The septa are exclusively entocœlic, as FOWLER has also given for *Madracis asperula*. The directive pair is plainly marked out in most sections, and the (dorsoventral) plane is directed in individual polpys of the same colony more or less towards the middle point of the colony. The polyps seem by this means to be oriented to a certain degree according to a main axis. This is plainly seen in the nodular, more acrogenous colonies, whereas it disappears altogether in flat colonies. I found, moreover, very often that the musculature uniting the mesenteries in paired fashion is developed one-sidedly only there, where the mesenteries include septa; on the other hand, the contractile threads are developed equally on both sides of the mesenteries where no septa occur, *i.e.*, close below the oral disc of the polyp. This gives, therefore, the impression that the one-sided development of the musculature is in a certain connection with the septa ("Korallen Studien," II., *Madracis pharensis*, 'Arbeiten aus dem Zool. Inst. zu Graz,' 1891, p. 317).

I subjoin diagrams F and G, illustrating interesting cases of pinnate insertion of

the septa in one or two Jurassic genera, founded on personal observations. KOBY observed some of these stages in the corresponding types of the Swiss Jurassic fauna. These cases occur within a group of genera whose other features declare them to be allies of Palæozoic Zaphrentids. I have erected for these Jurassic types and their later representatives a new family of Madreporaria, the Amphiastræidæ (see p. 275).

Diagram F. Diagram G.



Observed cases of the development of *septa* in pairs. The successive stages may be compared with those in the development of *mesenteries* (diagrams A and B) m = main septum, c = counter septum, a = alar septa.

A comparison of the septal pairs with the "embryonic pairs" of mesenteries drawn in diagrams A and B shows very clearly that there were types (and they were very numerously represented) still existing in Jurassic seas, in which the slow, paired mode of septal development was adhered to (*cf.* pp. 280–283). The same types counted usually eight, ten, or twelve septa in their so-called primary cycle; if eight, the arrangement was bilateral; if ten or twelve, it might still be bilateral, but showed a tendency to be practically radial. From these facts, together with the known facts of embryology, it will be admitted to be pretty well proved that the sub-orders Tetracoralla and Hexacoralla are based on a feature which became gradually in the course of time removed backward in the life-history of the individual until now it is presented only in embryonic stages. The diagram of the recent polyp *Seriatopora* shows twelve septa bilaterally arranged, correlated with the retention of the primitive feature of a pair of fossulæ. I have entered the numerals against the mesenteries in diagram E according to the same system followed in diagrams A to D, for the purpose of demonstrating the upholding of the significance of the "embryonic pairs" in this Recent coral.

10. Brief Review of Madreporarian Evolution.

It is a familiar fact that many "radially-symmetrical" Madreporarian corals are still distinctly bilaterally symmetrical in young stages. *Fungia* is a well-known example. The wide-spread occurrence of bilateral symmetry in the polyps of cœnenchymatous colonies has been frequently drawn attention to in this paper (*cf.* p. 271). These are cases of bilateral symmetry among recent corals. As soon as fossil corals are studied, the number of bilateral types is seen to be very great in the geological ages between Palæozoic and Recent time.

Bilateral symmetry is much more widely spread amongst Triassic and Jurassic corals than it has been the custom to admit. It is a constant feature in many genera, and in others all stages of transition are seen between bilaterally symmetrical calyces, even in some cases with a fossular depression, and radially symmetrical calyces.

On the other hand, radial symmetry in Triassic and Jurassic corals had no greater connection with the numbers 6 and 12 than with 8, 10, 14, and in fact all multiples of 2. Six is the first number at which radial symmetry is attained in the mesenteries of the embyro, and as such, it seems to have become early fixed for the primary cycle in many cases, more especially where the calyces were small (Oculinidæ). Moreover, if the septa are entocœlic only, the first cycle of septa can only have six and not twelve (*cf.* diagram B). Even then, the number eight seems to have been very often hit upon (*Stephanocœnia, Astrocœnia, Stylina*).

The broadest internal feature of difference between Palæozoic and later corals is, perhaps, best expressed in saying that a single well-developed reproductive mesentery, or one pair, seems to have characterized the majority of the former; while, with a few

exceptions possibly in the Triassic and Jurassic periods, reproductive filaments occur in later corals, at least in one pair, and usually in a great number of pairs of mesenteries. The correlated features have already been noted, *e.g.*, the extension of the original fossula or a deepening of the calyx; a columella for the better support of the mesenteries, and the adaptation for this purpose of the Palæozoic tabulæ; "hastening" in the processes of budding and in the development of the embryo.

It was not until *Cretaceous* time that the condition of *radial symmetry* became general. It may then be said to have made itself a *sine quâ non* in all colony-building types of Madreporaria except the cœnenchymatous families Pocilloporidæ and Madreporidæ. With this exception, there has been universal radial symmetry in the Madreporarian corals of Cretaceous, Tertiary, and Recent seas.

Nothing more than the mere tradition of their ancestry affects the corals of these ages, displaying itself now and then in the form *of a columellar mid-line*, or in the *appearance* of bilaterality where, in reality, the parts are not bi-symmetric, and at the same time not radio-symmetric. In short, a lamellar columella is probably a carefully-retained inheritance in some cases and in others a freak of atavism. Where the strength of the skeleton can do without it, it becomes obsolete. *The same may be said of the pillar-like columella. In the dwindling of this columella we are probably now seeing the end of the basal tabulæ, once common to all Madreporaria.*

One great innovation, which has reacted against the development of a columella, was the *synapticula* and in general *a lighter skeletal structure.* The synapticulate Thamnastræinæ branched from Cyathophyllids and appeared with Astræinæ in Triassic and Jurassic time. They were at once highly successful. The Cretaceous period brought new forms of Astræinæ and the genera *Cyclolites* and *Thamnastræa* chiefly represented the Thamnastræinæ, but Early-Tertiary* time saw the complete ascendency of the synapticulate Lophoserinæ, Funginæ, and Eupsammidæ over the Thamnastræinæ. The Turbinolidæ, E. H., attained in the Cretaceous and Early-Tertiary periods to full development; since then they seem to have steadily continued. It is also important to observe that contemporaneously with a rich Turbinolid fauna, the "recent" Perforate types appeared: Madreporidæ and also Poritinæ. The Later-Tertiary period continued directly the Cretaceous and Early-Tertiary fauna; at the same time, the form of the coral skeleton tended to become ever lighter, and fragile cœnenchymatous genera had special advantages over the more compact in reef-building.

The general character of the post-Jurassic fauna bears a distinct impress when compared with the Triassic and Jurassic fauna. Amongst other features, the numbers six and twelve then came more and more to the front in radial symmetry, although fissiparous and multi-septate Astræids continued the irregularity which had been natural to them from the first. The number was wholly arbitrary, as is evidenced by

* Early-Tertiary corals have been made the subject of a recent monograph by Reis:—"Die Korallen der Reiter Schichten," 'Geogn. Jahreshefte Bay. Landesuntersuchung,' II. Jahrg., 1889.

the fact that it became often fixed in genera remote from one another, while nearly related genera, or even species, differed.

The broad conclusions which I draw from such a review of the Madreporaria are :—

A. *Palæozoic.*—A *change,* which was advantageous, showed itself in Cyathophyllids and in Cyathaxonidæ, as early as Silurian and Devonian times; other types, which did not participate in the change, or could not rapidly enough adapt their disconnected habit of growth to it (*e.g.*, the Cystiphyllids), became extinct; before the close of the Palæozoic era, rather abnormal "columellar" genera were fashioned (*e.g.*, the Clisiophyllids), but were apparently unsuccessful; at the same time a large group of genera (Zaphrentids) seemed to make no sign of change.

B. *Triassic and Jurassic.*—The Madreporarian fauna was a mixed one, including many unaltered, or little altered, Zaphrentids, a few true Cyathophyllids, a great number of altered Cyathophyllids (Astræidæ, Thamnastræinæ, &c.), and a smaller number of altered Zaphrentids (Turbinolidæ, Eusmilinæ pro parte). The varied aspect of Astræid colonies, and the graceful branching corallum of such members as the Oculinidæ, are characteristic for the period. The Triassic fauna is remarkable for its small size, so far as we yet know it. In Jurassic seas, however, large simple corals were common (*Montlivaltia, Plesiosmilia,* etc.). The young forms show paired development of septa in certain examined cases, but cyclical arrangement (primary cycle of uncertain number) of the septa is the rule in the mature calyx.

C. *Cretaceous, Tertiary, and Recent.*—Lightness of the skeleton is the most marked feature, and the widespread occurrence of synapticulate groups gives quite another impress to the fauna.

The *simple* corals decrease in size, while *compound corals,* colonial and cœnenchymate types, show constant tendency toward farther modification. Cyclical development of the septa is present in the embryo, and the number of septa in the primary cycle is very generally twelve.

Several large families of recent Madreporaria, Fungidæ, Eupsammidæ, Madreporidæ, Poritidæ, although their relationship to Triassic and Jurassic ancestors may be determined, present a Madreporarian fauna quite as distinct in its character from the fauna of those two periods, as the Early-Mesozoic fauna was, in its time, different from the Palæozoic fauna.

Without the Triassic and Jurassic fauna, it might be possible to speak of Tetracoralla and Hexacoralla; with this intermediate fauna, however, the Madreporaria afford one of the most brilliant examples of a single evolutionary MOTIVE *reacting on the whole region of the body in the neighbourhood of the main part affected, and inducing an important series of correlated changes.*

11. *Recapitulation of Phylogenetic Changes.*

It will be useful to recapitulate briefly here the direction in which evolutionary changes have acted on the two great groups of Palæozoic Madreporaria—Zaphrentidæ and Cyathophyllidæ. I need not repeat the character of the changes and their various modes of correlation so as to produce the wonderful variety of our living Madreporarian fauna. Recapitulating merely the actual changes, these were :—

1. *An increase in the number of mesenteries, and more especially in the number of gonad-bearing mesenteries.* Higher differentiation of the musculature of the mesenteries and elongation, inwards and outwards, of the *mesenterial loculi.*

2. Greater firmness and lightness of the septa ; the grouping of the calcareous fibres became more and more complex, and gave rise in many families to a complicated system of ridges and granulations on the septal surfaces.

3. Instead of one, two, or four fossular pits for the corresponding number of reproductive mesenteries in the base of a calyx, the whole base became deepened, an axial style or columella projecting into the hollow of the deepened calyx. A very great number of mesenterial filaments could thus be accommodated. This change is the basis of the gradual incoming of radial symmetry in place of bilateral symmetry in the Madreporarian calyx.

4. The central tabulæ were modified as columella and pseudocolumella, and a large number of septa usually connected up at their inner ends with the columellar structure.

The architectural form of the calyx was thus considerably improved in respect of its *skeletal strength associated with economy of space.*

5. The "outer dissepimental zone" was also modified in a large number of families, and in a manner much like the modification of the tabulæ. By becoming round or erect, instead of being flat or vesicular, they gave place to *synapticulæ.* This change allowed the soft parts to remain very deeply sunk in the skeleton, even while upward growth continued at the lip of the calyx, and thus afforded a much larger area of *endodermic surface* to perform the gastral and other functions of the polyp. The change gave *increased vital activity associated with economy of space.*

6. Introduction of a definite "wall" at some part of the calyx. In Cyathophyllidæ the wall was formed in the calyx, either near the centre at the limit of the dissepimental outer zone with the central tabulate area, or near the periphery. In either case it was formed by septal thickening, and is called a "pseudotheca."

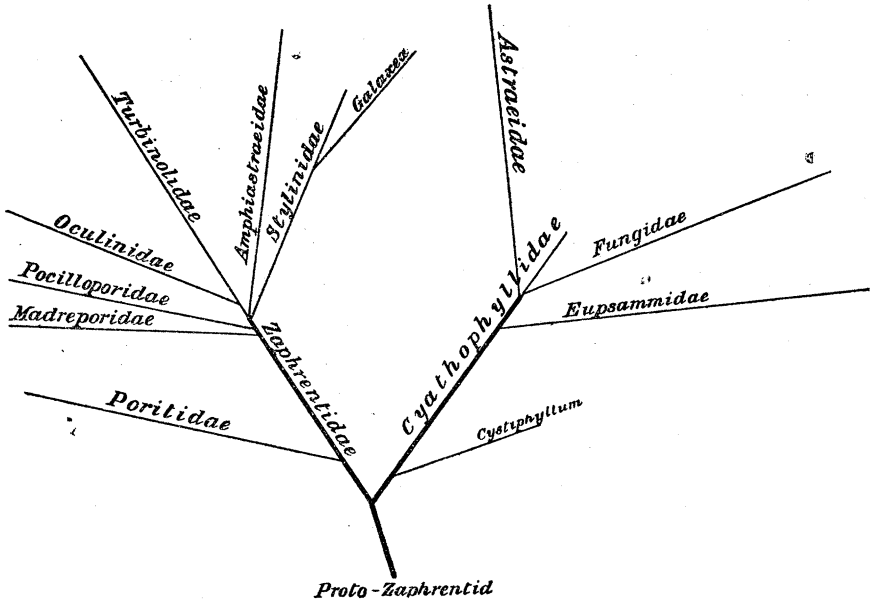
In Zaphrentidæ the wall was formed *at the periphery* as a modification of the innermost part of the epitheca. The wall, in this case, was a structure independent of any septal thickening (the latter might or might not be present) ; it shows, when studied microscopically, lines of calcification set at right angles or obliquely to these in the septa, and is called a "true theca," or simply "theca."

In a great number of simple corals, or branches of branching colonies, no wall was introduced.

7. Retrogression of the primitive basal and peripheral "epitheca" in many genera. This change largely depended on the introduction of a wall within the calyx in Cyathophyllidæ.

Amongst the descendants of the Zaphrentidæ, the epitheca is still well developed in most of the simple corals, is retrograde in the colonial types.

I append the following plan of recent families descended from these two chief Palæozoic mother-stocks of Madreporarian corals.



12. *Influence of Geographical Changes on the Palæozoic Polyps.*

Every geologist knows that in Central and Northern Europe the period between the deposition of Carboniferous limestones and the advance of the Rhætic and Jurassic Ocean was a long geologic age of disturbance and for the most part upheaval. The Permian and Triassic periods saw Europe undergoing the fluctuations of Archipelago conditions. Shallow, muddy basins, broad deltas, salt lakes, and low coasts occupied the North-Western areas. Central Europe saw in Middle-Triassic time one longer period of marine interruption, represented by the deposit of Muschelkalk. Even in this limestone deposit corals are very rarely found, but the intervening ages of Permian sandstones and conglomerates, as well as the Bunter pebble and sandstone beds, are naturally devoid of coral remains.

The Madreporarian fauna of Central and Northern Europe found itself subjected in Late-Carboniferous and Early-Permian time to highly unfavourable conditions. Pressed in by land to the West and North-West, an eastwards or southwards wandering was the only possible escape, and we may presume it was effected by the hardiest genera.

The Russo-Asiatic Ocean became the general harbourage for the descendants of the European Madreporaria, until in Middle-Triassic time bays and fiords in the Muschelkalk sea of Central Europe again offered the necessary conditions for coral existence. At the same time a series of physico-geographical changes were taking place in the Eastern Alps, accompanied by submarine volcanic activity along the Southern zone. And we find that local coral faunas abounded in the form of numberless reefs and banks.

The Central Europe to which the Mid-Triassic Madreporaria returned, showed very different contours from those of the Early-Carboniferous era. Climatic conditions and the physical environment were still variable, and as those are known to have marked effect on the particular character assumed by a coral fauna, we need not feel surprise when we find that the Triassic representatives in Europe were limited to reef-faunas, bearing strong local impress in the different regions.

It would therefore be wholly unfair to draw general conclusions from a comparison between the freely-developed pelagic and reef-faunas of the Palæozoic era in Europe and the limited reef-faunas of a few localities in Mid-Triassic time. It is otherwise, however, if we compare Palæozoic with Jurassic Madreporaria. The assemblage of coral forms in the Jurassic ocean is quite as representative as that in Mid-Palæozoic seas. At the same time, the interval between the two geologic eras is immense; and the vicissitudes which the corals must have undergone, in their constant wanderings to and fro, cannot have been without their effect.

For I am far from the opinion that it was a typical "Hexacorallian" fauna which the Jurassic sea brought into Europe, or a *suddenly* changed one. I have in the foregoing chapters given too many sound proofs of the agreement in structure and homologies of parts which may be traced throughout the main families in both eras, and of the large number of transitional types.

It seems to me that the relatively frequent and widespread changes in the geography of the Carboniferous, Permian, and Triassic eras more than sufficiently account for the "evolutionary motive" which I have above advanced in explanation of the changes in Madreporaria.

Many analogies might be found in other marine creatures. The instinct of preservation of *type* is as undeniable as the instinct of *self*-preservation. And surely the difficulties in the support of existence can never have been greater or more protracted for Madreporaria than those which drove them out of our regions in Permo-Triassic time. The effort to overcome those difficulties had the result of higher differentiation of the mesenteries and alteration of form in all the hardiest, most numerously represented, Palæozoic families.

One leading cause—physical changes of climate and environment, inducing a fiercer struggle for existence; one continuous counterbalancing effort—self-preservation and preservation of type—worked out a correlated series of changes in the animal kingdom of Madreporaria during the long interval of time between the Mid-Palæozoic and Late-Mesozoic geologic eras.

CHAPTER X.—TRANSITIONAL NATURE OF TRIASSIC AND JURASSIC GENERA.

Seeing that many of the homologies which I have indicated between Palæozoic and Recent Madreporaria are, so far as I am aware, expressed here for the first time, I think it desirable to treat certain intermediate types rather more in detail. This is moreover necessary, since the general conclusion to which I have arrived differs very considerably from the opinions of the only author* who has up to this time made a special study of Triassic corals.

The interest of the Triassic Alpine fauna is many sided; at present I confine myself to the evolutionary features. Professor FRECH wrote, in 1885, at the close of his paper on the Upper Devonian Corals of Germany (*loc. cit.*, p. 942): "On zoological grounds we can scarcely refuse to accept that the Tetracoralla were the ancestors of the Hexacoralla. The geological occurrence speaks also for this hypothesis. The change ("Umprägung") seems to have taken place during the period of deposition of the Bunter Sandstones, since the few Permian forms belong still without doubt to the Tetracoralla, whilst the known genera from the Muschelkalk and Alpine Trias are connected with the living."

The standpoint taken here rests on a general *hypothesis*, and assumes a change of a sweeping nature to have taken place during *one* geologic era; no corals in that era being forthcoming in evidence of the change.

The same standpoint was retained by Professor FRECH after detailed examination of the Triassic fauna of various Alpine localities. We read again ('Palæontographica,' *loc. cit.*, vol. 37, p. 113): "The great change of the Anthozoan fauna had been carried out before the Muschelkalk and after the Permo-Carboniferous."

My own examination of the same specimens enable me to criticize the grounds on which Professor FRECH'S statement is based. According to that author, the coral fauna includes :—

I. *Madreporaria.*

1. Fam. *Astræidæ.*
   Gen. *Thecosmilia, Isastræa, Phyllocœnia, Stylina, Astrocœnia, Stephanocœnia, Montlivaltia.*
   Sub-fam. *Stylophyllinæ*, FRECH. Gen. *Stylophyllopsis, Stylophyllum.*
2. Fam. *Thamnastræidæ.*
   Sub-fam. *Thamnastræinæ*, FRECH (*vide antea*, p. 189).
   Gen. *Thamnastræa.*
   Sub-fam. *Astræomorphinæ*, FRECH.
   Gen. *Procyclolites, Astræomorpha.*
3. Fam. *Spongiomorphidæ*, FRECH.
   Gen. *Heptastylis, Spongiomorpha, Stromatomorpha.*

* FRECH, "Die Korallenfauna der Trias," 'Palæontographica,' vol. 37, 1890.

II. *Pterocorallia*, FRECH (= *Rugosa*, M. EDW. = *Tetracoralla*, HÆCK.).

1. Fam. *Cyathaxonidæ*, E.H.
   Sub-fam. *Gigantostylinæ*, FRECH.
   Gen. *Gigantostylis*.
2. Fam. *Zaphrentidæ*.
   Gen. *Pinacophyllum*, *Coccophyllum*.

III. *Alcyonaria*. IV. *Tabulata*.

(The latter sub-divisions I leave out of consideration, as my paper concerns the first two only.)

It is clear from the names given to the subdivisions I. and II. that Professor FRECH draws a sharp limit between certain families and genera which he exclusively regards as Madreporaria and others which he regards as "the last remnants ('Superstiten') of the Palæozoic Pterocorallia."

The impossibility of defining such a limit is proved, in my opinion, by the presence even of a single genus such as *Coccophyllum*. The overlapping of the Palæozoic families upon Mesozoic families has been admitted by several authorities. Take, for example, Professor NICHOLSON'S treatment of the *Turbinolidæ* ('Manual,' *loc. cit.*, p. 266):—"The Recent genera *Guynia* and *Haplophyllia*, again, are remarkable in the fact that the symmetry of the corallum is tetrameral, and they thus serve to lead us to such ancient types as the Cyathaxonidæ of the *Carboniferous* rocks. . . . The *Silurian* corals which have been included in the genus *Cyathaxonia* belong, however, to the genus *Lindstrœmia*, which may also be referable to this division (Turbinolidæ) of the Madreporaria, though it will be here provisionally placed among the Rugosa." The Silurian genus *Duncanella*, as well as the genera *Petraia* (Silurian to Carboniferous) and *Polycœlia* (Silur. to Permian) are farther treated by Professor NICHOLSON as probably members of the Turbinolidæ (*cf.* also *antea*, pp. 280–286).

I need not, therefore, go farther in showing how prejudiced a picture Professor FRECH'S sub-divisions are apt to give the student.

More general inferences with regard to the systematic significance of the same Triassic genera may be made on the basis of research in the present paper. I shall apply the nomenclature of families and sub-families proposed at the end of this paper, and re-arrange the Triassic genera in FRECH'S list according to what I regard as their phylogenetic significance.

MADREPORARIA.

A.—*Of Cyathophylloid Ancestry.*

Fam. *Astræidæ*

Sub-fam. *Astræinæ.*

Gen. *Thecosmilia* . . . . . *Montlivaltia.*

(As above, excluding *Stylina, Stylophyllopsis, Stylophyllum.*)

Fam. *Fungidæ.*

Sub-fam. *Thamnastræinæ.*

Gen. *Thamnastræa,* Le Sauvage, em. Pratz.

Sub-fam. *Funginæ.*

Gen. *Procyclolites,* Frech.

The Sub-family Astræomorphinæ, Frech (= Pseudoagaricinæ, Pratz), is fully discussed below.

Fam. *Eupsammidæ.*

pro parte { Gen. *Stylophyllopsis,* Frech. / Gen. *Stylophyllum,* Reuss, em. Frech.

B.—*Of Zaphrentoid Ancestry.*

Fam. *Turbinolidæ.*

Sub-fam. *Turbinolinæ.*

Gen. *Gigantostylis,* Frech.

Fam *Amphiastræidæ* (see p. 328).

Gen. *Pinacophyllum* and *Coccophyllum.*

Two species represent the genus *Pinacophyllum,* Frech; I would refer the typical species *P. parallelum,* Frech, undoubtedly to the Amphiastræidæ, a family numerously represented in Jurassic strata. The second species is referred by Frech, with mark of interrogation, to the genus *Pinacophyllum.* It had been determined by Reuss as *Fletcheria.* Frech referred both species originally, in 1889, to the genus *Amplexus,* removed them in 1890 to the new genus *Pinacophyllum.*

Fam. *Stylinidæ.*

Gen. *Stylina.*

C.—*The Family Spongiomorphidæ,* Frech, is exclusively Triassic.

Frech has compared it with the Stromatoporoids on the one hand, and the Turbinaridæ on the other. Its near affinity to the genus *Astræomorpha* is also pointed out by Professor Frech. Probably the Spongiomorphids are most closely allied with the Poritidæ; they might almost rank as a sub-family.

In the above list I have endeavoured to indicate the main lines of systematic treatment relative to pre-Triassic and post-Triassic forms. One of the most striking features is the great *richness* of the Triassic fauna in members of the Eupsammidæ, Astræidæ, Fungidæ, and its *poverty* in those of the Amphiastræidæ, Turbinolidæ, and Stylinidæ. This observation goes far to confirm some of my arguments in the preceding chapter. The "*precocity*" of the change from bilateral to radial symmetry in the Palæozoic Cyathophylloids finds expression in the rich variety of form attained by their descendants as early as Triassic time. On the other hand, the *tardiness* of the change in the Zaphrentoids is consistent with the fact that the Turbinolidæ had not attained a steady type even in Jurassic time, and their full development was postponed until the Middle-Cretaceous age and its favourable oceanic conditions.

The general resemblance between the recent representatives of Astræidæ and Amphiastræidæ (*cf.* diagram, p. 331) which caused them to be placed in one family (Astræidæ), becomes all the more readily understood when the near relationship of their early ancestors is held in view. I have already referred to Professor NICHOLSON'S indications of genera intermediate between the three sub-divisions which he made ('Manual,' p. 284) of Palæozoic Madreporaria: Cyathophylloidea, Zaphrentoidea, Cystiphylloidea. Professor FRECH (*loc. cit.*, p. 83) draws attention to the same feature: "It has been frequently pointed out of recent years (amongst others, also by NEUMAYR), that the various classificatory features ('verwandten Merkmale') are not sufficiently significant for the separation of the Cyathophylloids and Zaphrentoids."

Those are side-lights which give clearness not to one family or one era of Madreporaria, but to the whole group from the earliest time to our own.

The Triassic Sub-family Stylophyllinæ, FRECH.

The interest of this sub-family, erected by Professor FRECH, rests in its decided Palæozoic character. The habit of the corallum is typically simple; when colonies form, they do so by "endothecal" or "tabulate" budding, and look like colonies of *Cyathophyllum*. The septa are made up of short, thick spines; often the spines are irregularly set and never properly combine as a septum. The base of the polyp is either tabulate or dissepimental; the theca thick and rugose. Bilateral symmetry is frequently shown; radial symmetry is chiefly present in larger well-developed specimens and then is never cyclical, the septa being indifferently long and short.

In spite of all those features of identity with Palæozoic forms, Professor FRECH has given reasons, at considerable length, for his opinion that the genera of this sub-family are probably sprung from *Montlivaltia*. Had the genera occurred in Palæozoic strata, I feel almost sure a place would, by most authors, have been found for them possibly between Cyathophylloids and Cystiphylloids, and I think, therefore, I

am justified in presenting another view of the case to that already published ('Triaskorallen,' *loc. cit.*, pp. 42–47).

Professor FRECH'S diagnosis of the sub-family may be given in full: "The two (or three*) genera" of the Stylophyllinæ "form a peculiar side-branch of the Astræids, which is almost limited to Trias, and has not until now been more sharply defined. The forms belonging to it have, as a distinguishing feature, strong septal spines remaining in part or wholly free (as in the Thamnastræidæ). The septal spines are, however, not built up by nodules. Moreover, synapticulæ and horizontal bars (pseudosynapticulæ) are absent. The dissepiments are strong and are developed sometimes as horizontal lamellæ or tabulæ."

The discussion "On the apparent relationship of *Stylophyllum* with Palæozoic corals (*Calostylis* and *Cystiphyllum*)" leads to the statement at the end that "a group (Stylophyllinæ) of Triassic and Liassic corals, belonging with certainty to the Astræidæ, is, in many points about their inner structure, reminiscent of old Palæozoic forms like *Cystiphyllum* and *Calostylis*." This reminiscence is said to be comprehensible in any one of three ways:—

(1.) "*Stylophyllum* descends from one of the Palæozoic genera."

(2.) "*Stylophyllum* is to be looked upon as an atavistic form."

(3.) "It is a question of one of the frequently occurring cases among fossil corals, that 'hard parts very much like one another occur in very different sub-divisions' (NEUMAYR)."

The last of the three explanations is the one which Professor FRECH accepts, his conclusion being: "According to the morphological investigations, it may be presumed that *Stylophyllopsis* branched off from *Montlivaltia*."

Setting aside, for the present, the above statement of FRECH'S opinions, I shall enumerate a few of the observed facts. The species *Stylophyllum paradoxum*, FRECH, is one under which an unusual variety of forms has been included. In fact, one of the most striking features in almost any species of *Stylophyllum* is that few specimens can be said to be really alike; and that, although the differences may be slight from one specimen to the next, there are extremes at the two ends, so to speak, of a specific series, which seem to have little in common. This I take to be thoroughly natural, if *we regard the sub-family as a Triassic assemblage of nearly-related species undergoing differentiation in one direction and another, and fairly rapidly.* Advance and retrogression would act hand in hand in such an assemblage.

A specimen of *S. paradoxum*, FRECH, figured by him in Plate 14, figs. 25, 25A, may be taken as an average in the matter of calycinal size and character of the septa. There the septal spines are seen to be scarcely arranged in regular longitudinal series, but rather each growth-period was practically marked by an independent set of small "spiniform" invaginations of the aboral body-walls. With this the

* The two main genera are *Stylophyllum* and *Stylophyllopsis*. A third genus of latimeandroid habit is called *Meandrostylis*, and treated as a sub-genus of *Stylophyllum*.

presence of broad tabulæ or large dissepiments is correlated. This specimen was originally described by SCHAFHÄUTL ('Neues Jahrb. d. Mineral.,' 1851, p. 413), as *Cyathophyllum ceratites* (*non* Goldf.), and one can scarcely feel surprise that the generic title should be a Palæozoic one. Still more Palæozoic in appearance are the very small specimens (*loc. cit.*, Plate 14, fig. 9), in which few spines are present, and these are grouped in threes and fours here and there.

The species *Stylophyllum pygmæum*, FRECH (*loc. cit.*, p. 56), shows remarkable agreement in habit and general features, to judge from the illustrations on p. 56, with the Jurassic form "*Lithodendrom mitratum*," QUENST. (*cf.* 'Natth. Kor. Palæontographica,' vol. 21, 1875–76, Plate 51, fig. 9). I would be inclined to place this species in the family of Amphiastræidæ, in the neighbourhood of the genus *Coccophyllum*.

On the other hand, the large specimens (Plate 14, fig. 12) bear, what might be called in contrast, a Mesozoic impress, *i.e.*, the spines are definitely arranged in radial lines, and are sufficiently compacted to form septa extending from the rim of the calyx to the centre. At the same time, the "endotheca" varies, being sometimes more dissepimental, at other times more tabulate in character.

A Triassic species like this *Stylophyllum paradoxum* or *pygmæum*, showing such variety and with an outspoken Palæozoic appearance, is, in my estimation, most simply explained as an evidence of structural transition. Further, Professor FRECH is incorrect in stating that the sub-family which he erected for *Stylophyllum* and *Stylophyllopsis* dies out in Liassic time (*loc. cit.*, p. 47).

The Jurassic "Nattheim" coral fauna* presents a genus certainly of more fixed character than that accorded to those of the Stylophyllinæ, but including species of almost identical characters with species of the said Triassic and Liassic genera. I refer to the genus *Epistreptophyllum*, MILASCH., which was figured and described fourteen years before Professor FRECH'S work on "Triaskorallen." Having compared the Nattheim originals with the Triassic originals of Professor FRECH, and also with certain species occurring in the "Stramberg" Jurassic fauna, I am in a position to state that in some cases it is impossible to find generic distinction between the Triassic and Upper Jurassic forms. Therefore this "peculiar side-branch of the Astræids" was not "almost limited to Trias," as Professor FRECH states.

The Triassic specimens of *Stylophyllum* and *Stylophyllopsis* which come into question in this comparison with the Upper Jurassic genus *Epistreptophyllum* are always the largest and best developed in any particular species, *vide Stylophyllum paradoxum*, FRECH (Plate 14, fig. 12); *Stylophyllum tenuispinum*, FRECH (Plate 14, figs. 28, 28A); *Stylophyllopsis polyactis*, FRECH (Plate 15, fig. 17); *Stylophyllopsis Lindströmi*, FRECH (Plate 12, fig. 2).

Nor is *Epistreptophyllum* an isolated Jurassic genus—some poor remnant of a long

* BECKER and MILASCHEWITZ, "Die Korallen der Nattheimer Schichten," 'Palæontographica,' vol. 21, 1875–76, p. 210.

past! On the contrary, it is one of several genera characterized by the fact that the "spines" (growth-segments) of the septa are more or less unattached both in a longitudinal and in a horizontal direction. About the middle of the septum the tendency is for the spines to be compacted, but centrally and often peripherally the tendency is for them to be freer. Lateral coalescence of the septal surfaces occurs frequently. Besides, these genera show frequent signs of *bilaterality*. Such genera are *Dermosmilia*, KOBY;* *Baryphyllia*, KOBY; *Haplaræa*, MILASCHEWITZ.

A moment's consideration will suffice to show that this Triassic and Jurassic series of genera leads to the family of Eupsammidæ, destined to play a very important *rôle* in the next following Cretaceous and later time. The Table of Classification (*antea*, Part I.) points out that the unfilled apertures left in the septa of the Eupsammidæ, and very often also in the Lophoserinæ, are due to incoherence of the "septal spines" referred to in my table on p. 252 as the "successive growth-parts" of septal trabeculæ. The individuality of the "septal spines" is one of the ancestral features in the group of Madreporaria (*cf. antea*, pp. 253–261), and it is a feature which has in the course of time become more and more seldom. Amongst Recent types it is found in very few families.

It is, however, only natural that in the Triassic age, a period rich in atavistic and transitional types of Madreporaria, there should be such septa more or less loosely built up of septal spines in genera possibly remote from one another. The systematic position of the genus must be determined in accordance, as far as possible, with other features, such as the relations of septum, wall, and basal structures, the main direction of the spines and their method of coalescence if any.

Yet Professor FRECH *emphasizes this feature as the distinguishing feature of the sub-family Stylophyllinæ.* The other features which he gives—absence of synapticulæ and variable development of dissepiments, sometimes in vesicular, sometimes in tabulate form—are not in themselves of sufficient weight for the erection of a new sub-family. The result is that a number of specimens have been grouped together, and form an unnatural sub-family, said to be of exclusively Triassic and Liassic age. Amongst these specimens one here and there may be picked out and shown to have quite different systematic affinities from its neighbours. If I were to accept this sub-family as Professor FRECH has described and classified it, I should, in my opinion, overlook some of the *important Triassic connecting links between Palæozoic and Jurassic genera.* The majority of the specimens included in this sub-family are ancestral forms of Eupsammidæ, others belong to the Amphiastræidæ, and still others show no essential difference from Palæozoic forms of Cyathophyllidæ and Cystiphyllidæ. I find it impossible to agree with Professor FRECH in his treatment of all the specimens as a narrowly-limited group for themselves which had branched off from the Astræidæ!

* KOBY, "Polypiers Jurassiques de la Suisse," Geneva, 1880–89, 'Mém. de la Soc. Pal. Suisse,' vols. 7–16, pp. 194, 546.

The so-called Stylophyllinæ, FRECH, may be descended from side-branches of Cystiphylloids, Cyathophylloids, and Zaphrentoids, but only a certain number of the specimens represent a fixed, definite form differing from ancestral types. Wherever such a form exists among the so-called Stylophyllinæ, it can readily be compared with certain Jurassic genera. The systematic position of the Jurassic genera in question is in the Eupsammidæ, yet of a character very nearly approaching many early types of Fungidæ.

The Triassic Sub-family Astræomorphinæ, FRECH (= *Pseudo-Agaricinæ,* PRATZ).*

The Fungidæ may be looked upon as struggling towards definite form and structure in Triassic and Jurassic time. The Thamnastræinæ attained full development rapidly. In Triassic time only one genus is described by FRECH—*Thamnastræa.* At the same time, in the Triassic fauna of St. Cassian, several others occur with the septal structure characteristic of the *Microsolena* members of the Thamnastræinæ in Upper Jurassic time.

The Triassic genus *Astræomorpha* was looked upon by PRATZ as an ally of the Thamnastræinæ (= Pseudoastræinæ, PRATZ, *pro parte*), and was grouped by him more especially with the genus *Siderastræa.* I have discussed the relations and characters of this genus in my monograph of the Stramberg fauna, in connection with several Upper Jurassic genera. It is, however, necessary here to point out that the Triassic genus *Astræomorpha* cannot be associated in one and the same sub-family with the Tertiary and Recent genus *Siderastræa.* The "*Siderastræa*" sections given in Part I., pp. 178–181, of this paper show the essential agreement in trabecular structure and in the calycinal features between *Siderastræa* and the various members of the Fungidæ. At the same time, a comparison of the same sections with those given by PRATZ for *Astræomorpha* show important differences. PRATZ was not quite right in his description of the septum of *Astræomorpha*: "Ein jedes Septum macht vielmehr den Eindruck eines selbständigen unregelmässig gestalteten Trabekels." Some well-preserved specimens in the Munich Museum show on weathered septal surfaces that the septum is in reality composed of a number of upwardly-directed trabeculæ, which are placed almost perpendicularly to the upper edge of the septa. The trabeculæ are extremely fine, and are disguised by the strongly-built horizontal ridges which project into the interseptal loculus. The ridges are often developed as knotted thickenings united by thinner parts. So that, in tangential sections through adjacent septa, the general impression given is strikingly similar to that of recent Poritidæ.

FRECH has pointed out the probability of relationship between the genus *Astræomorpha* and the curious Triassic family Spongiomorphidæ, and the resemblance between the latter family and "Perforates," more especially the Cretaceous genus

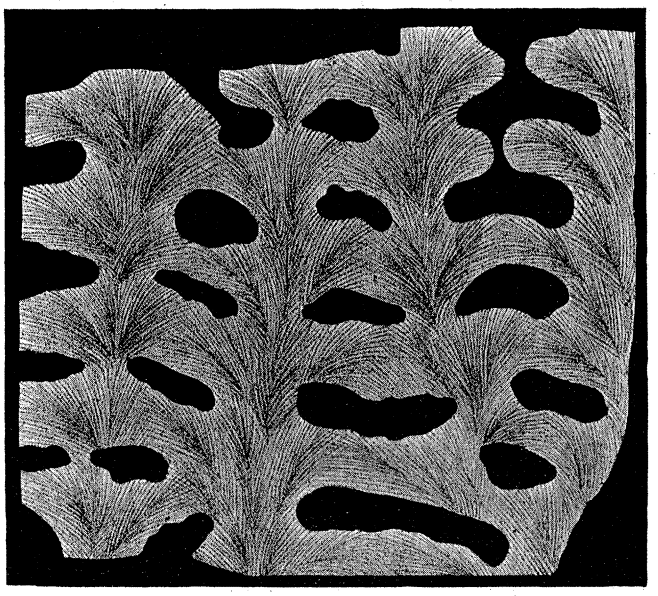
* *Cf. antea,* pp. 182–187.

(*Actinacis*). I am inclined to think the recent genus *Porites* is the genus amongst the "Perforates" which is most closely associated with these Spongiomorphid Triassic antetypes. *Turbinaria* seems to me to have in its irregularly-built cœnchyme a character which renders it distinct from *Porites* on the one hand, and from *Astræomorpha* and the Spongiomorphidæ on the other.

The general habit of *Astræomorpha*, its closely-set calyces, indistinct wall, net-like structure of all the skeletal structures, the small number of septa, styliform columella, richly-distributed dissepiments are a combination of features found, so far as I know, among recent genera only in the Poritidæ. But they are features which at once distinguish the genera in question from the Fungidæ. And I would not agree with NEUMAYR and FRECH in saying that "Microsolena (a Thamnastræid) builds a bridge to the Poritidæ" (*antea*, chap. v).

On the contrary the other indication given by FRECH of a possible connection between certain Perforates, *Astræomorpha*, and the Spongiomorphidæ, seems to me preferable. I give a microscopic section of *Heptastylis* (fig. 75) for comparison of its

Fig. 75



Heptastylis. Longitudinal section, showing the erect trabeculæ and horizontal synapticulæ. Fascicles of fibres are seen here and there in the section.

structure with *Porites*. It is one of the Spongiomorphids which shows distinct calyces, and which can with ample justice be compared with younger types among the Poritidæ.

One fact still deserves to be mentioned about *Astræomorpha*, since I have not yet seen it in published descriptions. It is that in many calyces there are traces of bilateral symmetry in the arrangement of the septa. Sometimes a main septum is

at once distinguishable. Again, other calyces in the same colony are as distinctly radial in their symmetry.

The above considerations lead me to entirely split up the sub-family Pseudo-agaricinæ, PRATZ = Astræomorphinæ, FRECH. The Recent genus *Siderastræa*, placed in it by PRATZ, is a Fungid. The Triassic genus *Procyclolites*, placed in it by FRECH, has, I believe, a much greater resemblance to simple Thamnastræinæ and Funginæ than to *Astræomorpha*. The latter genus may alone be left as a certain representative of the sub-family Astræomorphinæ, FRECH. This sub-family is probably best included under Poritidæ, at any rate, I shall provisionally place it here.

The Triassic Family Spongiomorphidæ, FRECH.

I would be much more inclined to look upon the Spongiomorphidæ than on the Stylophyllinæ as a peculiar Triassic group which soon became extinct. The resemblance to the Stromatoporoids is pointed out by FRECH, and is the most that can be said of the possible ancestry of the Triassic family. FRECH sub-divides the Stromatomorphidæ into cyclic and acyclic forms, according to the arrangement of the trabeculæ in definite calyces, or the absence of any such arrangement.

The Genera Astrocœnia *and* Stephanocœnia.

These two genera appeared for the first time in the Triassic period, had a very wide distribution in Jurassic time, and, since then, have been on the wane. It is doubtful if they are represented in recent seas. HELLER* described a coral from the Adriatic Sea, which he called *Astrocœnia pharensis*, but HEIDER,† after a detailed examination of the coral, referred it to the genus *Madracis*, one of the Oculinidæ.

The Triassic species are distinctly in a state of transition, and have still much in common with Palæozoic corals. Their septa are extremely short, and sharply distinguished from the large central area representing the tabulate area in ancestral types. In this area the spines are arranged without any definite radial or vertical system, repeating the structure seen in Cystiphylloids, or, in smaller measure, in the central part of *Endophyllum*. In Jurassic species the central (columellar) area is apparently diminished, the pali of *Stephanocœnia* having a definite order relative to the septa, and surrounding a central columellar palus.

It may be said, moreover, that no two of the Triassic species have the same number of septa in the primary cycle.

Stephanocœnia alpina has septa in two cycles of 10; *S. juvavica* has a very irregular arrangement, scarcely cyclical; the number varies from 24 to 30;

* HELLER, "Zoophyten und Echinodermen des Adriat. Meeres," 1868, p. 27.

† HEIDER, "Korallenstudien II., *Madracis pharensis*, HELLER, sp." 'Arbeiten aus dem Zool. Inst. zu Graz,' vol. 4, No. 2, 1891.

S. Schafhäutli is quite regular, with 3 cycles (6 + 6 + 12); *Astrocœnia Waltheri* has two cycles of 10; *A. Ohmanni* two of 8; and *A. hexactis* two of 6. The variations in the number of septa are seen, therefore, to be like those so characteristic of *Stylina* and its allies. Probably this is one of the reasons why *Astrocœnia* and *Stephanocœnia* were for so long placed systematically under the Eusmilinæ, E.H., in the neighbourhood of *Stylina*. They were then removed to the Astræinæ on account of their toothed septal edges. A prominently-toothed septal edge rarely occurs in any other family than Astræidæ and Fungidæ, but it has now become familiar that very often the septa of the main cycles may have toothed edges, and these of the subordinate cycles in the same calyx have edges almost smooth. The microscopic structure is, however, the same in both cases, and is the feature which must be considered in determining the systematic position of a genus.

Sections which I have made of Jurassic specimens of *Astrocœnia* and *Stephanocœnia* show agreement in the septal microscopic structure with the cœnenchymate type, *Stylophora* (*ante*, pp. 93, 94), in which the septa are neither deeply toothed nor prominently granulate. I am inclined to look upon both genera as closely allied with the family of Pocilloporidæ. Not only the septal structure, but also the general habit of the corallum, the well-developed epitheca, the irregular secondary infilling in the angles between adjacent calyces are features presenting strong similarity.

Frech has given longitudinal sections, illustrating the typical characters of the Triassic species of *Astrocœnia* and *Stephanocœnia* (*loc. cit.*, p. 33, figs. A and B). He draws attention to the difference between the loose, spinate columella in *Astrocœnia*, which is connected with the septal ends and the distinct pali in *Stephanocœnia*. Secondary compacting of the loose spines in the columellar area would produce naturally the effect of a longer septum, with irregular-sized teeth towards the centre. I have observed such appearances in many Jurassic specimens both of *Astrocœnia* and *Stephanocœnia*. This kind of septum I may call *heteromorphous*, where central spines once free from the septum become compacted with it so habitually as to be almost specific. It was already foreshadowed in Palæozoic corals and is of common occurrence in Poritidæ, Trochocyathinæ, and in some recent Astræidæ.

One important difference may be observed between the typical Jurassic species of *Astrocœnia* and *Stephanocœnia* and the representatives in Triassic age. It is that in the latter tabulæ occur centrally, while in the Jurassic species there are no tabulæ. A second interesting point is the entire uncertainty in the number and arrangement of the septa in the Triassic species, eight occurring now and then as the number in the primary cycle. While Jurassic species show regular cyclical arrangement of septa, and usually in hexameral or dodecameral type.

Systematic Significance of Triassic Corals.

Summarizing the above observations which I have myself made on Triassic and

Jurassic corals, I find the utmost corroboration of the *slowness* of the so-called "change" in the aspect of the Palæozoic fauna. To refer again to my list of Triassic corals given on p. 300, for comparison with Professor FRECH's list, p. 298, the result, as I draw it, is as follows :—

Division C is almost exclusively of *Palæozoic* character, very few species finding direct comparison with post-Triassic forms.

Division B includes genera which (with only one exception, *Stylina*) were actually placed by Professor FRECH under *Palæozoic* families. They indicate the strong Palæozoic impress still retained by numerous Triassic species.

Division A includes—

(1.) *Stylophyllinæ*, FRECH, a sub-family newly erected by Professor FRECH, showing, however, remarkable evidence of having been in active process of change, associated on the one side with Palæozoic forms, on the other identical with the early types of Eupsammidæ.

(2.) *Procyclolites*, which ought to have a quite different systematic position from *Astræomorpha*, with which it had been classified by Professor FRECH. Its microscopic structure resembles Palæozoic carinate Cyathophylloids, and it is possibly best looked upon as a curious antetype of the synapticulate Funginæ, resembling certain Cretaceous types even more than the known Jurassic relatives.

(3). *Thamnastræinæ* represented by the typical genus *Thamnastræa* of distinct Mesozoic character, and introducing the great Jurassic concourse of this extinct sub-family of the Fungidæ.

(4.) *Astræidæ*. This large family, although so profusely represented in the Triassic fauna, is of distinct post-Palæozoic character. Indeed, its preponderance in individuals, together with the striking radiate character, have done much to encourage the idea of a palæontological break between the Palæozoic and Triassic-Recent coral faunas. Yet the curious fact is that everyone admits, in a general way, the descent of this family from the Palæozoic Cyathophylloids. The latter may be said then to have most completely undergone a change in form during the interval that elapsed between Carboniferous and Triassic time. At the same time, true Cyathophyllids are present in the St. Cassian Triassic strata,* which is a somewhat older deposit than the Zlambach strata above discussed.

According to those results, I find it utterly impossible to accept Professor FRECH's dictum that "*The great change of the Anthozoa had been carried out before the Muschelkalk and after the Permo-Carboniferous period.*" I have indicated, in direct contradiction of this, the connection afforded by the *Jurassic* corals with the main groups of Triassic corals, and have brought forward evidence of a continued series of

* WILHELM VOLZ, "Vorläufige Mittheilung," "Ueber die Korallenfauna der St. Cassianer Schichten," 'Jahresb. Schles. Ges. Vat. Cultur, Naturw. Sect.,' June, 1894. There, under the sub-division *Rugosa* (in contradistinction to *Madreporaria*), the families Cyathophyllidæ (gen. *Cœlocœnia*) and Zaphrentidæ (gen. *Pinacophyllum*) are represented—each by a single genus.

changes going on during the Triassic and Jurassic ages, changes unmistakably transitional between the Palæozoic and Recent Madreporarian fauna.

CHAPTER XI.—SUB-ORDERS OF MADREPORARIA.

Edwards and Haime's Sub-Orders.

Edwards and Haime grouped the types and families which have been treated in this paper, under the sub-orders *Madreporaria Rugosa, Aporosa, Perforata.* My reasons for not accepting the sub-divisions *M. aporosa* and *M. perforata,* follow from the detailed study of skeletal features carried out in Part I. Reference may be made to chapter viii. above. The sub-order *M. rugosa* was, in the first instance, erected for Palæozoic corals (see "Brit. Foss. Corals," E. and H., "Introduction," p. 64). These are usually enveloped in a rugose epitheca, and were said to have a "septal apparatus, never forming six distinct systems as in all the preceding Zoantharia (*Aporosa, Perforata, Tabulata*), but appearing to be derived from four primary elements." The terms (1) Tetracoralla, and (2) Hexacoralla, were afterwards given by Hæckel in the same sense as Edwards and Haime's sub-orders, (1) *M. rugosa,* and (2) *M. aporosa* + *M. perforata,* respectively.

The two foregoing chapters in the present paper sufficiently point out the conventionality of these two sub-orders. The feature of "tetrameral" septal symmetry is one which was subject to slow phylogenetic change, taking place sometimes completely, sometimes less completely in genera descended from one and the same ancestral type, and in no measure limited to a particular period of geological time.

The terms Euthecalia and Pseudothecalia.

Relation of the Edge-Zone (Randplatte) to the Theca.

Of recent years Heider suggested the possibility of subdividing Madreporaria into *Euthecalia* and *Pseudothecalia.* Zoologists have also been inclined to lay some weight on the presence or absence of an edge-zone ("Randplatte") surrounding the main visceral chamber of the polyp.

Heider studied the "edge-zone" in *Cladocora* and *Caryophyllia,* and described it as a smooth lappet clothing the outer surface of the calicinal wall. The cœlenteron was typically continued into it, divided up into mesenterial loculi continuous with those of the main cœlenteric cavity.

From what is already known about the edge-zone in recent types, it may be demonstrated to be a polypal feature correlated with any one of two possible skeletal features:—

(1.) The presence of a pseudothecal thickening at some part of the calyx

(Astræidæ), or of a thickened synapticular development, *i.e.*, a modified form of pseudotheca (Fungidæ, Eupsammidæ).

(2.) The occasional retardation in growth of the theca relatively to the septa (Turbinolidæ, Oculinidæ).

This relationship observed between "edge-zone" and "skeleton," in living genera, affords a standpoint from which I have studied fossil genera, and I arrived at certain general principles explaining the probable history of the edge-zone in pseudothecate types. It seems to have been in the first place well developed in some of the colonial Cyathophyllid types, such as *Acervularia*, *Phillipsastræa*, and probably had primitively the function of a nurse-organ, allowing rapid development of buds. This is very certainly the part which it played in many Jurassic genera (ex. *Amphiastræa*, *Diplocœnia*, *Placophyllia*). Frequently the outer area, corresponding to "edge-zone," is beset with a whorl of buds. Without doubt the "narrowing of a calyx," so common in Palæozoic genera, is a similar morphological process and led, in many cases, to the formation of a temporary edge-zone.

The genus *Cyathophyllum*, with its tabulate, well-marked, central area, and broad, vesicular, outer zone, may be regarded as the antetype of most forms whose polyps have edge-zones, and this because the relations of septa, pseudotheca, and epitheca, are essentially unchanged in the simple *Cyathophyllum*, and the simple Astræid, Fungid, or Eupsammid. Yet one cannot generalize from the skeletal features since, in certain types, a pseudotheca does not occur, and there is no marked difference in the basal deposit, central, and peripheral areas.

Neither can one generalize very safely from the polypal parts, since the edge-zone may be well developed or rudimentary in apparently nearly-related genera. For example, *Dendrophyllia* is an Eupsammid in which the edge-zone has distinct mesenterial loculi; whereas in *Astroides*, another Eupsammid, the edge-zone is a simple layer, without cœlenteric loculi.

Heider,* who carefully pointed out the difference in the character of the edge-zone, was inclined to ascribe *great* importance to it, and suggested its influence on the formation of the theca. According to Heider, the types with a well-developed locular edge-zone were those in which a pseudotheca was present, while the types in which the body-wall was a mere plate of tissue were those in which an eutheca, or true theca, was developed. I am not of opinion that any such distinction can be carried out. *Galaxea*, with a true theca, has a locular edge-zone.

Heider suggested that all the Madreporaria might possibly be, on this basis, arranged in two main suborders: "Euthecalia" (ex. *Astroides*, and perhaps *Flabellum*),†

* Heider, 'Korallenstudien,' *loc. cit.*, 1886, p. 178.

† Heider's definition of the two subdivisions is made on the basis that all skeletal structures are laid down by the mesoderm (*cf.* pp. 9–11). He defines the *Pseudothecalia* as those in which the body-wall, with its three layers of endoderm, mesoderm (= mesoglœa, Bourne), and ectoderm, remains unchanged at the peripheral portion of the calyx. It is the same in polyp and edge-zone, and lays down no skeletal wall-lamella (Mauerblatt). The septa are secondarily united by their lateral surfaces,

and "Pseudothecalia" (ex. *Cladocora, Dendrophyllia, Rhodopsammia, Balanophyllia, Caryophyllia*, etc.). It is true that *Caryophyllia* appears in the published sections to have a pseudotheca, and to be in this respect more like Astræidæ than like the majority of Turbinolidæ. On the other hand, KOCH'S description of the development of *Caryophyllia* mentions the appearance of wall or ring-folds between the septa. HEIDER has thrown some doubt on these observations. Yet *Caryophyllia* is one of the best-known genera, and precisely this uncertainty shows how impracticable it would be at present to carry out a subdivision of Madreporaria into these two sub-orders. Already one may safely say most Astræidæ which have a wall are "pseudothecal." But in the case of all other families there are species and genera which require careful examination before general results can be drawn up.

ORTMANN has suggested three orders of Madreporaria, based on the thecal characters: (1) Euthecalia, (2) Pseudothecalia, (3) Athecalia.* His observations were directed largely to the appearance of the centres of calcification in the skeletal structures. He showed by transverse sections that the theca possessed tangentially-placed centres of calcification in the following:—*Flabellum, Euphyllia, Galaxea, Desmophllum, Pocillopora, Amphihelia, Lophohelia, Acrohelia.* Transverse sections of most of these genera may be seen also in the papers of FOWLER and BOURNE, frequently referred to.

ORTMANN'S arrangement of families is—

Order *Euthecalia.*

Sub-order Pocilloporacea, fam. Pocilloporidæ; *Pocillopora* the type examined.
Sub-order Stylinacea, fam. Stylinidæ; type examined, *Galaxea.*
Sub-order Eusmiliaceæ, fam. Euphyllidæ; type examined, *Euphyllia.*

Under these sub-orders naturally more families are to be included, but I cannot find any complete list given by ORTMANN.

and this forms the "pseudotheca." In the Euthecalia the peripheral part of the aboral body-wall is said by HEIDER to lay down a calcareous wall-lamella within its mesoderm layer, an "eutheca," with which the septa later unite.

FOWLER, in the course of anatomical studies, has frequently referred to the difference in the behaviour of the peripheral region of polyps with regard to an edge-zone. He, however, always places *Astroides* in the same category as *Dendrophyllia*, possessing an edge-zone intimately associated with the polypal cavities. This is unquestionably the correct view. Still, even if HEIDER cites one example incorrectly, the other, viz., *Flabellum*, gives very clear expression to his meaning. The difference of the wall in *Flabellum* and in an Astræid is a skeletal feature of the highest systematic importance, *especially when the relation of the "eutheca" to septa in simple forms and to cœnenchyme in colonial forms is properly appreciated.* For example, the insertion of new costæ alternately to the septa is a feature only present in an eutheca, never in pseudotheca. Again, in cœnenchymatous forms new costæ may be introduced in such numbers, or be so near each other in the wall of small calices (ex. *Porites*), that little room remains for "wall-lamellæ," and the calyx is then often described as without a wall, immediately surrounded by cœnenchyme. At the same time the mere presence and relative position of the costæ shows the homology of the extra-calicinal portions of the colony, *i.e.*, the cœnenchyme with the firmly-built theca, thecal costæ, and epithecal thickening in simple forms.

* Athecalia (ORTMANN), ref. *antea*, "Note on the Porous Theca," p. 249.

The Turbinolidæ and Oculinidæ are also placed under the Euthecalia.

One name is unsatisfactory in the above list, viz., Stylinidæ. The typical Mesozoic Stylinids have a pseudotheca, and not an eutheca. *Galaxea* differs from them in this respect.

Otherwise, my results agree with those of ORTMANN, in so far as all the above families have *thecæ*. Several of the Turbinolidæ and Trochosmiliaceæ, E.H., are at present being examined in this respect in the Munich Museum.

Order *Pseudothecalia*.

The Astræidæ.

Order *Athecalia*.

In this order ORTMANN places all the remaining Madreporarian families, including such types as *Fungia*, *Merulina*, *Lophoseris*, *Coscinaræa*, *Siderastræa*, *Turbinaria*, *Montipora*, *Alveopora*, *Porites*, *Madrepora*, *Dendrophyllia*, and traces them back phylogenetically to the Triassic Thamnastræidæ (= Pseudoastræinæ, PRATZ).

My results disagree with ORTMANN in this respect. If I were to accept main Orders based upon the characters of the Theca so far as yet known, I would arrange the *recent* Madreporian families as follows:—

Order Euthecalia.	*Order Pseudothecalia,*
Turbinolidæ,	Astræidæ (*excl.* Eusmilinæ, E.H.),
Oculinidæ,	Fungidæ (*incl.* Pseudoastræinæ, PRATZ),
Amphiastræidæ (type *Euphyllia*),	Lophoseridæ,
Pocilloporidæ,	Eupsammidæ.
Madreporidæ,	
Poritidæ.	

The Order *Athecalia*, ORTMANN, is, in my opinion, unnecessary, and has been based on the principle of the absence of, or porosity of, the wall. ORTMANN'S diagnosis relative to the wall in *Athecalia* is "a true wall (theca) is absent; the septa are united with one another by *synapticulæ*. These are either distributed upon the septal surfaces or combine so as to form a porous, loosely-made *cœnenchyme* or a *porous* false wall. Septa of the neighbouring calyces confluent or breaking up into the cœnenchyme or the false wall," *loc. cit.*, p. 495.

I have referred to the various points in this diagnosis in a previous chapter (*antea*, pp. 206 and 261–268). It remains to say that the cœnenchyme of *Turbinaria* and *Madrepora* is of an entirely irregular character. Synapticular rods are combined with flat dissepimental plates, and are placed now vertically, now obliquely, now horizontally. They cannot be compared morphologically with the regular trabeculate outgrowths in Fungidæ and Lophoseridæ. Besides, they are distinctly outside the

calyx. The sections which I have given of the calyces in those types show that at the peripheral limit of the calyx a thecal ring of calcification exists, which is in greater part independent of the septa.

These are skeletal features. The actual anatomical features of the polyp are in favour of my view. FOWLER'S work has shown very clearly the near affinity which exists between *Pocillopora*, *Seriatopora*, and *Madrepora*. The whole tendency of my work has been to show that the thick, peripheral deposit around the calices of the simple Turbinolidæ proves the calicoblastic activity of the same region of the polypal wall which is supported upon *cœnenchyme* in these colonial thecate types. Whether the cœnenchyme is porous or compact I regard as a minor feature. Moreover, in types which are said to have compact cœnenchyme, occasional spaces are left unfilled at parts of rapid growth, ex. *Stylophora*.

In spite of a certain attractiveness in the subdivision of the Madreporaria into two main Orders, *Euthecalia* and *Pseudothecalia*, as above arranged, I do not feel that it is fully justified in the present position of research. The very fact that the Eupsammidæ at present include one or two forms which zoologists have shown to have either no edge-zone, or a very rudimentary one, warns against premature acceptance of these sub-divisions. The most probable explanation of this is a certain retrogression in the edge-zone, and correlative increased active development of the remote neighbourhood of the polypal wall. The point is however not clear.

Again, the Stylinidæ show in their other skeletal features relationship with the Oculinidæ, yet they have a pseudotheca.

Further, *both pseudotheca and theca may be totally absent*, and yet the coral show by its septal and basal structures clear points of affinity with genera in which a wall is developed. It would be thoroughly artificial to gather such types together and remove them from what has hitherto seemed a natural position.

The farther we go back in time the greater is the number of genera which seem to have only epitheca and septa, and no tangential thecal structure. *I regard this condition as the primitive condition among Madreporaria*, and one which has been retained to the present day by a few genera, while others have developed various wall structures (*cf.* pp. 316, 317).

Embryology gives also some insight into this question, since we find in all thoroughly examined cases, that the embryo has *no theca*, but only a basal skeletal disc of attachment representing the embryonic epitheca. The primary skeletal invaginations are purely radial, and are pouched up vertically from the basal body wall resting on the skeletal disc.

It seems fairly natural to suppose that this embryological stage presents a typical picture of some primitive Madreporarian.

I picture the ancestral Madreporarian as a small disc or ring (*cf. Duncanella*) of living tissue attached by its whole basal surface. Tentacular feelers were sent out on the upper surface of the disc, and on the lower, very often stolonal or irregular

cœlenteric expansions of the disc were rendered permanent as a means of better attachment. The base of the disc and the rootlets or rugæ became strengthened by calcareous cell deposit, and formed a part of the primitive "Rugose epitheca."

A few phases of evolution having been successfully passed through, the enterprising coral may be pictured as taller and stronger with a whorl of tentacles and a number of rootlets. Its basal body-wall was pulled up and tucked in at the sides, but curled loosely round the whorl of tentacles, and so far hooded the polyp when the tentacles were retracted.

In every tuck calcareous cell-deposit gathered here and there, just as it did in the basal disc. The primitive "septal trabeculæ" and "spines" thus formed, were therefore continuous with the epitheca, and, in fact, between adjacent "septal" tucks, the ectoderm continued actively depositing epitheca.

If the curls and wrinkles of the peripheral ring of the body-wall were particularly loose, it might easily happen, with further growth, that only the innermost wrinkle kept up the original connection with the septa, while the outer wrinkles became more variable. Thus the inner part would be differentiated as a theca, and would be protected by the less regular deposit of the farther wall-wrinkles. The so-called theca and epitheca are inherent parts of one and the same tangential structure.

Should calicoblastic activity in the peripheral area prove, on the contrary, to be relatively small, and the main area of deposit be in the radial folds, the tendency towards higher complication of the septal structures would be given. Rapid upward growth of the septa demands some mode of support, and correlatively the pseudotheca would be developed. The most usual position of the pseudotheca in Palæozoic genera is at the limit of the dissepimental and the tabulate zone. The steeper inclination of the dissepiments and the depression of the polypal body-wall towards the centre of the calyx were probably the chief factors in determining the secondary appearance of a pseudotheca at that part.

At the same time, it is highly probable that the first cause of a pseudothecal development was the narrowing of the calyx so characteristic of Palæozoic corals, and connected with the process of budding.

In the course of time, the increasing strengthening of the septa and the pseudotheca would lead naturally to retrogression in the development of the epitheca. More especially would such retrogression make itself felt in colonies where vegetative budding within the calyx went on to any large extent. Thus the Astræiform colony became a fixed type.

One other modification of the primitive Madreporarian may be mentioned. Where a brood of young corals grew up together, any wall-outgrowths, *e.g.*, rootlets, readily caught each other for support; and since the coelenteron of each polyp was continued into the ramifications, the fusion of these meant an open connection between adjacent polypal cavities. Probably this was the most primitive form of a Madreporarian colony. It was at any rate very early attained in Madreporarian evolution

ex. Eridophyllum, Michelinia, etc. Old-fashioned Palæozoic colonies such as *Eridophyllum,* are admitted to have a "Rugose epitheca" and "irregular continuations"; newer-fashioned colonies, of *Turbinaria* for example, are said to have a "theca" and a "cœnenchyme"; yet I see no real morphological difference between the old and the new fashion. The costate wall has been developed as a wonderfully complete canalicular system, but the cœnenchyme in the case of Madreporidæ, Pocilloporidæ, and Poritinæ is nothing more than a ramifying modification of the primitive tangential structure (*cf. antea,* pp. 261-268).

I have thus traced the history both of the solid Turbinolid "wall" and the "Perforate wall" of the allied reef-builders back to the basal skeletal disc of the primitive Madreporarian. The theca with epithecal surface is probably more ancient than the free "inner wall" or "pseudotheca" of Cyathophylloid and Astræid types and many other facts corroborate this conclusion. The bilateral symmetry of the polyps of *Seriatopora* and *Madrepora* is in keeping with the primitive nature of their cœnenchyme.

With regard to the phylogeny of the theca, pseudotheca, and cœnenchyme in Madreporaria we may distinguish the following evolutionary stages:—

I. The ancestral stage frequent enough in Palæozoic corals—a "Rugose epitheca" without any centres of calcification in connection with the septal centres.

II.—(*a*). *Theca in solitary corals.*—The differentiation of an inner part of the epitheca as a theca possessing centres of calcification connected with the septal centres. In this case there is never more than *one wall,* composed of theca and epitheca together.

II.—(*b*). *Pseudotheca in solitary corals.*—The epitheca remains as it was, but a ring of septal thickening is marked out within the calyx at a greater or less distance from the epitheca. It appears as an "inner wall," the epitheca as an "outer wall."

II.—(*c*). *Cœnenchymate, colonial types.*—A permanent connection is formed between the polyps of a brood by means either of a light skeletal framework in the place of thick walls, *i.e.,* by a *porous* wall-growth on the "thecate" type *ex.* Madreporidæ, or on the "pseudothecate" type *ex.* Eupsammidæ, or by means of *superficial compact or sub-compact deposit* laid down in the area between adjacent thecæ, themselves compact: *ex.* Pocilloporidæ. The skeletal structures laid down between polyps have no fixed type; the rim round the growing horizon of the brood is marked by an epithecal pellicle. This epithecal pellicle is only the outer specialized zone of the so-called cœnenchyme between the polyps. It is more strongly and firmly developed and has a protective function, while the cœnenchymal part has only a circulatory function.

III.—*Pseudothecate, colonial types.*—Two distinct stages are presented, (1) the fascicular or branching colony where each member of the colony may have its pseudotheca and its epitheca well developed and appear two-walled. This stage is the original form of Cyathophylloid and, generally, of Astræiform colonies. (2). The

"fissiparous" and "meandroid" stage, where the inner wall in the middle, or near the periphery of the calyx, is the only apparent wall, and may by constant self-division of a polyp come to include several calyces. The epithecal deposit may be almost abandoned or retained strictly as a means of attachment for the colony. Meandroid colonies springing from quite different genera behave similarly in this respect, and the stage is highly characteristic of the most advanced colonial types of Astræidæ and Lophoserinæ.

The mere fact that the primitive basal and tangential structure went through these evolutionary stages, makes it impossible to use the *morphology of the theca* as a basis for the main subdivisions of Madreporaria. Clearly an Astræid which was directly descended from a Cyathophyllid might differ in this respect and have to be placed in an entirely different subdivision from its ancestral types.

Again, species of *Montlivaltia* with an epitheca, and neither theca or pseudotheca would possibly have to be removed from pseudothecate Astræids, similarly *Microsolena* from the Fungidæ and placed alongside of certain species of *Zaphrentis* and other Palæozoic corals which also had not advanced beyond the primitive stage.

Grouping of Families in the Madreporaria.

No feature has remained so steady during the long geologic ages as the fine microscopic structure of the "trabecula," or as known in its primitive form, the "septal spine." Indeed the whole microscopic structure of the septum has undergone little change. In very many cases absolute identity may be demonstrated in the fine structure and growth relations of the septa alike of the oldest and the youngest Madreporarian genera. At the same time evolution reacted also on the septa, and has induced in advanced types far greater complication than existed so far as is known in any of the primitive genera. No complication however introduces any new microscopic elements of structure. The same *fundamental lines of structure* established in the septa of primitive Madreporaria are followed in the most highly differentiated recent types; elaboration has strictly followed the first principles of septal structure. Further, *dimensions* and *form* may vary in closely related genera, but never the actual *microscopic building-up of the Septal trabecula.*

It is, therefore, to the *microscopic structure of the trabecula as well as to the fundamental lines of structure followed by trabeculæ in the septum* that I have looked as the basis of any grouping of families amongst the Madreporaria. Subordinate to that, the general habit of families helps to indicate their affinities. The following five groups of coral families are not intended to be part of a classificatory system. They will merely serve to summarize and accentuate some of the main aspects of this paper.

I take for granted all the definitions and explanations of terms which I gave in the last chapter of Part I. of this work. I refer for instance to such terms as "simple" and "compound" trabeculæ (*antea*, p. 141), "area of divergence" (p. 140), "trabecular

part" (p. 235), "growth-segment" of the septum (pp. 234, 236, 237), "fascicle" of fibres (p. 118), "centre of calcification" (pp. 125–128), etc., etc. It will also be remembered that the true original use of the term "*spine*" was (1) for spiny-looking *short projections from the inside* of the calicinal wall projections which did not, however, unite together in vertical series so as to form a septum; (2) for spiny-looking projections *up from the base* of a calyx, also not uniting to form a septum. These are the only legitimate uses of the term "spine." A *trabecula* on the other hand must have some method of attachment with its neighbours to give rise to a septum. It understands also a certain length, a sequence of growth.

MUROCORALLIA.

The Palæozoic corals had septa either composed of trabeculæ, or represented by a series of spines, and were in this sense as in others the strict forbears of all younger forms of Madreporaria. The broadest distinction which can be drawn for Palæozoic types refers to the direction followed by the trabeculæ in the septum. In some genera (ex. *Pholidophyllum, Acanthocyclus*) the *trabeculæ are directed almost horizontally inwards from the epithecate wall, and keep the same horizon of height as the wall.* Naturally, the inference is that the fleshy body-wall of the polyp was pouched inwards from the periphery, and folded radially along the septal lines just at the same level as it lay around the wall. Thus the radial and the tangential skeleton kept pace side by side in growth. A still further point is afforded by the microscopic structure, which shows that the main body of the calcareous fibres were deposited along the *sides* of the septal flaps while very little or none at all formed along the middle, *i.e.*, the apical angle of the fold. The laterally-deposited fibres are not in union along the middle of the fold, whose place is signified in the skeleton by a band varying in breadth and appearance according to the original amount of deposit laid down there, if any, and the particular nature of the subsequent changes undergone by it.

This *middle band*, which I now distinguish as the representative partly of the apical or upper deposit of the septal fold, partly of the original unfilled space between the two flaps of the septal fold, has been called the "primary septum," "dark line," etc., by former authors, while the part which I have called the *lateral* deposit has usually been spoken of as the "stereoplasm" or "secondary thickening" of the septum. The application of these terms looks fairly easy in the case which I am just discussing of septa with horizontally placed trabeculæ, or the trabeculæ making only a very low angle with the wall, but they are terms which only cause mistake and difficulty when one tries to apply them generally throughout Madreporaria, and I therefore deprecate the use of them at all (*antea*, pp. 89, 125–128, 198, 256–259).

Suffice it here to note that the septa which have their trabeculæ making a low angle with the wall, or quite horizontal, show on microscopic examination of a trans-

verse section a fairly distinct and continuous median band dividing the two side wings of the septum. The horizontal or low-angled position of the trabecula is characteristic (among the Palæozoic Madreporaria) of the *Zaphrentid* forms, in short, of these types which have a broad tabulate area in the middle and a very narrow dissepimental zone at the periphery practically embodied in the strongly built epithecate wall. The septa in these types are as a rule short, extending little into the lumen of the calyx. It is chiefly among these Palæozoic types, too, that the septa are so often vicariously represented by rows of short spines projecting inwards from the wall.

A general glance through the Palæozoic genera possessing these correlative features points to the *predominance of the tangential elements* of the skeleton. In the epithecate wall lay apparently the strength and power of resistance of the coral, the soft polypal parts being rigidly protected *within* the calyx, sunk, so to speak, below the hard outer rim of wall and epitheca. The septa, spines, and tabulæ formed merely an internal framework, which never elaborated itself to any very high degree of differentiation. The battle with the waves and with natural enemies concentrated itself clearly on the wall. There we find, in allies of these corals, all sorts of spines and tubercles, quite echinid sometimes in type, no doubt serving for the better protection, or possibly sometimes balancing of the coral.

Besides the Palæozoic Zaphrentidæ, two other families, the *Turbinolidæ* and the *Amphiastræidæ*, whose ages range from Palæozoic to Recent, have their septa built up on the same principle and show precisely the same relations of growth between the wall and the septa. A still further structural point which these three families have in common is the possession of a well-built *theca*, whose fibrous elements are set in a direction at right angles to those of the septa. I have, therefore, grouped these three families together under one main subdivision of the Madreporaria. And I have chosen a name to indicate the pre-eminence of the wall, viz., MUROCORALLIA.

The actual size of the trabeculæ will be found to vary greatly within this group. Sometimes they are extremely narrow, even thread-like to the naked eye, sometimes they are of quite appreciable width. But these of any one coral vary remarkably little in size. Their fibrous structure is always the same—*simple*, with a single "axis" or "centre" of calcification (whose shape is lens-like or rod-like when cut crossways), and the calcareous fibres are placed rectangularly outwards on either side. Owing to the low-angled position of the trabeculæ in the septum, transverse sections usually cut for a long distance through one trabecula, or pass very obliquely from one trabecula to its neighbour; hence the uncalcified axial line of one trabecula or another is always visible in the thin section and gives that appearance of a "dark band" or "light band," as the case may be, between the lateral deposit of fibres.

Very often the "dark" or "light" appearance penetrates to some distance on either side of the actual median line, marking off, as it were, an inner set of the calcareous fibres from the outer. This may, indeed, possibly have helped at the first to make she term "primary septum" be accepted. But the actual fibrous deposit is con-

tinuous throughout; it is only that the crystalline deposit laid down at or near the edge of the septal fold is sometimes set at a different angle from the later deposit, sometimes also it contains a larger quantity of uncalcified cell-material and undergoes in consequence slightly different chemical changes.

It remains to mention the structure of the "wall" in these types. The "true theca" (eutheca, p. 310, *seq.*) has its own centres of calcification, and the term was originally applied to the particular kind of theca in which microscopic transverse sections display a "dark line' with independent centres of calcification in the wall just like the one seen along the mid-line of the septum. But, from what I have already said about the septal "dark line," it will be easily understood that the presence of a similar line in the wall simply indicates that the polypal flesh took the form of a fold over the wall, the two flaps hanging down inside and outside the wall. Suppose, now, that no part of the polypal flesh hangs down outside the wall, there would be no "dark line" to mark an apical edge. Thickening of the wall would go on one-sidedly, namely, on the inside. This is the usual case among Palæozoic Zaphrentids. Suppose, again, that only a very small lip of the polypal flesh hung down outside the wall and the interior of the calyx was fairly deep, then the thickness of wall deposit would be greater on the inside and the dark line indicating the upper edge of the fold would be nearer the outside than the inside of the skeletal wall. Conversely, if the outer lip was much deeper than the inner wall lining, the position of the "dark line" would be nearer the inside. I have already mentioned the observation in *Galaxæa*, and have referred to Dr. FOWLER'S similar observations on *Lophohelia*, where the position of the "dark line" in the wall varies according to the age of the polyp.

Now, this is extremely interesting, and shows how the so-called "true" theca is but a modification of the primitive epithecate wall of corals (*antea*, p. 316). For, as any polyp forms the habit of having a lip of flesh around its wall (in other words, an edge-zone or "Randplatte") (1), the epitheca is necessarily laid down *below* instead of *at* the rim of the calyx; (2) a fold of flesh encloses the upper part of the rim or wall, with the result that a "dark line" marks the apical edge, and a two-sided calcareous deposit corresponds to the double flap of polypal flesh.

But one has only to study living Turbinolids to convince himself of the worthlessness of fixing any great classificatory value on the state of development of the epitheca or the depth of the edge-zone of polypal flesh outside the wall. I look upon the primitive theca such as we see it in the majority of Zaphrentids as a *true theca*, inasmuch as the laminæ composing it are placed *tangentially*, and are not lateral thickenings of septal deposit which have met across an interseptal loculus, as in the case of a pseudotheca.

CŒNENCHYMATA.

Exactly the same "*simple*" structure of the septal trabeculæ, and the same low-angled or horizontal direction of the trabeculæ in the septum, characterise several

colony-building families of Madreporaria—the Madreporidæ, Pocilloporidæ, Oculinidæ, and Stylinidæ. Moreover, the relations of growth between wall and septa are virtually the same. But an important difference of habit has led me to place these families in a separate group. The *Zaphrentidæ* are exclusively solitary corals; the *Turbinolidæ* may be also said to be solitary corals, for only one or two isolated cases of a branching colony have been cited; the *Amphiastræidæ* include both solitary and colonial corals, but the corallites of a colony always retain a high degree of individuality, since each member of a colony is surrounded by its own distinct epithecate wall.

On the other hand, these families—the Madreporidæ, Pocilloporidæ, Oculinidæ, and Stylinidæ—only exist as colony-builders. The colonial aspect also is the most marked feature about them, it is in the living state that of innumerable tiny polyps embedded in a common cœnosarc. The polyps carry on the active vital functions, the cœnosarc is circulatory and nutritive, very often also it carries on a sexual budding. In the dry skeleton one sees the corallites surrounded by skeletal deposit, which varies a good deal in its actual form, but goes generally under the name of "cœnenchyme." It is in reference to this striking and invariable feature in these families that I have chosen the name of *cœnenchymata* for the sub-division.

At the same time, not *all* cœnenchymatous corals are included here, only those which possess the characteristic trabecular and septal features.

The trabeculæ then are all *simple*, they are almost uniform in size in any one coral, they are either perfectly smooth externally or are marked by regularly-spaced small granulations, their apices end smoothly at the septal edge, or give rise to very fine serræ of equal size, like the trabeculæ themselves.

The position of the trabeculæ in the septum is like that of the *Murocorallia*, whenever, as in them, the septa are not prominent, but keep the same horizon of height as the wall or are even sunk below it. It is true that amongst this group there is a tendency for the septa to become rather more prominent and correlatively for the trabeculæ to take up a higher angle with regard to the wall. Similar advance is being made indeed among the Turbinolids. Still, these external appearances to which I have just been referring, are good practical guides in classification. Of course, the sure guide is always the *microscopic*, the *simple* character of the trabeculæ, the lens-shaped axes of calcification, and bi-symmetric arrangement of fascicles.

Whilst these are all resemblances in the structural plan of the *Murocorallia* and the *Cœnenchymata*, a difference at once arises in consequence of the cœnenchymatous development. Costal radial structures are present in the cœnenchyme, and their trabeculæ are placed in a direction exactly opposite to that followed by the trabeculæ in the septa. The costal radial structures may be continuous with the septa through the wall of the corallite, or they may be introduced at the wall alternately between septa. The reverse position of the trabeculæ in septa and costæ may be seen in the illustrations of cœnenchymatous types above (figs. 2, 35, 56).

A true wall (*cf.* pp. 158, 159) was primitively present in all these families, and has been retained in the great majority of genera. But especially among the Stylinids, more rarely among the other three families, the true wall became obsolete, and the inner limit between tabulæ and dissepiments became fixed as the wall of the corallite. This only helped to enlarge the area occupied by cœnenchyme in these types, although the original limit is, in many cases, perhaps still indicated in living polyps by the fact that a fairly wide lip or "edge-zone" with mesenteries extends beyond the wall of the corallite, and continues the mesenterial canals beyond the visceral cavity of the polyp over the costæ and cœnenchyme. This edge-zone passes then imperceptibly into true cœnosarcal flesh, clothing these parts of the cœnenchyme which are more remote from the corallites, and as a rule less regularly built.

Septocorallia.

I have already described under *Murocorallia* the one type of trabecular structure and direction in the septum, which characterised a very large number of the earliest known corals. The other type which stood in strong contradistinction to it was shown by the ancient Cyathophyllids. The septa of the Cyathophyllids were as a rule of considerable breadth, that is, they projected a long distance into the lumen of the calyx. Correlated with this, is the fact that the central tabulate area was relatively small, while the broad peripheral area had a rich, basal deposit of dissepiments in the interseptal loculi. The septa had a greater extent of surface, speaking generally, in Cyathophyllids than in Zaphrentids, and that fact in itself sufficiently explains the greater elaboration of their trabecular structure. Strength and firmness seem to have been the law governing the septal skeleton, and clearly the attainment of this might call for considerable deviation of plan in the arrangement of trabeculæ according to the dimensions or shape of the septum.

In the Cyathophyllids the ground-plan was to have all the trabeculæ pointing to the upper edge of the septum. It may be observed in living corals that the shape of a septum frequently goes on changing during the growth of a young polyp, and the first-formed trabeculæ cannot, in that case, point to the ultimate upper edge of the septum in its mature shape and position. But the actually growing trabeculæ do so all round the septal edge. The shaping of themselves, so to speak, according to the shape of the septal edge at any particular period, causes the trabeculæ to be very different in their size. Some are much broader and, indeed, thicker than others. The smaller are always distributed near the inner edge of the septum, the larger occur at the more exposed parts of the septum, *i.e.*, usually where the curve of the upper edge is greatest.

The actual arrangement of the trabeculæ in the mature Cyathophyllid septal type, is that the trabeculæ are (1) either *all* directed *inwards* and upwards from the epithecate wall towards the centre of the calyx, or (2) the trabeculæ fan out

right and left in the septal plane, passing on the one hand *inwards* and upwards, on the other hand *outwards* and upwards to the septal edge. The latter variety is by far the most general, the first variety being practically limited to some early types. In both varieties the trabeculæ meet the septal edge at high angles; their apices indeed form practically right angles with it in the case of curving septa. Curved septa are however rather exceptional among Palæozoic genera. They are present notably in one or two genera, whose affinities have usually been considered doubtful, I mean the low discoid genera, like Palæocyclus and Hadrophyllum, where the septa although low have a well-curved edge and trabeculæ, diverging in fan-like form right and left.

It will at once be seen that this arrangement of trabeculæ is bound to give a different aspect to the septal edge. Whereas in the Murocorallian type the trabeculæ lie *along* the septa, making a very small angle with its upper edge, they seem here to stand up in the septum and present their apices freely at the growing upper edge. A transverse section is bound to show some difference in appearance, and the difference will be greater in proportion as the trabeculæ in the latter type happen to be big and strong—in other words in proportion as their axes are at greater distances from one another, for each trabecular axis shows a certain uncalcified part in section, while the fibrous part of the trabecula is disposed more or less radially around the axis. The trabecular axis instead of being lens-shaped in transverse section, is really only a point or group of points in well-preserved specimens, and the term "centre of calcification" was originally given to describe exactly such a trabecular axis seen in transverse section.

In the first part of this paper I have described in full the sections made through several leading types of Astræidæ and Fungidæ (*cf.* pp. 127–189). It is therefore unnecessary for me to repeat here the details of the microscopic structure characteristic of these two large families of Madreporaria. The important fact is that these younger families agree with the Palæozoic Cyathophyllids in the essential features of trabecular structure, and in the position of the apices of trabeculæ at the upper edge of the septum. Some of these younger types have precisely the same distribution of trabeculæ in the septum as the older types. Others again have a more elaborate system. Instead of having only one area of divergence in the septum from which trabeculæ fan out to the right and left and vertically upwards, these elaborate forms have several such areas (*cf.* figs. 14, 15, 37, 38). These variations are always associated with a specially large size of septum, or with rich toothing and granulation of the septum. As I have already said, however, no degree of elaboration alters the fundamental law that the free apices of the trabeculæ are at all periods of growth directed towards the upper edge of the septum for that period.

The differences in the septal structure of the Palæozoic Zaphrentids and Cyathophyllids would seem to indicate a simpler development of the mesenterial muscles in the former. Certainly these differences have not become less in the younger

families descended from these, and the anatomy of the typical Turbinolid and a typical Astræid gives full evidence of the fact that the simpler septal structure answers to a less pleated, less highly differentiated condition of the muscular thickening of the mesenteries.

It is in the same three families, viz., the Cyathophyllidæ, Astræidæ, and Fungidæ, that the *compound trabecula* reaches its highest and most varied development, and that the granulations of the septum in consequence are most elaborate. Many of the forms have been described above (figs. 68, 69). The apparently radial symmetry of the fibres around an axis is in reality the result of the small bunches of fibres which I have called "fascicles" being arranged around an ideal axis. The appearance of several centres in transverse sections of a compound trabecula is produced by the section meeting the origin of the several fascicles. Now some of the genera belonging to these families are entirely composed of compound trabeculæ, others again have compound trabeculæ compactly cemented together by simple trabeculæ, in still others the trabeculæ are all simple, but they differ greatly in size and are grouped together in such a way as to make the effect rather that of flat, spread-out compound trabeculæ (*cf.* *Mussa* p. 133, fig. 18, and p. 123, fig. 14).

A true wall exists in very few of these types. It may be said generally that the primitive members possessed an epithecate wall, but that this wall had already become retrograde in the greater number of Mesozoic types. On the other hand a pseudotheca had made its appearance in a fair number of Palæozoic types and became almost general in the younger families. The retrogression of the theca and the incoming of the pseudotheca is a skeletal feature correlative with the whole tendency displayed by these three families—the tendency to increase the importance of the septa. The septa and not the wall have practically the whole weight of the polyp to support, and hence arose their spined or dentiform edges and their thickly granulated sides.

The predominating part played by the septa in the skeleton of these types has induced me to choose *Septocorallia* as the name of this group of three families—the Cyathophyllidæ, Astræidæ, and Fungidæ. The name is also designed in contrast to the group of *Murocorallia*.

Spinocorallia.

Although by far the larger number of the Palæozoic *Madreporaria* belong to the *Murocorallia* and *Septocorallia*, there still remain a few types, *Cystiphyllum* and its allies, with a quite peculiar character of septa. Some indeed had no septum properly speaking, but only consecutive rows, regular or irregular, of loose spines placed upon the basal skeletal elements. These spines frequently grew together and gave rise to a patchy, interrupted kind of septum. The Palæozoic types of this character are usually classified as Cystiphyllidæ. The Mesozoic period saw a farther development of such genera. The spines frequently attached themselves both lengthways and sideways so as to produce septal trabeculæ. Still, however, many spines remained

free and prevented the same regularity of plan in the arrangement of trabeculæ which marks the septa of other types. Even among the recent representatives of these forms, the septa seldom show any very well-defined law determining the direction of their trabeculæ, and the looseness of many of the "trabecular parts" still indicates their past history as loose spines set in the calyx. I have classified these Mesozoic and younger forms in the family of Eupsammidæ.

Wherever a definite arrangement of trabeculæ is presented by an Eupsammid genus it approaches most nearly to that of the *Septocorallia*. It shows either highly-inclined parallel trabeculæ or irregular fan-shaped groups of trabeculæ. The trabeculæ are short, and successive trabeculæ rarely fit on exactly end to end, with the result that irregular gaps are left in the septum. It is just this irregularity which essentially distinguishes all Eupsammids from Astræids and Fungids.

The microscopic structure of trabeculæ, which unite as a septum, likewise agrees with that of the *Septocorallia* in the main, but the axes are lens-shaped, the groups of calcification centres elongate, and the arrangement of the fibres assumes in consequence more the appearance of bisymmetry than of radial symmetry in transverse sections. Nevertheless, the trabeculæ are really grouped, and the fascicles have a very distinct character, the primary part of the deposit near the origin of the fascicle showing crystalline fibres set rectangularly to the axis, while as the deposit is farther remote from the origin the crystalline fibres become more and more oblique in their setting. And it is this very principle, together with the lens-like form of the axes which produces in transverse section of an Eupsammid septum the appearance of an inner and outer septal deposit on both sides of the mid-line. No doubt this kind of appearance gave rise to the idea of a four-leaved septum held by some palæontologists. But these are appearances shown only by particular sections, and owe their explanation to the facts I have just indicated.

If I were to go on appearances, I might say all septa in which the trabecular axes are lens-like in shape and close together, *appear* to be at least *two-leaved* in transverse sections, in some cases *four-leaved*. Whereas all septa in which the trabecular axes are thread-like or rod-like in shape, and are not very close, *appear* to be a *single-leaf* in transverse section, in some cases *three-leaved* (*i.e.*, where the deposit near the origin of fascicles differs in its crystalline setting from the deposit more remote). But these appearances cannot lead with any security to a systematic analysis of corals.

Thus, one must not be deceived by the appearances of Eupsammid transverse sections. The affinity of this family is undoubtedly rather with the Astræidæ and Fungidæ than with the Madreporidæ in spite of EDWARDS and HAIME'S classification of it along with the last-named family among the "*Perforata*" (*antea*, p. 201). And this seems all the more reasonable in the light of the parallel fact that its Palæozoic antetype, the Cystiphyllidæ, has marked affinities with the Palæozoic antetype of the Astræidæ and Fungidæ, namely, with the Cyathophyllidæ.

The same fundamental feature which distinguishes the septa of Eupsammids gives also the peculiar character to its wall, costal, and cœnenchymal elements. The free spine is everywhere the skeletal basis, and has given rise in a number of genera to an irregular synapticular network around the periphery, where costal and basal elements combine to build up a porous wall structure. The same elements extend as a porous cœnenchyme in colonial types. The true wall present in primitive types became then greatly modified in the course of time.

The predominance of the spine in all primitive types of this group, and its influence in the particular line of evolution followed by all the skeletal parts in younger types, have suggested to me the name of *Spinocorallia* for the group.

I provisionally include the ancient family of *Archæocyathidæ* within this group in addition to the Cystiphyllidæ and Eupsammidæ. I do so with some hesitation, since I have not had an opportunity of personally examining the Archæocyathidæ, and can only judge of the affinities of the family from published descriptions.

Porosa.

The family of Poritidæ is practically specialized as a reef-building type. Considerable areas are covered by the spreading growths of genera belonging to this family. Their most striking structural features seem to me to be the net-like meshes formed by their trabeculæ in all the radial and tangential skeletal parts, and the rapid succession of fascicles in individual trabeculæ. These features are undoubtedly correlated with their life-habits, since rapidity of growth and lightness of skeletal framework are both advantageous to an extensive reef-growth of any one coral. There is no great elaboration of calyces, simply a few septa, of quite uncertain number, are marked out here and there in a circular group. These circular groups are closely packed together or are far apart from one another, quite according to adventitious circumstances. In the main mass of any reef-growth the trabeculæ stand up erect in the septa of these calyces just as they do in the intervening skeletal parts. But often some particular position of the calyx has the effect of producing deviation from this rule, and causing the trabeculæ to grow obliquely. In small colonies it is frequently the case that the trabeculæ make an angle of about 70° or 80° with the calycinal rim and diverge inwards to the calyx, and outwards away from the calyx. This becomes even more marked in the calyces near the periphery of a small colony.

As may be imagined, the divergence of trabeculæ at once causes a resemblance between such colonies and an Astræid or Fungid colony. But we have here only an external resemblance. The relation of the septa both to the tangential and to the basal structures, affords important distinctions between the Poritidæ and both of those families. Microscopic examination, moreover, reveals fundamental differences in the fibrous composition of the skeleton.

Besides, I hold that as the Poritidæ are reef-builders on the grandest scale known

in the Madreporaria, it is the reef-type which should be taken as the standard for the family, and not the small astræiform colonies formed by some species.

Septal and mural trabeculæ in Poritidæ are only distinguished from the trabeculæ in the rest of the skeletal parts by being, as a rule, more closely matted together by interstitial secondary deposit. The microscopic structure in all trabeculæ of Poritidæ is always grouped, with the fascicles of any particular "trabecular part" arranged circularly at successive planes of origin. The branching-out of the fibres of the fascicles produces a corresponding bulging-out all round the trabecula at the emergence of these fascicles. Thus a succession of trabecular parts is like a nodose stem where the thick parts correspond to the emergence of numerous fascicles belonging to each nodular portion, but do not form the cross-bars (synapticulæ).

If one seeks to compare this with some of the Fungids which have fenestrated septa, it will be found that the fascicles have their points of origin at or near the base of each trabecular part in the latter, and the bulging-out practically forms the pseudosynapticulæ.

The pores characteristic of the skeleton of Poritidæ are between the small parts of the adjacent trabeculæ. Another set of pores, however, arise in consequence of the "true synapticulæ" (*antea*, p. 222), which cross the interseptal loculi, and whose size and structure repeats that of an individual trabecular part. Thus the whole framework has the appearance of similar rods set crossways. In most cases, however, a fine vesicular tissue of dissepiments is also deposited in the midst of the rod-scaffolding.

The Triassic Spongiomorphidæ described by Professor FRECH (*cf. antea*, p. 307) show the same essential features as the reef Poritidæ and may, I think, be safely included with them as an independent group, to which I give the name of Porosa. There are, too, certain ancient forms which from the descriptions seem to have much in common with Poritidæ. I refer to the genus *Thecia* and its allies. The ancestry of the Spongiomorphids and Poritids will have still to be thoroughly investigated. So far as my reading goes, the Theciidæ appear to be at least close allies.

It comes to be a question how far the recent Poritidæ are related with the recent Madreporids. The external signs on which EDWARDS and HAIME chiefly founded their group of *M. perforata*, including in it Eupsammids, Madreporids, and Poritids, carry no longer any real weight. Porosity of the septum may be seen to a certain extent in a few Astræids, most Fungids and Eupsammids, and in all Poritids, whereas the septum of Madreporids is, as a matter of fact absolutely compact. Such a feature only leads away from the fundamental laws of coral structure.

A sure indication of relationship between the Poritidæ and the cœnenchymatous group generally, is afforded by the peripheral arrangement of the skeletal elements. The introduction of new costal trabeculæ in the wall, the multiplication of costæ as the distance from the wall increases, the variation in the area covered by the cœnenchymate skeleton, and even in its precise form, are all features which show

strong resemblance of habit between the Cœnenchymata and the Porosa. At the same time, the calyces and the trabeculæ of the latter have too many distinctive features to permit actually uniting the two groups in the present light of our knowledge. It may be that zoological investigations will advance this matter, which is certainly one of the most interesting fields of research in the whole of the Madreporaria.

*Phylogenetic Scheme of Madreporaria.**

I now subjoin a general phylogenetic scheme designed for the purpose of showing at a glance the main lines of generic descent followed during the working-out of Madreporarian evolution. I have entered the most familiar Madreporarian genera upon particular curves corresponding to the geologic periods which seemed to mark the most distinct phases passed through by corals. These periods are—

(1) Cambrian to Devonian,
(2) Carboniferous and Permian,
(3) Triassic,
(4) Jurassic,
(5) Cretaceous and Old-Tertiary,
(6) Young-Tertiary and Recent.

Each of these six periods of time forms what I might call a natural moment or phase in the history of corals. Each successive age saw the retrogression or extinction of many of the types which had flourished in the preceding age, while some newer form of coral life reached its high-level of adaptation and success. I might institute six sub-orders of Madreporaria for these six geologic periods with quite as much right as underlies the sub-orders of Rugosa (*Tetracoralla*) and *Hexacoralla!* The result would, at least, be less misleading, since it would profess to be nothing but a convenient *historical* subdivision of the Madreporaria! And this is indeed a most useful method of studying any order of animal life—to trace the rise and fall of each successive wave of change that swept over it, to gather the poor broken types and watch the farther course of those that floated on, to scan the rocks of old ocean beds and reason out the why and wherefore of the main tumults of change and migration which shook the animal world.

These old sub-divisions of Rugosa, *Tetracoralla* and *Hexacoralla*, have therefore done their service to the knowledge of Madreporaria. They gave expression to an idea that the corals of the Palæozoic world ceased to exist and a new class of

* A few genera in the scheme (p. 331) marked with an asterisk have been erected lately by myself; the descriptions of them and illustrative figures will be found in my "Monograph of the Jurassic Corals from Stramberg" ('Paläontologische Mittheilungen,' Koch, Stuttgart, 1896).

corals began to people the seas in Triassic time. As the science of Palæontology advanced, this idea was felt by many to be out of touch with the march of evolution which could be traced satisfactorily in so many other orders of animal life. Research concentrated itself more or less on the question. QUELCH, ORTMANN, and others showed the weakness of the sub-divisions; the names were disowned, and others suggested. Still, the best palæontological authorities at home and abroad felt that for practical purposes none better were forthcoming than HÆCKEL'S or MILNE EDWARDS and HAIME'S, and have continued to give their countenance to names which express only an outworn idea.

My own opinion is that the most intelligent way of studying corals is not to approach them by means of any fixed system of sub-divisions, but by some such way as I have tried in drawing up the Phylogenetic scheme below, where the worker first studies the anatomy of the soft parts and the structure (microscopic) of the skeleton in one common type of each of the living families of corals. According to my classification there are ten of these. Then, having a general idea of the physical conditions characteristic of the six geologic periods enumerated above, it is no very difficult matter to work back through the outstanding types in each of the past ages. Thus one cannot fail to note how the types approach each other in the preceding ages, and how the whole many-branched order of living Madreporaria springs from probably two main trunks. [I have borrowed two names, the *Zaphrentoidea* and the *Cyathophylloidea*, to signify the two parent trunks, each with its ramifications of younger families. These names were given by Professor NICHOLSON* to designate Palæozoic groups of families; a third Palæozic group erected by him was the Cystiphylloidea. At the same time, as it may be open to misunderstanding if I include Mesozoic and Tertiary families under names which were previously of Palæozoic application, I think it well to suggest alternative terms for the two parent trunks. The Zaphrentoid families may be called *Madreporaria Haplophracta* in reference to the simpler structure of the septa, while the Cyathophylloid families may be called *Madreporaria Pollaplophracta*, referring to the more complicate structure of the septa :—

Zaphrentoidean Families or *Madreporaria Haplophracta:*
Zaphrentidæ, Turbinolidæ, Amphiastræidæ;
Stylinidæ, Oculinidæ, Pocilloporidæ, Madreporidæ.

* As used by Professor NICHOLSON, the terms Zaphrentoidea and Cyathophylloidea are to all intents and purposes identical with the use made in this paper of the names Zaphrentidæ and Cyathophyllidæ. The *family names*, *Zaphrentidæ* and *Cyathophyllidæ*, are not used in the same latitude of meaning by different authors. Professor NICHOLSON makes each of them only one member of a Palæozoic group of families, and to these groups he gives the names respectively of *Zaphrentoidea* and *Cyathophylloidea*. In my arrangement of families I have accepted the usual *wide* sense of the *family* names.

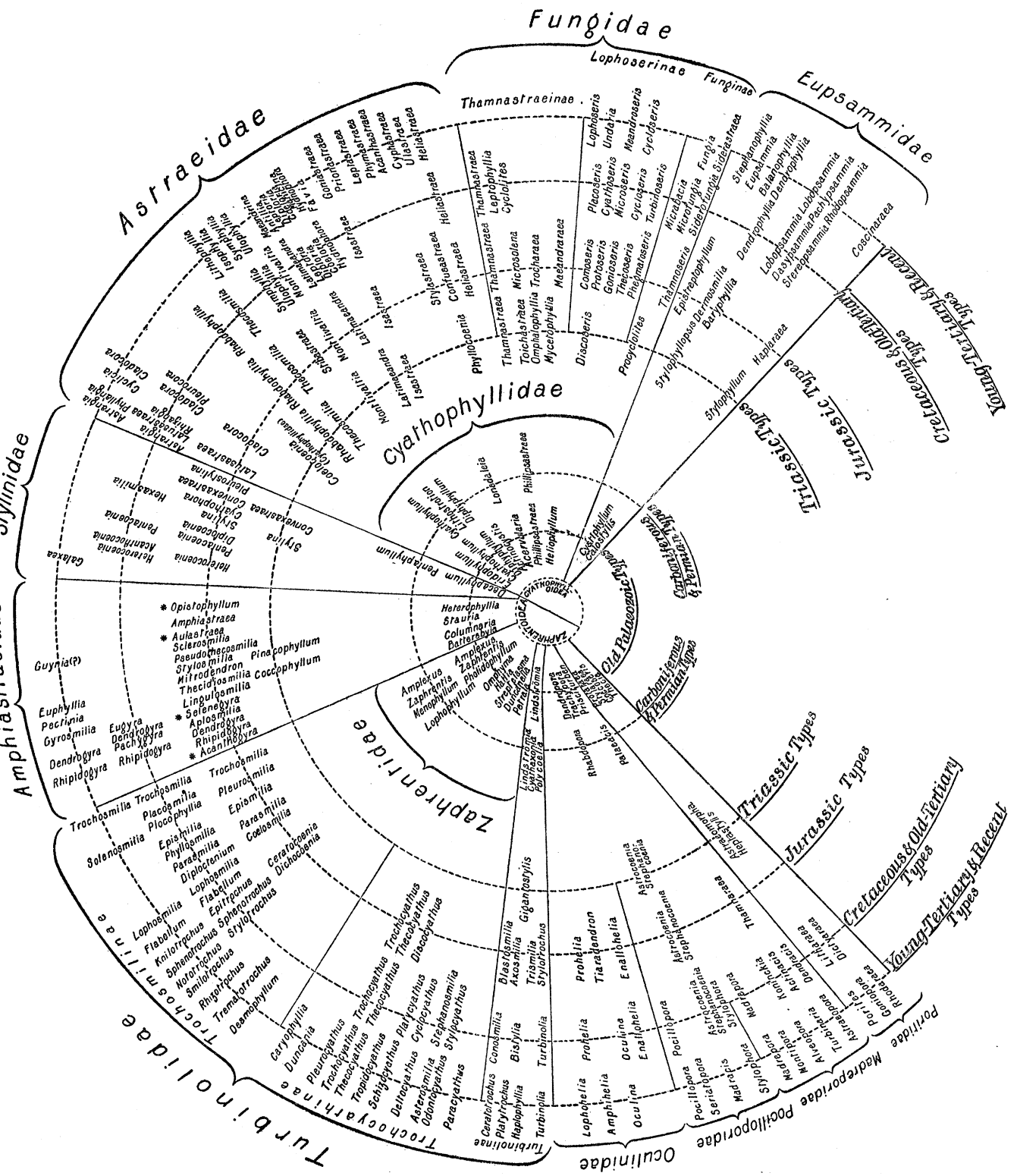
Cyathophylloidean Families or *Madreporaria Pollaplophracta:*
Cyathophyllidæ, Astræidæ, Fungidæ;
Cystiphyllidæ, Eupsammidæ.

The Haplophracta have retained very simple trabecular structure in their septa. The trabeculæ are small and uniform in size, the fibres are bisymmetrically arranged, the centres of calcification very closely set in the median plane of the septum. The septa of the forms included here have been usually described as "smooth-edged," and either with "smooth septal surfaces," or with "rows of granulations parallel to the septal edge."

The Pollaplophracta have attained greater variation and complication in the trabecular structure of their septa. The centres of calcification, instead of being uniformly spaced along the median plane of the septum, are aggregated more thickly at certain intervals. When the "centres" are placed serially in each aggregate, the fibres form a long elliptical figure in cross-section, but when the "centres" crowd still more closely together, the fibres radiate out and form practically a circular figure around them. Thus we pass from the bi-symmetric to the radio-symmetric trabecula, and the progressive stages are shown in the early members of the Pollaplophracta. Such elliptical and circular groups of fibres really correspond to a number of combined trabeculæ, and give rise to prominent granulate ridges on the septal surfaces, ending frequently in apical teeth at the septal margin. The elaborate structure of these septa is a skeletal feature in keeping with more elaborate musculature of the mesenteries in the living polyp, just as the simpler, smoother septal structure corresponds with less specialization of the mesenteries.

I divide, then, the Madreporaria into two great groups—an *old-fashioned*, primitive group, conservative of type, slow of advance, prone to retrogression—and a *progressive* group which has always been in the forefront of evolutionary advance, quick to adapt, seldom retrograde. These are characteristics true not only of the structural features of their septa, but throughout the whole calyx.

The affinities of the reef Poritids must remain doubtful until an exhaustive anatomy of their soft parts has been accomplished. It is possible that they may have sprung from an independent parent trunk, the same from which the Triassic Spongiomorphidæ, and certain Palæozoic types, *e.g.*, the Theciidæ took origin. —12*th October*, 1896.]


Fungidae
Lophoserinae
Funginae
Eupsammidae
Astraeidae
Thamnastraeinae.
Cyathophyllidae
Stylinidae
Amphiastraeidae
Zaphrentidae
Trochosmiliinae
Turbinoliinae
Trochocyathinae
Oculinidae
Madreporidae
Poritidae
Young-Tertiary Types
Cretaceous & Old-Tertiary Types
Jurassic Types
Triassic Types
Carboniferous & Permian Types
Old Palaeozoic Types

CHAPTER XII.—GENERAL SCHEME OF CLASSIFICATION.

Order Madreporaria.

Family :—*Zaphrentidæ.* E.H.

Solitary corals.

Septa always pinnate in their mode of increase; well-developed, occasionally represented by series of horizontally-placed spines projecting inwards from the wall.

One to four fossulæ present.

Base of the calyx formed by broad tabulæ; a very narrow zone of dissepiments is sometimes present peripherally.

Tangential thecal deposit* present within a well-developed epitheca.

Family :—*Turbinolidæ.* E.H. (emend. Ogilvie).

In this family I include, for the first time, a large number of genera which have been previously classified amongst the *Eusmilinæ* (fam., Astræidæ, E.H.). I also place here various Palæozoic and Triassic genera previously called *Cyathaxonidæ* (pp. 269, 270), and I have re-arranged the Turbinolid genera in Sub-families.

Solitary rarely colonial, corals.

Radial insertion of septa typical, pinnate insertion occurs in a few Palæozoic genera.

* Compare my remarks on "true theca" (p. 320). The absence of any distinct "thecal" centres of calcification in primitive Madreporaria indicates that invagination took place originally only in radial, *i.e.*, septal, lines. The "epitheca" was the primitive base and periphery in one.

Calcareous laminæ, if deposited on the complete inner surface of the epitheca, would give rise to *solid laminar deposit at the base of the calyx*, and to so-called "*secondary thickening*" *around the calyx.* In other words, the *basal deposit of Turbinolidæ*, such as we find it in living types, is probably only a remnant of the primitive epithecal lining of Madreporaria, and is certainly an exact homologue of the *wall* of Zaphrentidæ.

If we follow the history of this primitive epithecal lining farther, we find that while retained in the basal portion of the Turbinolid calyx, its form became modified round about the calyx, owing apparently to the pouching or rolling up of the soft tissues peripherally, as well as radially, during the upward growth of the polyp. Thus, too, the epithecal layer lagged behind, and a "true theca" became specialized, whose "centres of calcification" marked the position of the peripheral folds. The only difference between the "true theca" of Turbinolids and the primitive theca of Zaphrentids, is that the former is a double set of calcareous laminæ, the latter a single. Their structural relations to the septa are quite the same.

The *epithecal pellicle* of Turbinolidæ has usually the appearance of wound threads of calcareous substance, or it may be slightly coloured and look like a rough bark. In no case is it so purely crystalline as the calcareous deposit of the rest of the skeleton. Apparently, it contains a large amount of organic matter, as in the case of the median plane ("dark line") of septa and wall.

Base of the calyx never tabulate; usually a solid laminate deposit is formed, more rarely dissepiments occur.
A columella or pseudocolumella is almost always present.
A true theca or pseudotheca is present peripherally, in all cases coalescent with the epitheca.

Sub-family 1.—*Turbinolinæ.*

Solitary corals with round calyces and large styliform or fasciculate columella. No pali-septa, never lobed, their edges smooth.
Basal deposit laminate and solid, or scanty dissepiments.
Bilateral or radial symmetry of septa.*

Sub-family 2.—*Trochocyathinæ.*

Solitary corals, rare occurrences as colonies.
Calyx round, septa radially arranged.
Columella present or absent. Pali always present in one or more whorls.
Basal deposit laminate, or scanty dissepiments present.
True theca or pseudotheca present peripherally. Thecal centres of calcification are frequently zig-zagged round the calyx. Epithecal basal plate present—rootlets never developed.

Sub-family 3.—*Trochosmilinæ.*

Solitary corals with elliptical or elongated calyces.
Columella lamellar, may be replaced by pseudocolumella or be absent. No pali.
The upper edges of septa are frequently crested at the calicinal lip. True theca always developed.

Tribe :—*Desmophyllaceæ.*

Basal deposit absent or in the form of solid laminate thickening of skeletal parts.
Rootlets very often present (gen., *Desmophyllum*, *Flabellum*, *Sphenotrochus*, *Smilotrochus*, etc.).

* The double row of "dimples" in the wall of *Turbinolia*, between any two neighbouring septa and the additional costæ between the double series, is an interesting morphological feature, since it is one also presented by the cœnenchymatous types, *Turbinaria* and *Madrepora*. A Miocene Australian (solitary) genus *Trematotrochus* has pores in its theca in the same relative position as the "dimples" of *Turbinolia* and the "pores" of *Turbinaria*. The few colony-building Turbinolid genera are said to have buds which "ascend in growth and join others by their epitheca." This is precisely the process which the study of structural features led me to accept in explanation of the cœnenchyme in Oculinidæ, Pocilloporidæ, and Madreporidæ. The calyces in all those families show closest relationship with the Turbinolidæ (*cf.* chap. viii.).

Tribe :—*Trochosmiliaceæ.*

Basal deposit present as dissepiments.
Rootlets never occur (gen., *Trochosmilia, Pleurosmilia, Placosmilia, Circophyllia,* etc.).

Family :—*Amphiastræidæ,** OGILVIE.

Mainly colony-building, seldom solitary corals.
Colonies massive or bushy, rarely meandroid. The whole colony as well as the individual corallites covered with strong epitheca.
Septa never pinnately inserted in mature calyces; well developed or represented by horizontally-placed spines.
No fossula present; but bilateral symmetry of the calyx always well marked by means of a main septum.
True theca present.
Base of the calyx tabulate or dissepimental, the dissepiments in the peripheral part are usually placed at a high angle and give rise to a false "inner" wall.

Pinnate insertion of the septa has been observed in the young calyces of a few examined cases (*cf.* p. 291). And frequently the septa are pinnately arranged in the calyx with reference to a main septum, so that a group of longer septa is present posteriorly, and short septa are present in the anterior part of the calyx. In this family I would include the Palæozoic genus *columnaria,* which has hitherto been so variously placed in classification.

The Amphiastræidæ may be regarded as colony-building types directly descended from typical Zaphrentid genera. The families Zaphrentidæ and Amphiastræidæ are the only two in which bilateral symmetry of the septa is a constant systematic feature. In all other families its occurrence is occasional. In the same colony often one member may have it and another not. Bilaterality is atavistic in such cases. It may be inherited and constant in *Seriatopora,* certain genera of *Madrepora,* etc., yet the hexameral symmetry of related types and genera is sufficient to show that bilaterality is giving place to radial symmetry even in those cases.

The lamellar columella in the Trochosmiliaceæ is undoubtedly the representative of

* *Amphiastræidæ*:—This newly-erected family will be found fully described in my "Monograph of the Stramberg Upper Jurassic Corals" ('Palæont. Mitth.,' Stuttgart, 1896). One of its most interesting characters is the primitive nature of its modes of budding. The most usual is so-called "tabular" and "endothecal" budding. Or an incomplete inner wall is frequently formed within the calyx, and buds develop in the cut-off corners of the calyces. In other words an "edge-zone" is formed within the calyx during periods of rapid vegetative budding. Again the contraction of the calyx may give rise to one bud centrally; analogous contraction of the mother calyx may still be observed in a recent Turbinolid, *Schizocyathus.*

a "main" septum; in Jurassic species it is as a matter of fact a long septum. Yet we see how it gradually becomes less developed, gives place in recent genera to a pseudo-columella, or is rudimentary.

Family :—*Stylinidæ*, KLZ.

Colonial corals, massive, astræiform, or incrusting.
Septa never pinnately inserted and no fossulæ present.
Septal symmetry always radial, septa alternating in length and developed strictly in cycles (4 or 8, 5 or 10, 6 or 12 = primary cycle).
The septa leave a central space free, occupied by tabulæ or a columella.
Dissepiments present peripherally and throughout the cœnenchyme.
True outer theca sometimes, inner pseudotheca between calyx and cœnenchyme always present; cœnenchyme light, with costæ strongest at the calycinal rims.
Epitheca well developed on the base of the colony and frequently encircling the individual corallites.

The genus *Stylina* and its allies were classified by EDWARDS and HAIME in the sub-family Eusmilinæ, therefore in the family of Astræidæ. I have erected these genera into an independent family for reasons referred to above (pp. 157–160, 221) but only discussed fully in my "Monograph of the Upper Jurassic Stramberg Corals." In that work I compared them with some Palæozoic genera, especially with the genus *Decaphyllum*, which I now include with the Stylinidæ. There too I noted the many signs of a common ancestry which were displayed by the Jurassic representatives of the Stylinidæ and Amphiastræidæ. The latter, however, still kept a certain old-fashioned look and sameness, while the Stylinidæ, with their small star-like calyces, inner septal walls, outer costal and vesicular area, and infinite variety of colonial habit, were clearly in the forefront of that great influx of cœnenchymatous types which signalized post-Jurassic time.

Family :—*Oculinidæ*, E. H.

Colonial corals branching, massive or incrusting.
Cœnenchyme dense, compact; fine papillary ridges are usually present on the surface, more rarely it is smooth.
Costæ are distinct at the rims of calyces.
The calyces extend some distance above the surface of the cœnenchyme.
Septa well developed, few or numerous, bilaterally or radially symmetrical.
Pali occasionally present.

Columella or pseudocolumella always present.
Tabulæ or dissepiments may be sparsely developed.
Theca strongly developed, compact
The calycinal cavity is greatly diminished by secondary thickening of all the skeletal parts.
Rudimentary epitheca apparent at the base of the colony.
The mesenteries of the polyp are continued into an edge-zone at the lip of the calyx. The edge-zones of adjacent polyps are, however, rarely brought into direct contact, they become continuous with the common cœnosarc of the colony.

A comparison of the fine microscopic structure of the calyces of *Lophohelia* and *Amphihelia* with typical Turbinolidæ is sufficient to prove the identity even in minute details.

The earliest Oculinids were the Enallohelias of Jurassic age, and these had typically a well marked main septum in their calyces and smooth septa, the cyclical number varying in number, 6, 8, 10, 12. The calyces were definitely oriented and arranged in spiral or straight series on a dendroid stem. Recent Oculinidæ are radially symmetrical, and the calyces are approaching more and more to the Astræid type, with irregular cyclical development and exsert serrated septa.

The ancestral forms of Oculinids are the "Lobophyllias" of QUENSTEDT, forms in which the mother polyp gave off whorls of buds at regular intervals. The individuals of the whorl might one and all remain short, but retain their original connection with one another by means of the edge-zone of the mother polyp, or they might grow variously as branches.

Family :—*Pocilloporidæ*, E.H.*

Colonial corals branching, massive, or incrusting, with small calyces either sunk in the cœnenchyme or extending very little above it.
Cœnenchyme compact or sub-compact, with echinulate surface.
Septa, few in number, arranged with bilateral or radial symmetry; often represented by a series of horizontal septal spines.
Tabulæ or compact laminate deposit, seldom dissepiments.
Theca compact. The mesenteries of the polyp are not continued over the lip of the theca into an "edge-zone."

* I have included the common genus *Stylophora* and its allies in this family of Pocilloporidæ (*cf.* Phylogenetic scheme and pp. 308, 313).

Sub-family.—*Pocilloporinæ.*

Calyces round, irregularly distributed. Cœnenchyme compact.

Tabulæ present in the corallites; solid laminar deposit may occur near the surface.

Septa often represented by spines. Two septa, opposite one another, usually better developed than the rest.

Six of the mesenteries bear filaments, two of which are reproductive, four rudimentary.

Sub-family.—*Seriatoporinæ.*

Calyces oblong, regularly placed in series along the branches.

Cœnenchyme compact.

Solid laminar deposit; forms the base of corallites; tabulæ rare.

Septa usually twelve in number, two forming a mid-line coinciding with the long axis of the calyx; certain septa are rudimentary, associated with the presence of a pair of fossulæ on opposite sides of the mid-line.

Only two of the mesenteries bear reproductive filaments, an opposite pair at right angles to the septal mid-line; these filaments occupy the fossulæ.

Sub-family.—*Stylophorinæ.*

Calcyces round, irregularly placed.

No tabulæ, occasional dissepiments present.

Cœnenchyme sub-compact; unfilled spaces are left in rapidly-growing parts of the colony.

Six radially-arranged septa well developed; a varying number of rudimentary septa.

Columella present as a simple axial style coalescent with the ends of the six primary septa.

Family: *Madreporidæ.* DANA.

Colonial corals, branching, palmate, or incrusting, frequently forming reef-growths.

Calyces sunk or little prominent, small and with few septa.

Theca porous, cœnenchyme canaliculate, the canals communicating with the calyces by means of the thecal pores.

Septa bilaterally or radially arranged, compact; sometimes represented by a series of horizontal spines projecting inwards from the wall.

Basal deposit in the calyces may be absent; when present, it is in the form of tabulæ or solid laminate thickening.

The mesenteries of the polyp are not continued over the lip of the theca into an "edge-zone."

Sub-family.—*Madreporinæ.*

Mainly branching colonies, with a radially symmetrical end-calyx. Other calyces are usually oriented with respect to the axis of the branch, and vary in shape and in development. They project slightly from the surface of the branch.

No basal deposit present in calyces.

Septa six, radially arranged; two are usually specially developed, and form a calycinal mid-line; a varying number of septa are present in rudimentary form.

Sub-family.—*Montiporinæ.*

Colonies, dendroid, massive, or incrusting.

Calyces are placed in the surface depressions of the cœnenchyme. No end-calyx is present in branching types.

No basal deposit in calyces.

Septa 6 or 12; seldom more than 6 are well developed, and all may be represented by series of spines.

Sub-family.—*Alveoporinæ.*

Massive colonies, with closely-placed calyces.

Thecal pores large; cœnenchymal canals, little compacted.

Calyces sunk in cœnenchyme; cavities deep, tabulæ present in lower parts.

Septa 6 or 12, all represented by series of spines. Two opposite spines meet occasionally, as a calicinal mid-line. More often the spines of several series coalesce and wind round one another centrally, forming a pseudo-columella.

Sub-family.—*Turbinarinæ.*

Colonies, low, massive, or dendroid.

Calyces at irregular distances, rising slightly above the surface of the cœnenchyme, rarely sunken.

Septa 6 to 30, either well developed or rudimentary, but never represented by series of spines. A calicinal mid-line may be marked out by the elongation of one of the principal septa, or its coalescence with the septum opposite.

Pali often present, formed by coalescence of the inner ends of neighbouring couples of septa. The pali frequently have winding upward growth, and give the appearance of a large columella, present or absent.

Family: *Poritidæ*. DANA (*pro parte*).

Reef-growing, incrusting, or massive, rarely dendroid colonies, with solid well-developed epithecal basal-plate.

Calyces unequally distributed, in contact directly at their periphery, or with a development of cœnenchyme.

The whole skeleton is built up on a system of upright trabeculæ and stout cross bars, so that, in longitudinal section, it is scarcely possible to distinguish calyces.

Several trabeculæ may be partially compacted to form 5–12 primary septa, or individual broad trabeculæ may represent septa; frequently one or more trabeculæ are free centrally, as styliform columella and pali.

The cœnenchyme is not echinulate at the surface, but presents costate ridges, confluent or non-confluent.

Dissepiments richly developed throughout the skeleton; tabulæ may be present in the calyces.

The Palæozoic family of Theciidæ (*Thecia*, *Protaræa*, *Stylaræa*, *Coccoseris*) seems to be the ancestral types of our recent reef-builders. An interesting transitional genus is *Astræomorpha*, a Triassic genus, whose thick septa and calicinal features show more the character of the Palæozoic types, yet the fine structure proves its affinity with the recent *Porites* (*cf.* pp. 305–307). Longitudinal sections of *Astræomorpha* and *Porites* are essentially similar, while the intimate connection of the calyces at their periphery is characteristic in both.

The Theciidæ and several allied forms of Palæozoic age represent, to judge from their calicinal structures, early colony-building relatives of the solitary Zaphrentidæ, where the epitheca of young broods came laterally into contact. Primitive Madreporaria had no theca, hence tangential contact readily gave rise to a so-called cœnenchymatous colony (*cf.* pp. 315–317)—whether porous or compact is a further point of modification. The genus *Astræomorpha* may be held provisionally as the representative of a sub-family, Astræomorphinæ. The Palæozoic genera of the Theciidæ require detailed examination before they can be rightly placed. The Cretaceous and recent types of the Poritidæ may be provisionally treated as a sub-family, Poritinæ.

The typical reef-building members of the Poritidæ belong to this sub-family Poritinæ, and I shall therefore enumerate here the characteristic structural features observed in Porites. I am not in a position to thoroughly review the family of Poritidæ or to discuss the possible affinities of Palæozoic types with Favositidæ at present; I limited microscopic investigation to Mesozoic and younger genera.

In the following list of features I shall indicate the *superficial* resemblances of Porites with other recent families of Madreporaria.

The *microscopic structure* of the septa and pali in Porites is unlike that of any other Madreporarian type hitherto examined in detail. All skeletal parts of Porites have the same microscopic structure, so that its most characteristic feature is the *similarity in size and development of each growth-segment* however it may happen to be placed in the skeleton vertically, obliquely, or horizontally (so-called "synapticulæ").

The *calyces* are radially symmetrical, but the number of septa in the primary cycle is highly variable: 5, 6, 7, 8, 10, 12. A styliform columella is usually present, surrounded by pali as in the Oculinidæ and Trochocyathinæ.

The *septa* are made up of vertical or slightly slanting trabeculæ; when spaces are left unfilled, the surface appearance of the septum is much like that of a porous Eupsammid septum. The individual trabeculæ are often directed locally inwards towards the axial part of the calyx, but there is *no area of divergence at the periphery* (*cf.*, pp. 222, 223) of the calyx as Eupsammidæ, Astræidæ, and Fungidæ. Moreover, the microscopic structure of the individual trabeculæ in Poritinæ is different from trabecular structure in these three families. Numerous fine dissepiments are present.

The calycinal structures radiate outwards, considered from the centre, in *deltoid* fashion, and this feature is fundamental in many genera belonging to the Trochocyathinæ and Eupsammidæ. The so-called wall of the Poritinæ is a zig-zag ring of thecal deposit like that in most of the Trochocyathinæ. The porosity of the "wall" is based on structural relations quite different from those in Eupsammia, but homologous with those in the Madreporidæ. Each new layer of growth is indicated by fresh epithecal rims round the corallum, as is the case in encrusting types of Oculinidæ.

Spongiomorphidæ.

For the diagnosis of this family I refer to its founder Professor FRECH ("Triassic Corals," 'Palæontogr.,' 1890–91). I have had occasion to compare it with the Poritidæ above (p. 307), and think it would be best regarded as a *Subfamily*, of equal rank with the Poritinæ and included under the family of Poritidæ.

Family :—*Cyathophyllidæ*. E.H.

Solitary and colonial corals; colonies massive, bushy, or branching—never meandroid.

Base of the calyx distinctly subdivided into a central tabulate or columellar area and a broad peripheral area with dissepiments.

Septa arranged in the mature calyx usually with radial symmetry, indications of bilateral symmetry seldom; there may or may not be pinnate insertion of septa; fossulæ small or obsolete; septa well developed, never represented by a series of horizontally placed "wall" spines.

Theca usually present, coalescent with the epitheca.

Pseudothecal septal thickening occurs frequently, and at some distance from the true theca, forming an inner wall.

The Palæozoic types, as they have hitherto been classified, cannot be said to have been referred to families or even genera according to the fine microscopic structure of their septa. And it might, therefore, seem at first sight, as if the method I have advanced under the new sub-orders (pp. 329, 330) would be at complete variance with all existing grouping of corals. Curiously enough, it makes least change of all amongst the Palæozoic types. For the *microscopic structure of the trabeculæ and the relative arrangement of the trabeculæ in the septal plane* are both architectural features dependent upon the breadth of the oral disc and the required strength of the septa for the support of the corresponding aboral breadth. The same polypal conditions have determined the nature of the skeletal base. Hence a classificatory arrangement of Palæozoic corals, such as Professor NICHOLSON'S, where the chief weight is laid upon the particular relations of the calicinal base, is bound to coincide in its main features with the system I now follow. Either classificatory basis can indeed merely act as a corrective on the other in the examination of the primitive Palæozoic species and genera. As I have already said, I use *Zaphrentidæ* practically with the limits of *Zaphrentoidea*, NICHOLSON, similarly *Cyathophyllidæ* as the equivalent in the main of *Cyathophylloidea*, NICHOLSON; but *Cystiphyllidæ* only with the special meaning which is attached to the *family* of the same name by Professor NICHOLSON.

I have seen it stated, in several lately-published papers on Palæozoic corals, that the genus *Heliophyllum* may be incorporated with *Cyathophyllum*. It is said that the carinæ of *Heliophyllum* are not sufficient reason for a separation. I place considerable importance on the carinæ as a starting-point of a variation within the Cyathophyllidæ which may have been the origin of the main differences in the structures of recent Astræids and Fungidæ. But, in addition to this feature, there is the fact that in *Heliophyllum* the pinnate insertion of the septa is strongly marked throughout growth, whereas in the *typical* species of *Cyathophyllum*, which ought to be regarded as the standard of the genus, pinnate insertion is not observed in the mature calyx. NICHOLSON, on the other hand, made two distinct families—Cyathophyllidæ and Heliophyllidæ. I would certainly be inclined to regard them as sub-families.

In the Clisiophyllidæ (NICH.), in addition to the columellar area, a point may again be made of the invariable pinnate insertion of septa.

The following families have been already treated in full systematic detail in Part I., and their characteristic features will be found summarized in the Table (p. 252). Short diagnoses may be repeated here.

Family :—*Astræidæ*. E. H. (emend. Ogilvie).

Mainly colonial, seldom solitary, corals.

Colonies massive, branching, bushy, incrusting, meandroid.

No tabulæ are present centrally, dissepiments are distributed throughout, and form a compact calycinal base.

Septa never pinnately inserted; always arranged with radial symmetry; give rise frequently to a pseudocolumella centrally; compact; trabecular structure regular.

True theca only present in a few of the older types, coalescent with the epitheca. Pseudothecal septal thickening almost always present in the interior of the calyx. Epitheca surrounds simple forms, also the branches of bushy and dendroid colonies, but is limited to the base of massive and meandroid colonies.

The sub-families of Astræidæ are given above (Part I., pp. 163, 164). I have frequently referred, in the course of this work, to the significance of the pseudotheca in this group of corals, and its correlation with the retrograde state of the more primitive theca and epitheca round individual members of a colony. On this depends the homology between the broad outer disc, or "dissepimental zone," of Cyathophyllidæ and the costate, so-called *extracalycinal*, zone of Astræidæ—both representing, in the skeleton of a massive astræiform colony, the edge-zone, or "Randplatte," which laps over the edge of the wall in the free branches of bushy colonies, or in a solitary coral.

Although I retain the long-familiar name of Astræidæ, the family is very differently defined from Edwards and Haime's original use of the name. I have removed from it practically the whole of the sub-family Eusmilinæ, distributing these genera among the families Amphiastræidæ, Stylinidæ, Turbinolidæ, as given above (pp. 159, 162).

Family :—*Fungidæ*. Dana (emend. Ogilvie).

Solitary and colonial corals. Colonies massive, incrusting, palmate, meandroid, rarely dendroid.

Septa never pinnately inserted; radially symmetrical in mature calyx.

Septa porous or compact, frequently coalescing, *i.e.*, the inner ends of the shorter septa coalesce with the side surfaces of longer septa; trabecular structure regular.

Base of the calyx chiefly formed by synapticular bars; dissepiments irregularly developed or absent.

No true theca is developed; pseudotheca sometimes.

Sub-family :—*Funginæ.*

Low, solitary corals, or massive colonies, never meandroid.
Epitheca rudimentary, replaced in greater part by large basal spines.
Both "true" synapticulæ and pseudosynapticulæ (*cf.* p. 198) richly developed. Dissepiments well developed, rarely absent.
Septa usually compact, in some cases those of the higher cycles may be porous Coalescence of lateral surfaces largely developed.

Sub-family :—*Thamnastræinæ* (*cf.* pp. 186–190).

Solitary corals of discoid or turbinate form. *Colonies* massive, calyces confluent, frequently meandroid.
Epitheca well developed, forming a compact basal surface for the corallum.
No true synapticulæ occur. Dissepiments well developed.
Pseudosynapticulæ developed in horizontal rows representing successive growth-periods; the rows extend throughout the whole length of the interseptal and intercostal loculi.
Septa regularly fenestrated between individual trabecular parts. The spaces become sometimes solidified by secondary deposit. The divergence of the septal trabeculæ is in a single fan-system.

Sub-family :—*Lophoserinæ.*

Solitary corals, or low, foliaceous, and frequently meandroid colonies.
Epitheca, when present, is compact and not spinate.
Pseudosynapticulæ richly developed at and near periphery of calyces, but *not* forming complete interseptal and intercostal series.
True synapticulæ occasionally occur in the formation of a pseudotheca. Dissepiments few or absent.
Septa usually compact; when porous, the pores are not regularly distributed between adjacent trabeculæ, they may be in the course of the trabeculæ themselves. The divergence of the trabeculæ takes place, as a rule, in several fan-systems.

Family :—*Eupsammidæ.* E. H. (emend. Ogilvie).

Solitary and colonial corals. Colonies branching, massive, incrusting, bushy or stolonal.
Septa never pinnately inserted, radially symmetrical in calyx, rarely showing traces of bilateral symmetry.

Septa irregularly toothed and granulated, of irregular trabeculate structure, the "trabecular parts" often alternating in position and leaving pores of various sizes and shapes in the septal plane. Lateral coalescence of septal surfaces at their inner ends usually pronounced.

No true theca is present. Costæ highly developed. A considerable area is marked out peripherally as a porous pseudotheca; the structure of the base here varies from a rich vesicular deposit to a complicated synapticular network, and is associated with mural costæ (*cf.* "cœnenchymate types," p. 316).

Basal deposit within the calyx extremely various; synapticulæ, pseudosynapticulæ, dissepiments, more rarely tabulæ or solid laminar deposit.

A large amount of secondary thickening takes place on septa, pseudotheca, and base.

Epitheca, when present, is smooth or slightly rugose, never spined.

In this family I now include for the first time a number of Mesozoic genera which have hitherto had a somewhat uncertain systematic position. The characteristic feature of loose and irregular trabeculate septal structure shows itself throughout all. The most important of these are the Jurassic genera—*Haplaræa* (sub-fam. Pseudoastræinæ irregulares, PRATZ; fam. Fungidæ); *Epistreptophyllum* (sub-fam. Epistreptophyllinæ, ZITTEL; fam. Astræidæ); *Dermosmilia* (Dermosmilidæ, KOBY); and the Triassic genera, *Stylophyllum* and *Stylophyllopsis* (sub-fam. Stylophyllinæ, FRECH; fam. Astræidæ).

Family:—*Cystiphyllidæ*, E. H.

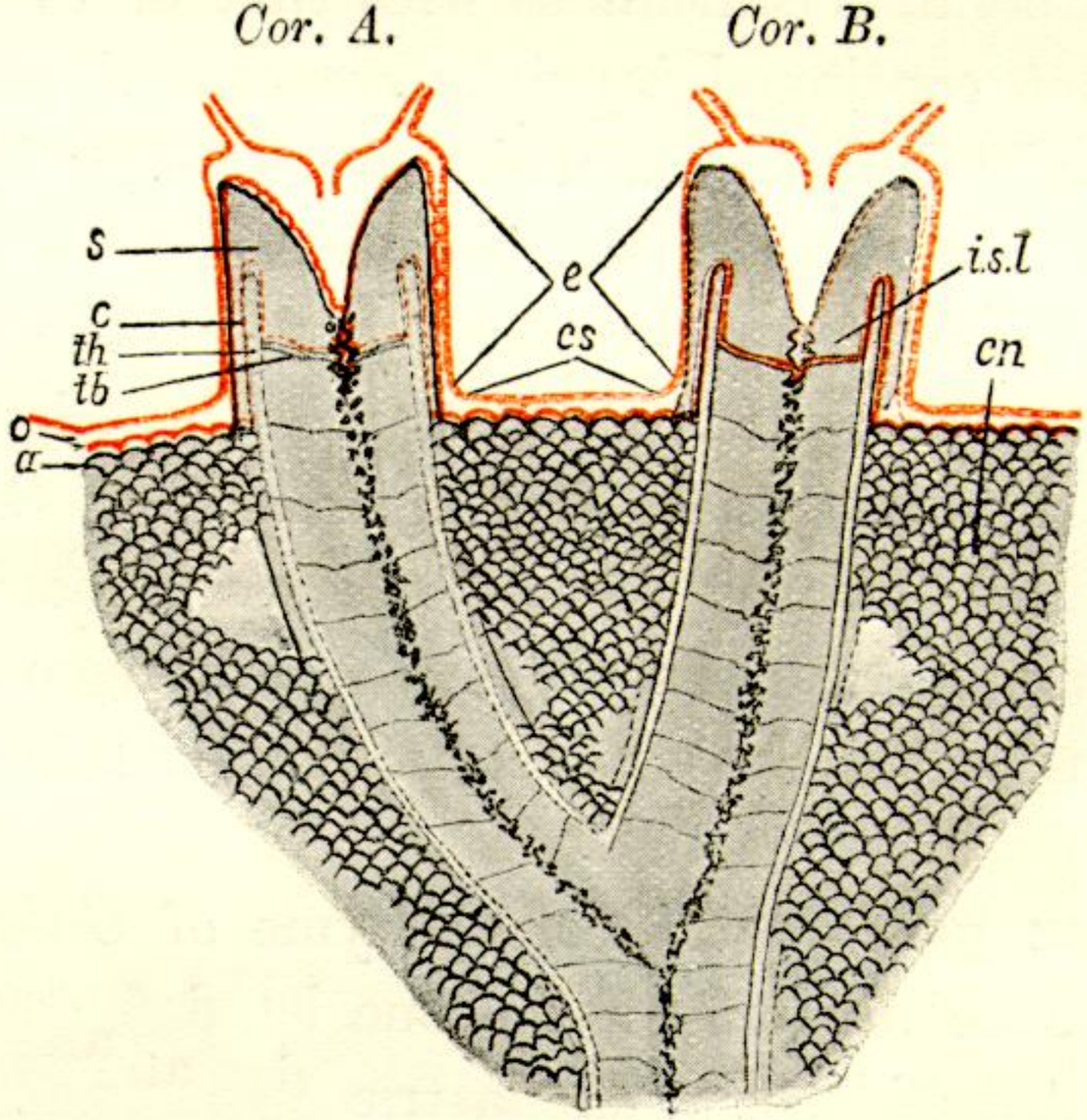
Family:—*Archæocyathidæ*, WALCOTT.

These two Palæozoic families may be taken from standard text books

List of Abbreviations used in Lettering the Figures.

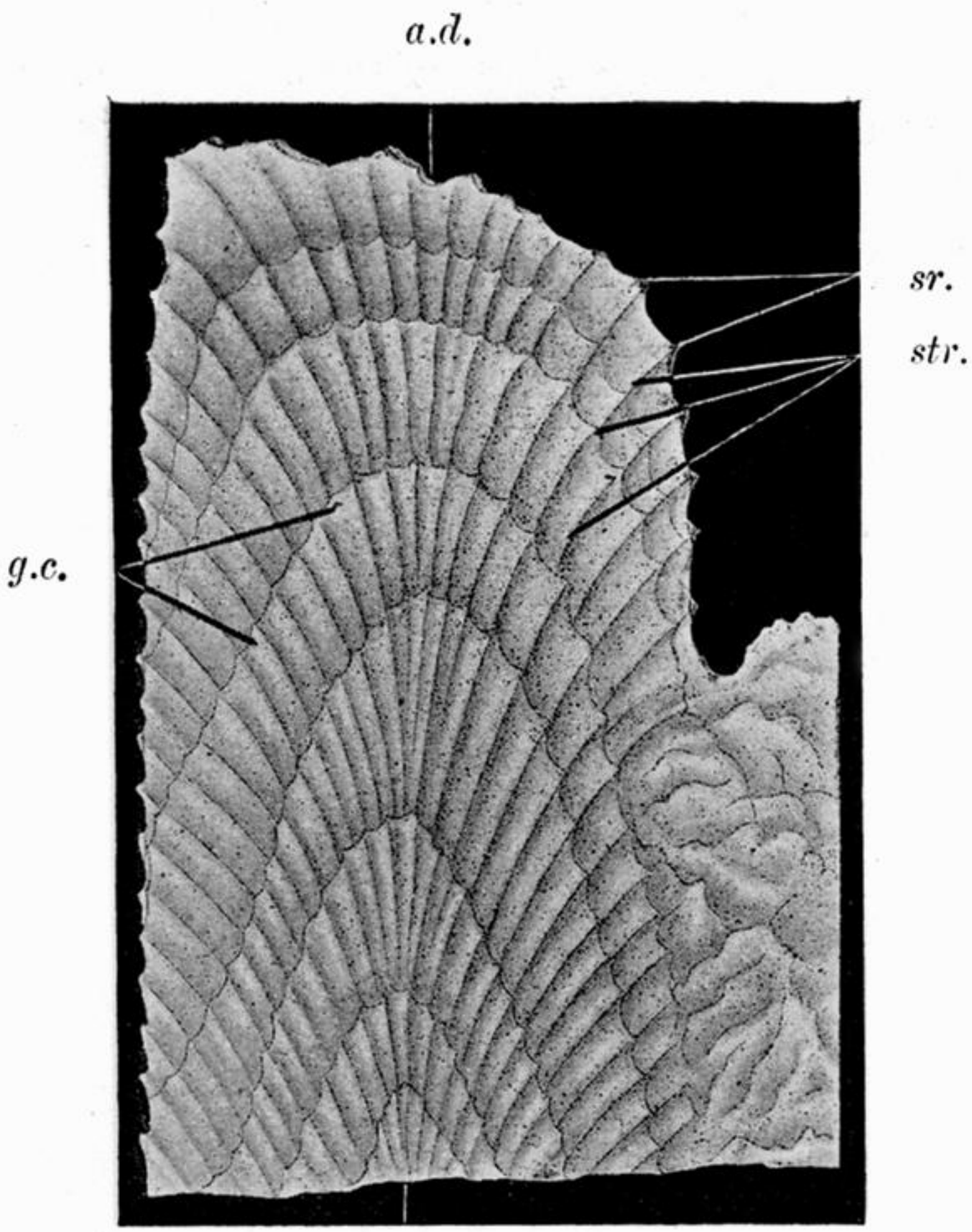
a. Aboral body-wall of polyp.
a.d. Area of divergence.
c. Costa.
c.c. Centre of calcification.
c.e. Costal edge.
cn. Cœnenchyme.
cn.p. Cœnenchymal pore.
co. Coalescence of septal surfaces.
col. Columella.
cor. Corallite.
cs. Cœnosarc.
c.tr. Calcification centre in trabecula.
c.th. Calcification centre in theca.
d. Dissepiment.
d.l. "Dark line" (Primärstreif).
e. Edge-zone (Randplatte).
ep. Epitheca.
f. Fascicle of fibro-crystals.
f.c. Fibro-crystals.
g.c. Growth-curve.
g.l. Growth-lamella.
gr. Granulation.
g.s. Growth-segment of septum.
h. Hyphæ (Fungi, etc.).
o. Oral body-wall of the polyp.
org. Organic cell-remnant.
p. Septal pore.
pa. Palus.
ps.col. Pseudo-columella.
ps.syn. Pseudo-synapticula.
ps.th. Pseudo-theca.
r. Septal ridge.
s. Septum.
sc. Scale (calcified calicoblast).
s.e. Septal edge.
sec. Secondary fibrous deposit.
sp. Spiniform tooth.
sr. Serra.
s.s. Septal spine.
str. Stria on septal surface.
syn. Synapticula.
tab. Tabula.
th. Theca (eutheca).
th.p. Thecal pore.
tr. Trabecula (*simp.* = simple; *comp.* = compound).
tr.ax. Ideal axis of trabecula.
tr.p. Trabecular pore.

Fig. 2.



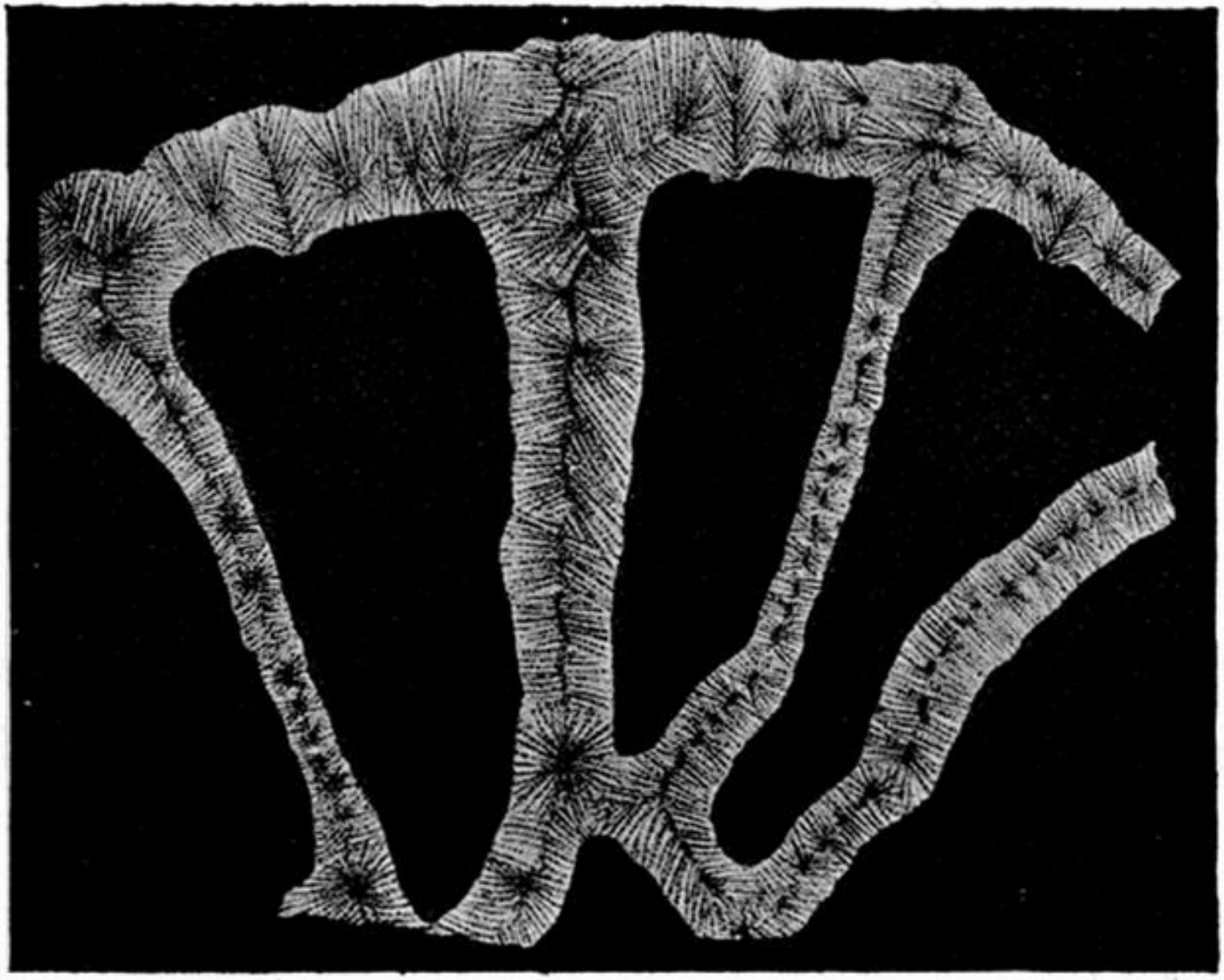
GALAXEA—cœnenchymatous type. *o.* = oral body-wall; *a.* = aboral body-wall; *cs.* = cœnosarc; *cn.* = cœnenchyme; *e.* = edge-zone; *s.* = septum; *c.* = costa; *th.* = theca; *tb.* = tabula; *is.l.* = interseptal loculus. (Compare the similarly treated figures, 22, 35, 36, 56.)

Fig. 3.



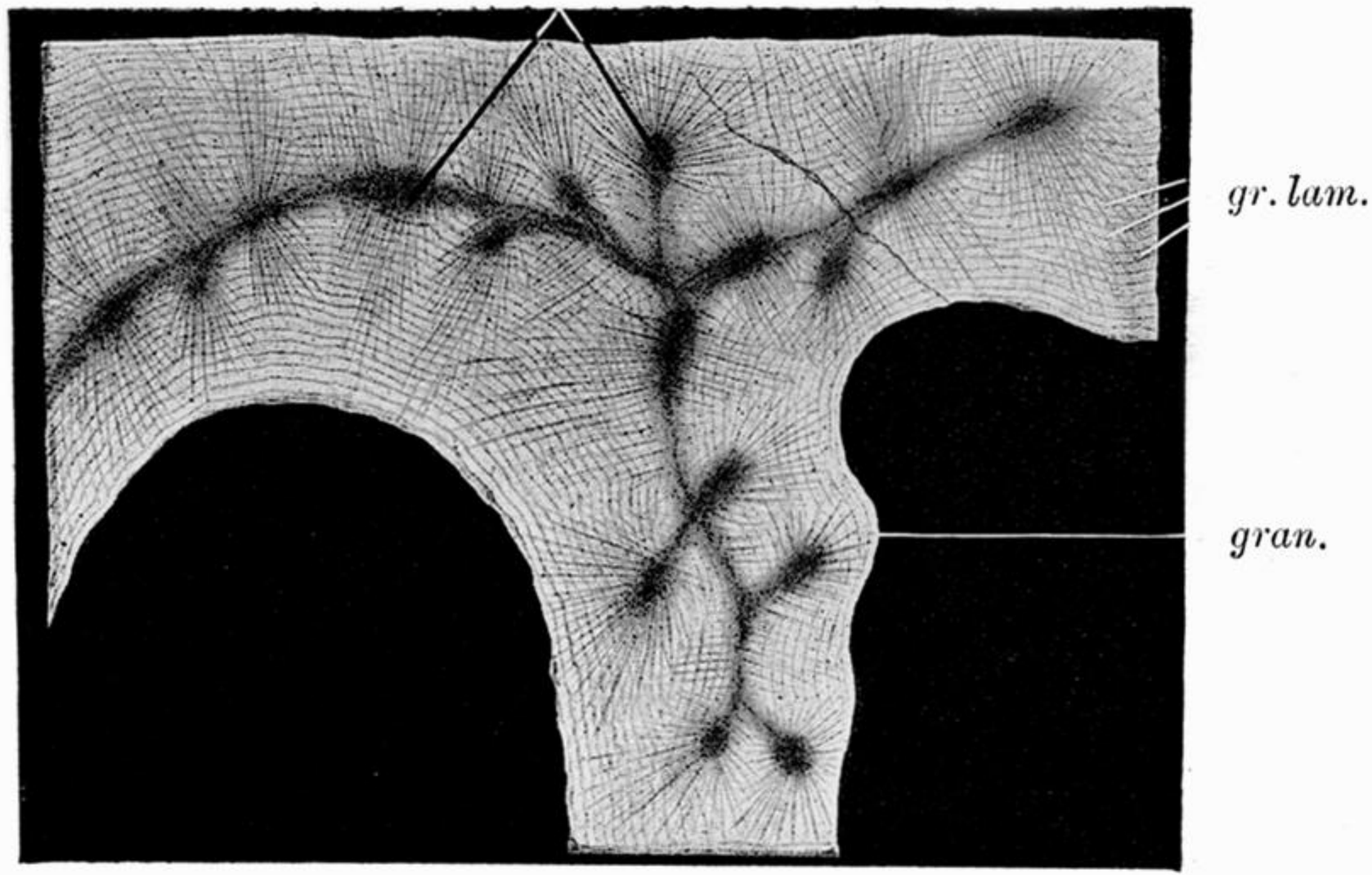
Lateral surface of a radial structure: *str.* = striæ; *sr.* = serræ; *a.d.* = area of divergence of striæ; *g.c.* = growth-curve.

Fig. 5.



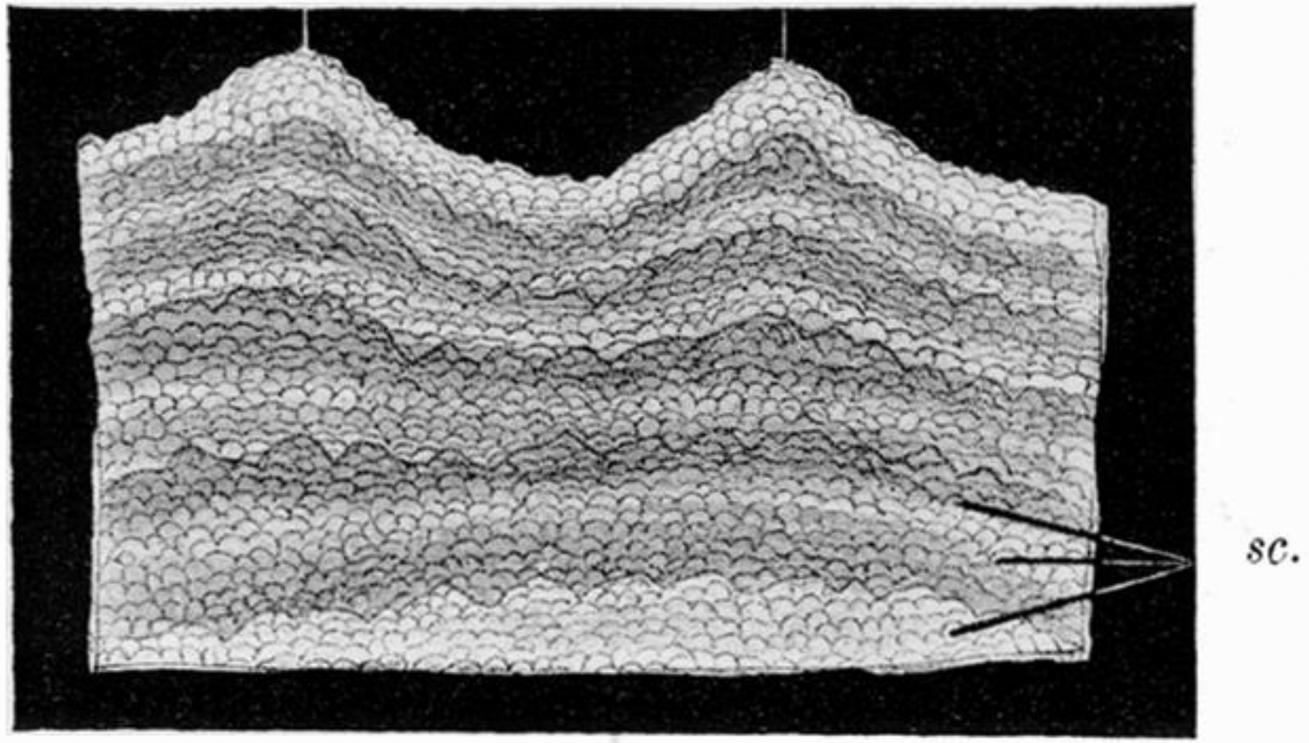
Transverse section of a few septa and part of the wall (low power).

Fig. 6.



Transverse section of part of septum and wall showing the radiating lines of structure passing out from the "dark points," and also the wavy cross-lines corresponding to successive "growth-lamellæ" (high power); *d.p.* = dark points; *gr. lam.* = growth-lamellæ; *gran.* = granulation.

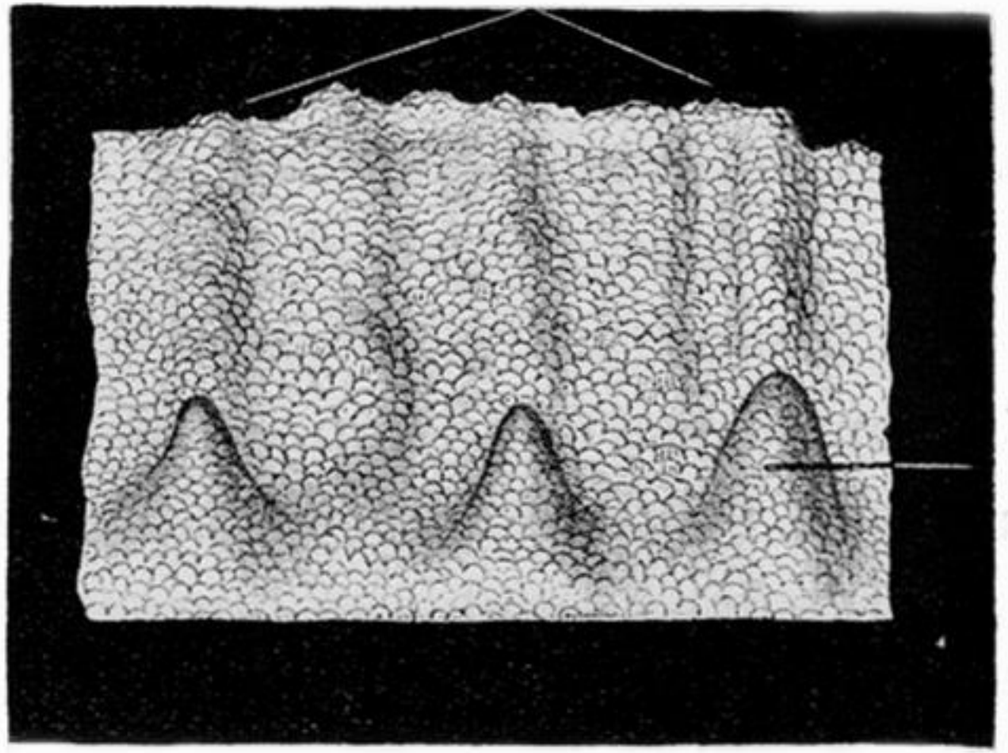
Fig. 7A.



sr. = serræ; *sc.* = scales.

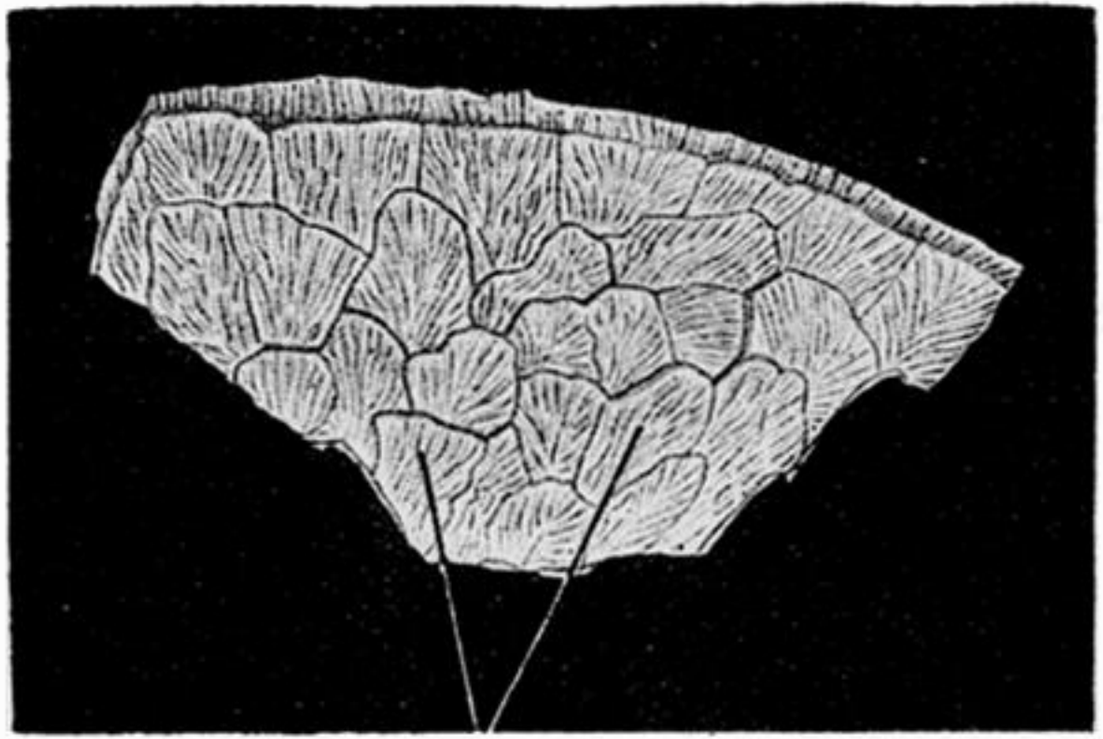
The irregular lines running roughly parallel with the serrated septal edge indicate growth-lamellæ which have been cut during the polishing of the section.

Fig. 7B.



s.e. = septal edge; *gran.* = granulation covered with the calcareous scales.

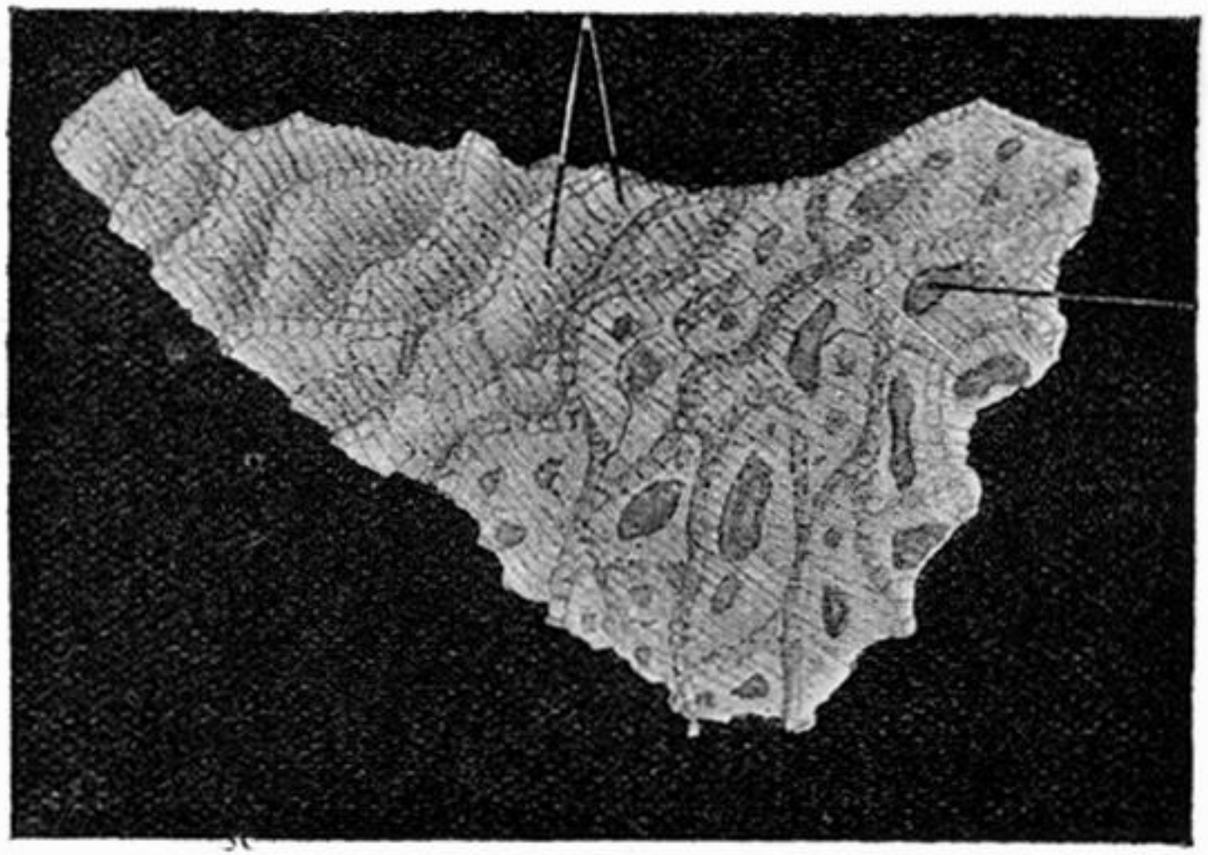
Fig. 8A.



sc.

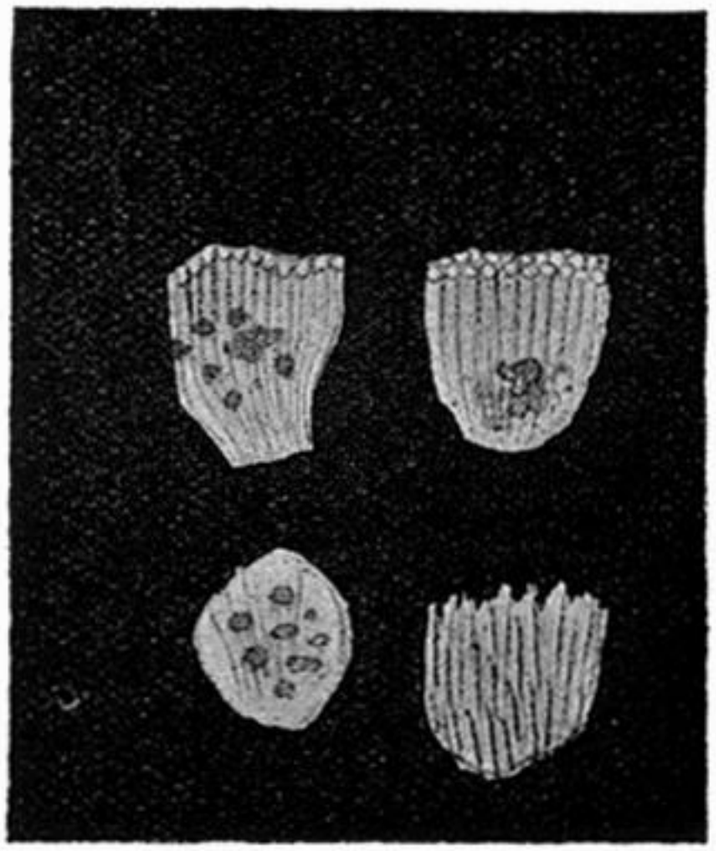
Calcareous scales on the surface of a dissepiment (from the cœnenchyme of *Galaxea*—highly magnified).

Fig. 8B.



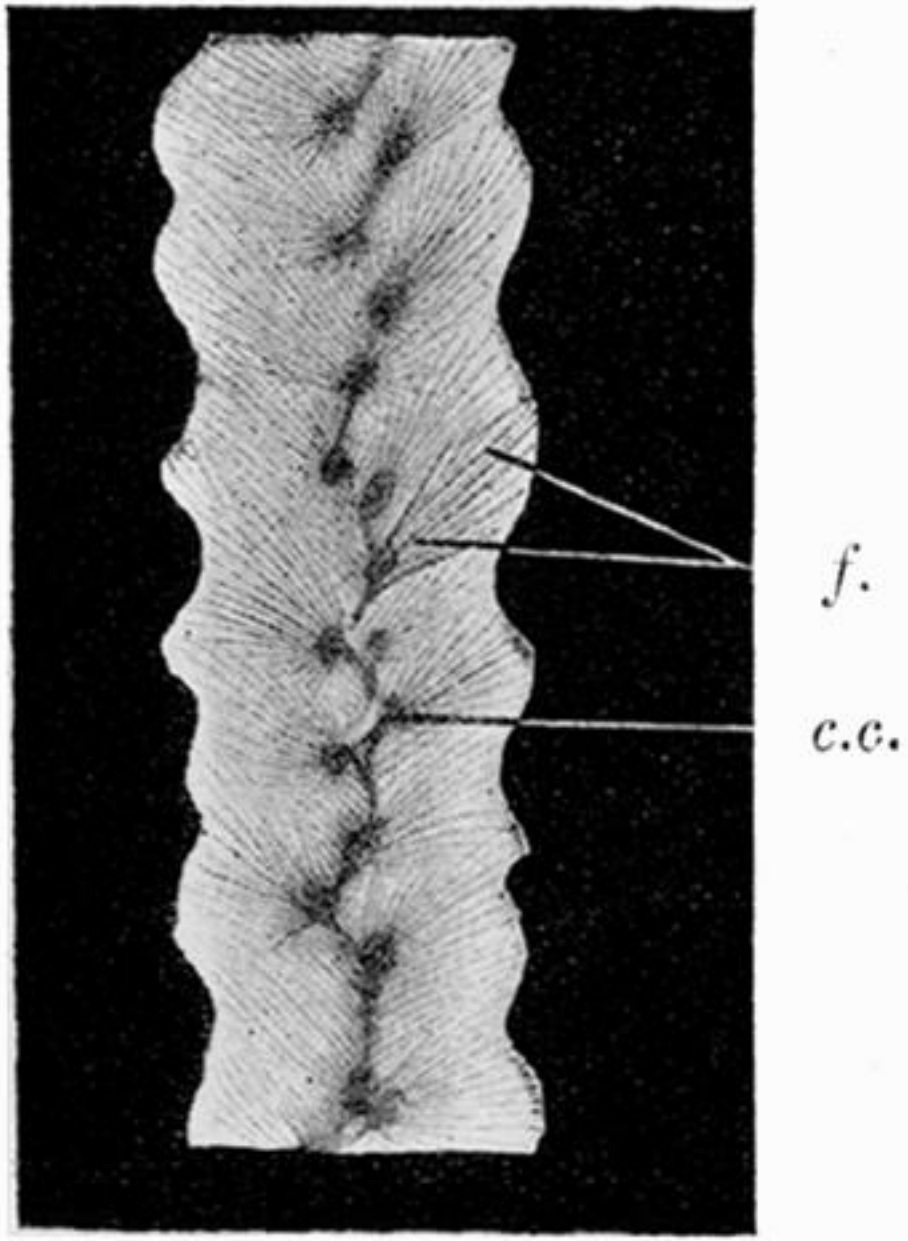
Galaxeo[e] dissepiment, showing several growth-lamellæ; those at or near the surface show organic remnants (*org.*) while those below have passed almost wholly into the fibro-crystalline (*f.c.*) condition.

Fig. 8C.



Individual scales separated from dissepiment = calicoblasts in various stages of calcification.

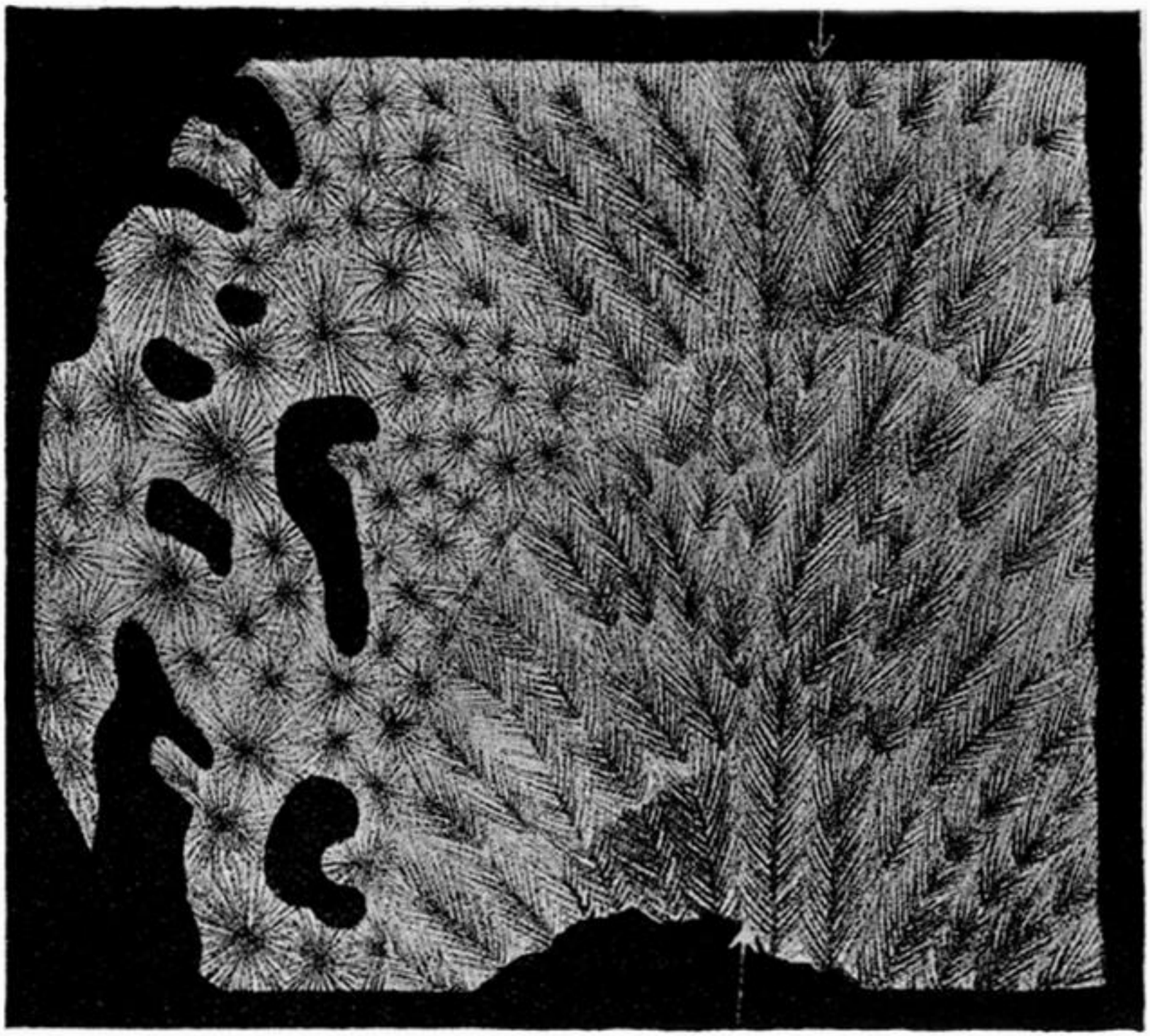
Fig. 9.



f. = fascicle of fibres emerging in a surface granulation.

c.c. = centre of calcification.

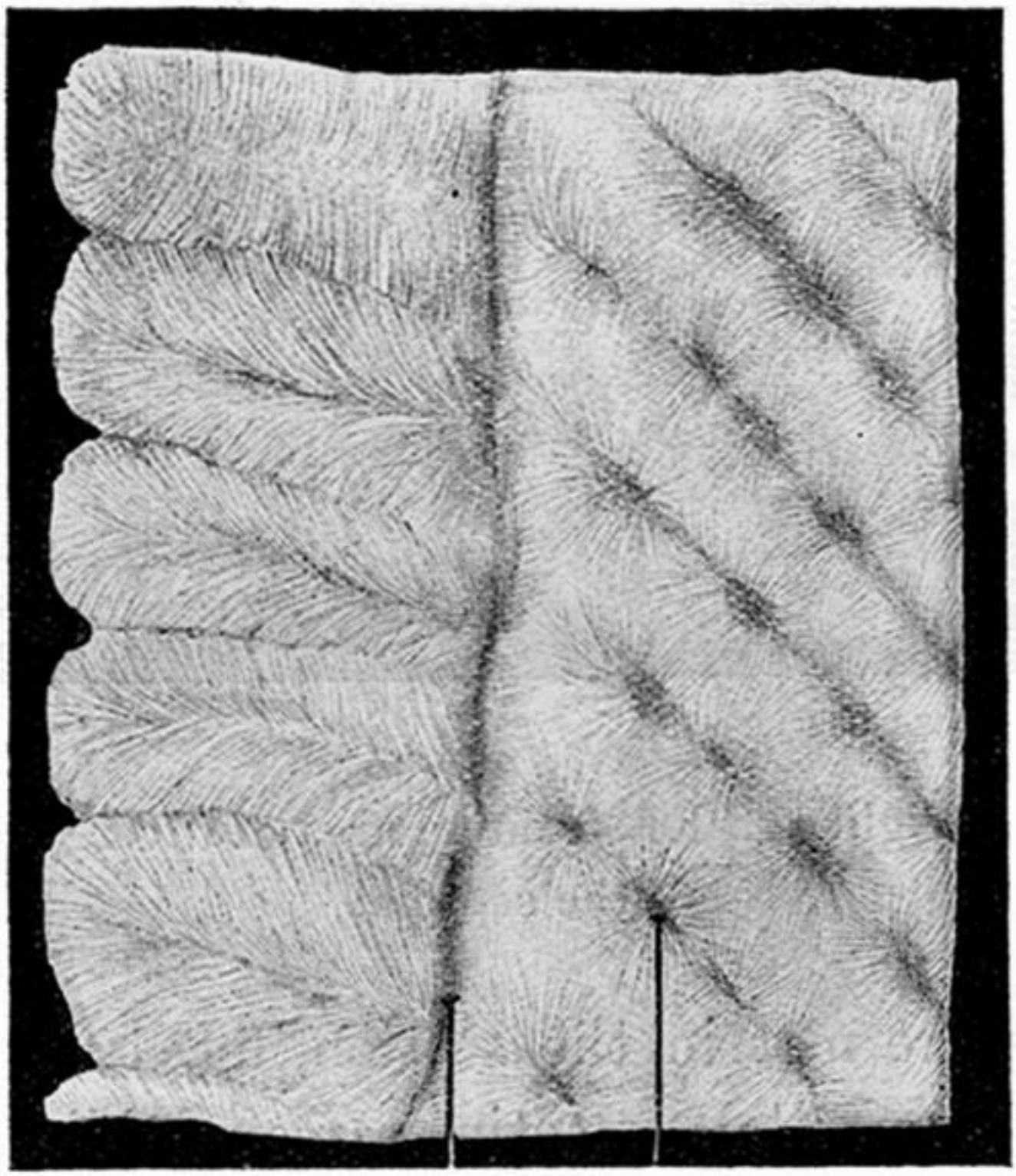
Fig. 10.



The striæ branch out to right and left from an area of divergence (*a.d.*) in the plane of the septum.

Fig. 11.

costa. *septum.*



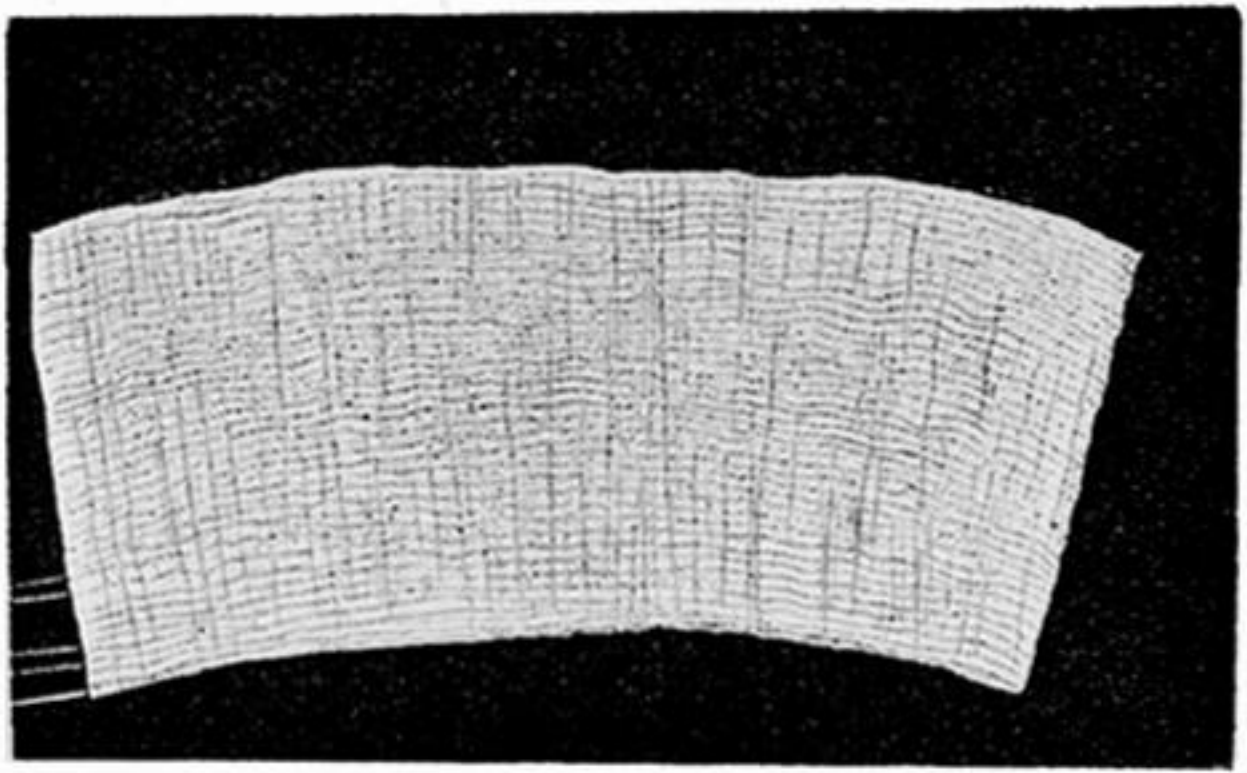
c.th. *c.tr.*

Radial longitudinal section through wall and septum of *Galaxea.*

c.th. = centre of calcification in the theca.

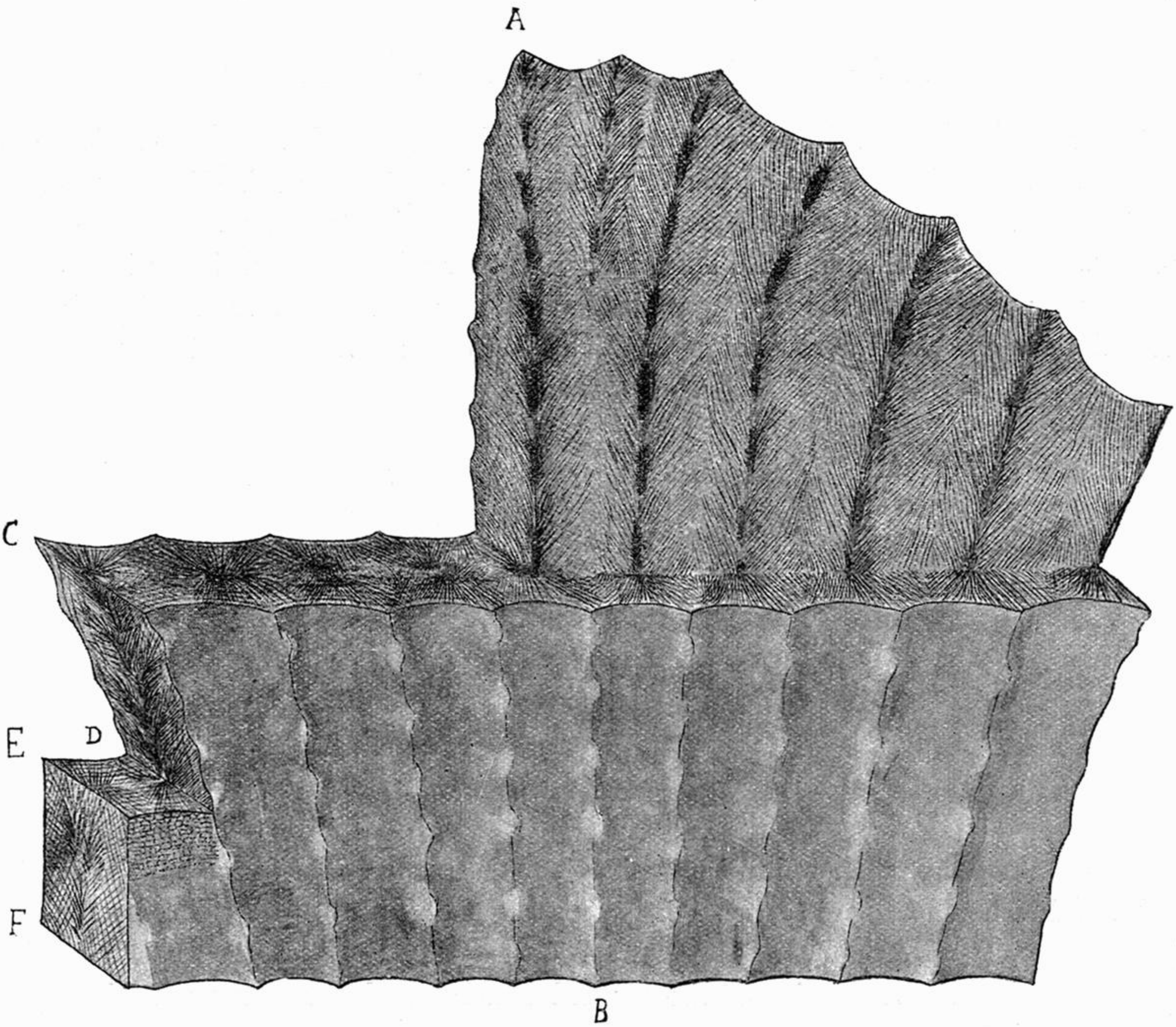
c.tr. = centre of calcification in the septal stria or trabecula.

Fig. 12.



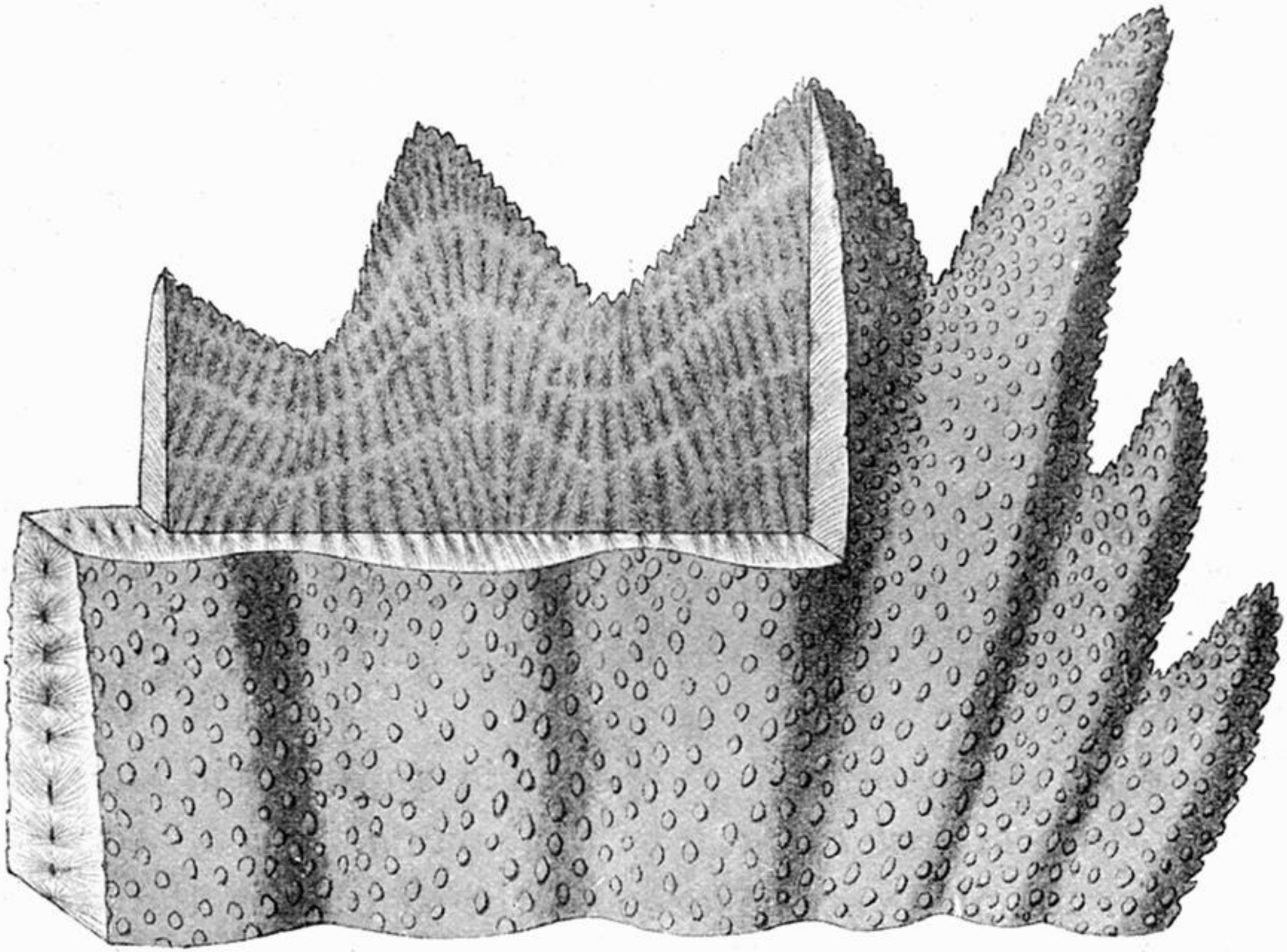
Galaxea dissepiment: *g.l.* = growth-lamellæ.

Fig. 13.



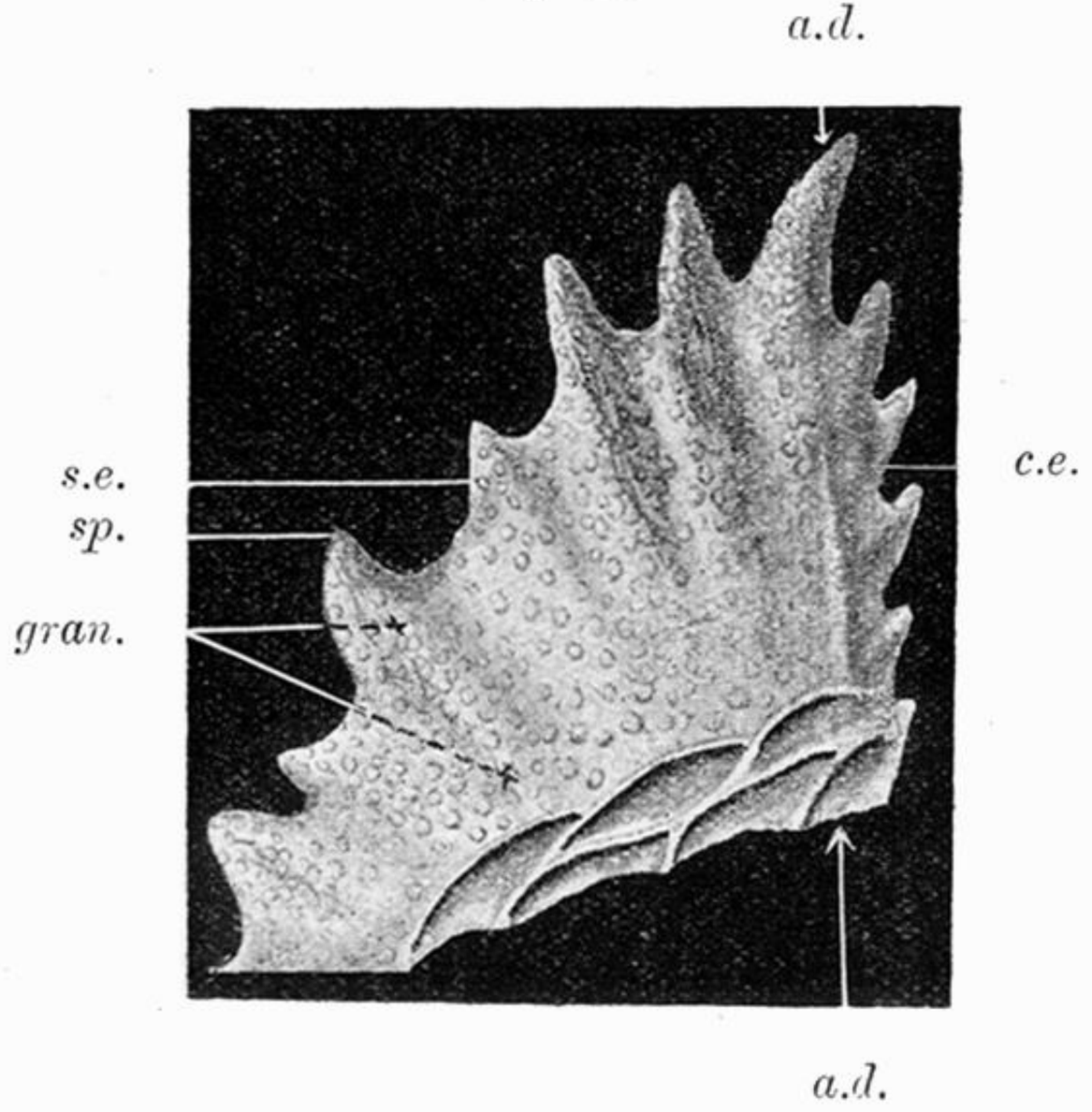
Diagrammatic view of the structure of a *Galaxea* septum.
AB direction of the "area of divergence" of septal striæ.
CD tangential section through a pair of striæ on the opposite surfaces of the septum.
EF tangential section cut obliquely to the direction of striæ.

Fig. 14.



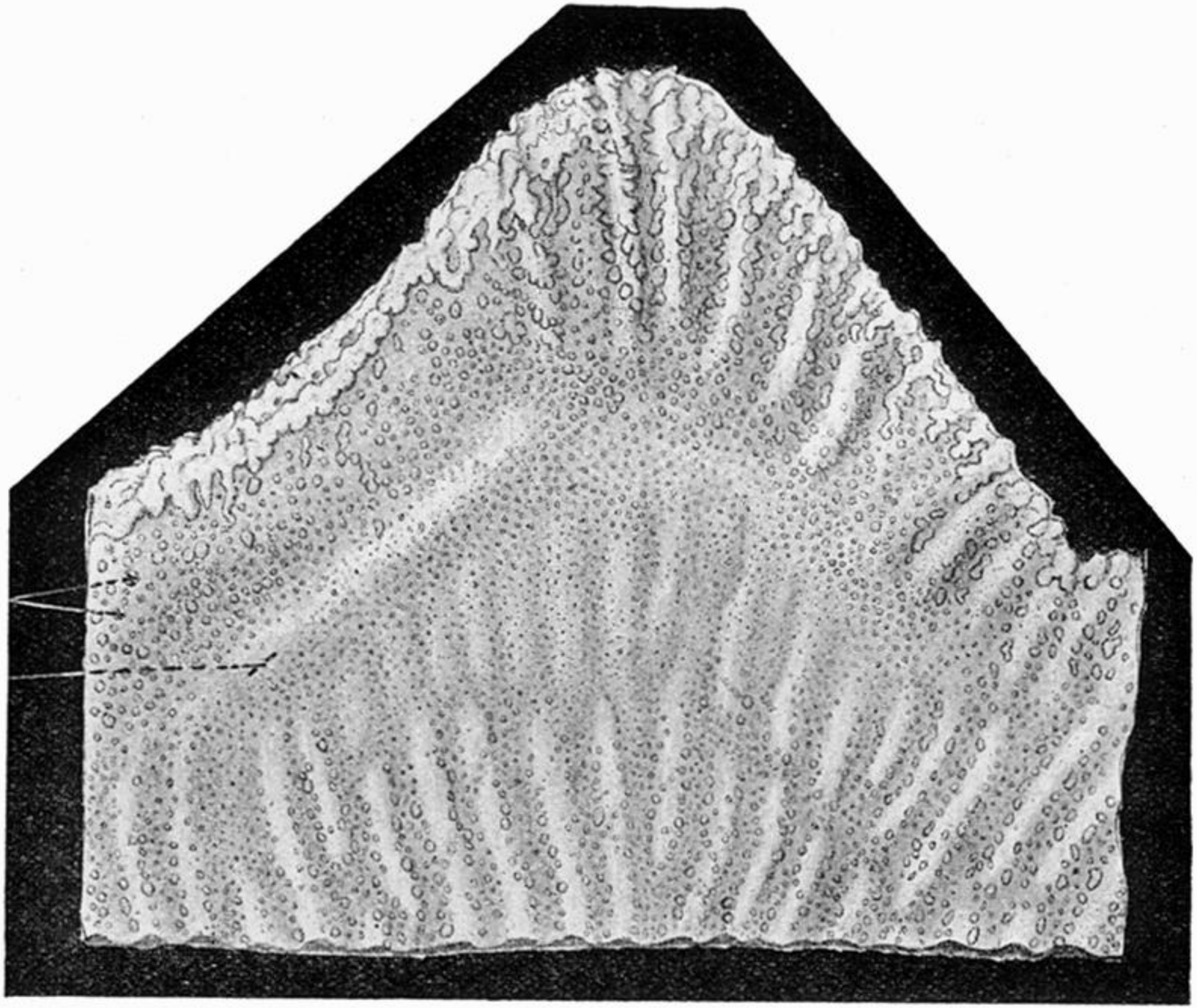
Similarly cut septa of *Mussa*, showing its more complex structure (ref., pp. 136–139). Four successive growth-segments are shown in longitudinal section. Distinct "fans" of diverging trabeculæ are present in each septal ridge. In *Galaxea* (fig. 13) the whole septum is composed of one such "fan" of diverging trabeculæ.

Fig. 15.



Upper or growing part of a *Mussa* septum; *s.e.* septal edge; *c.e.* costal edge; *sp.* spiniform teeth. *gran.* granulations coalescing on a septal ridge; *a.d.* area of divergence of septal and costal ridges.

Fig. 16.

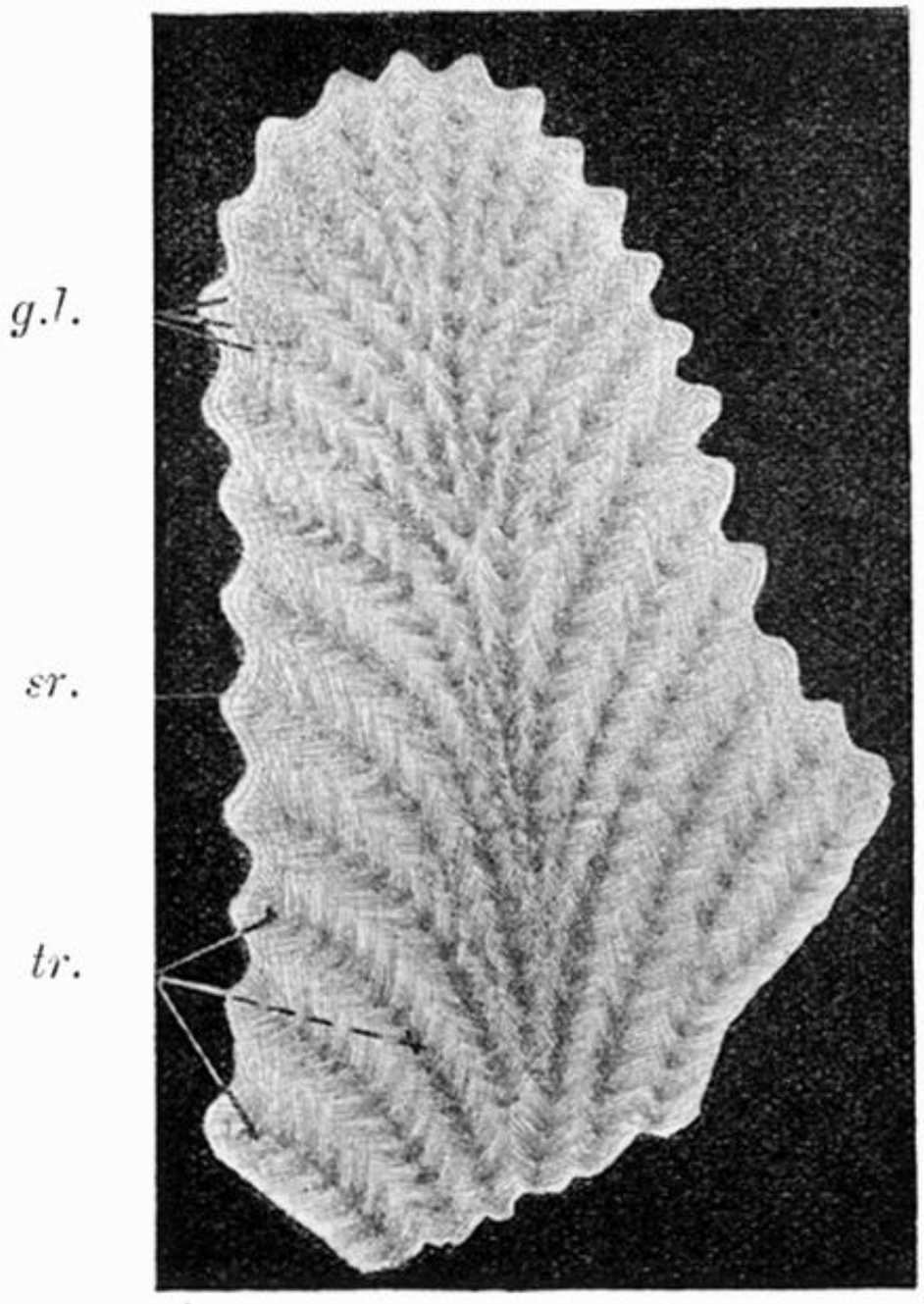


A single spiniform tooth (40 times magnified) of one of the small, fine septa in *Mussa*, showing upwardly diverging striæ (*str.*) growth-curves (*g.c.*) and variously sized granulations (*gr.*).

Fig. 17A.

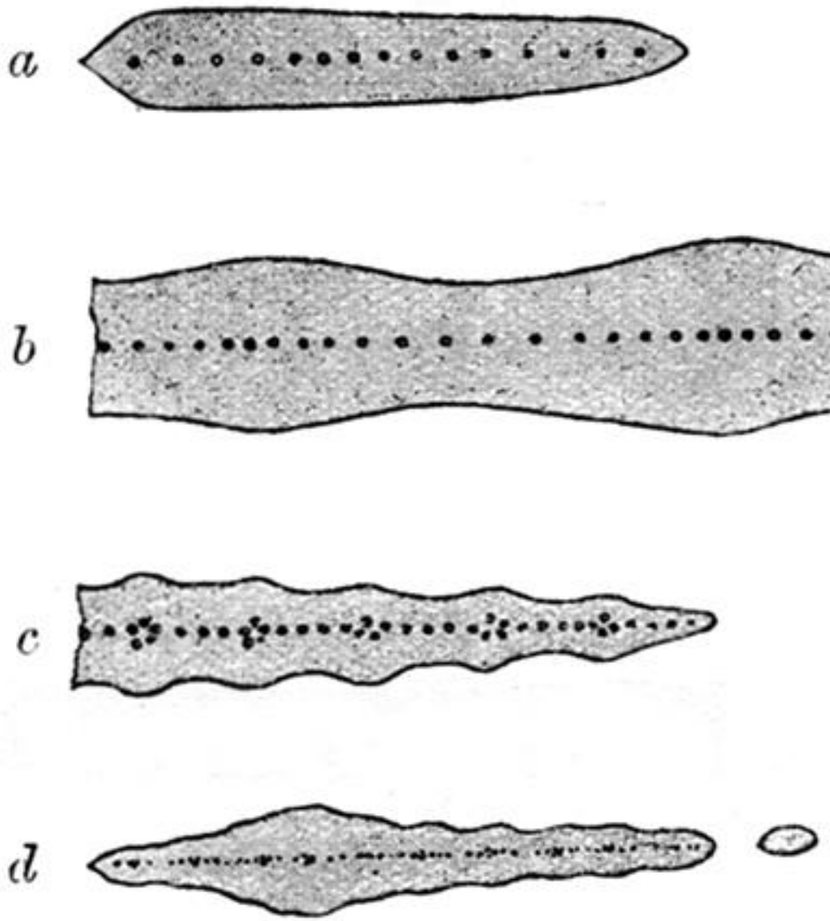
Two spiniform teeth in a thick *Mussa* septum (low power). *s.r.* septal ridge; *g.c.* growth-curves marking three successive growth-segments in that septal tooth.

Fig. 17B.



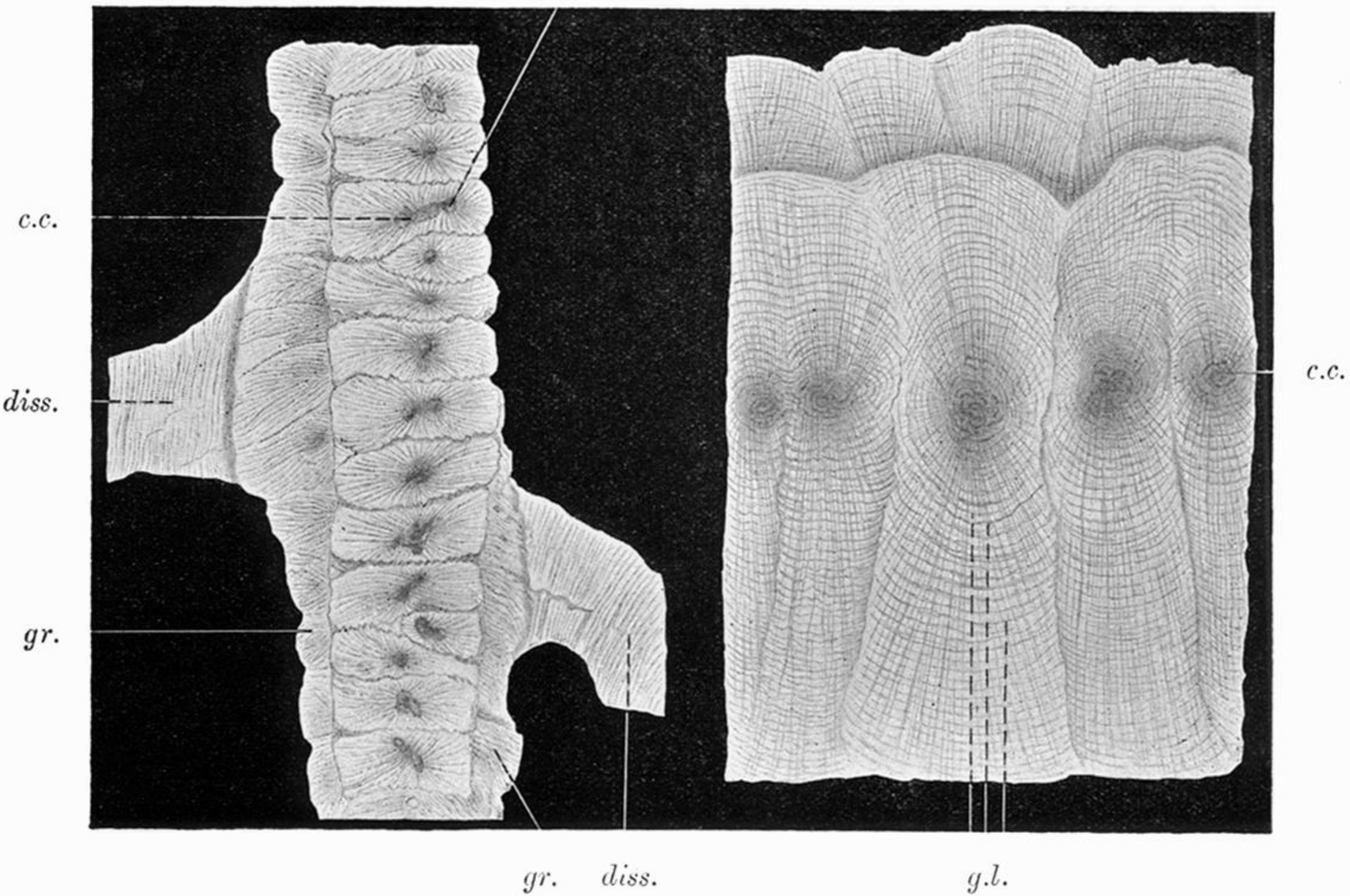
One tooth (high power). *tr.* trabeculæ; *sr.* serra; *g.l.* growth-lines. The "area of divergence" of the trabeculæ runs along the middle.

Fig. 18.



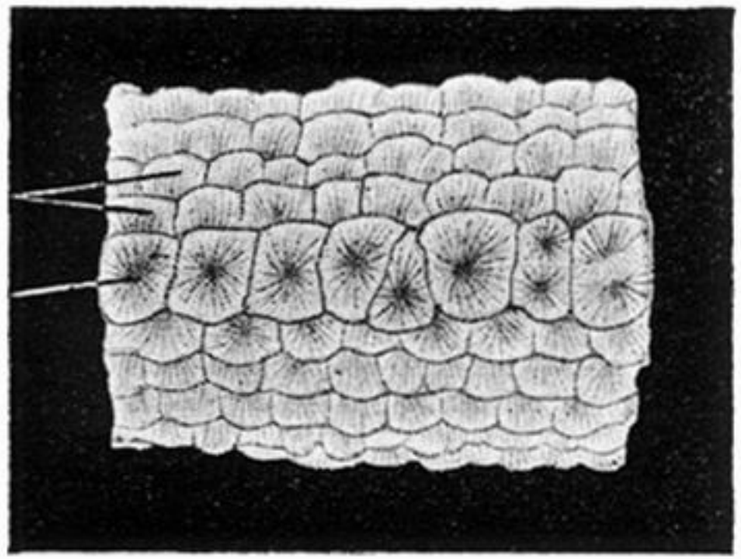
Scale diagram, showing the distribution of "centres of calcification" seen in transverse sections of various septal types.

Fig. 19.



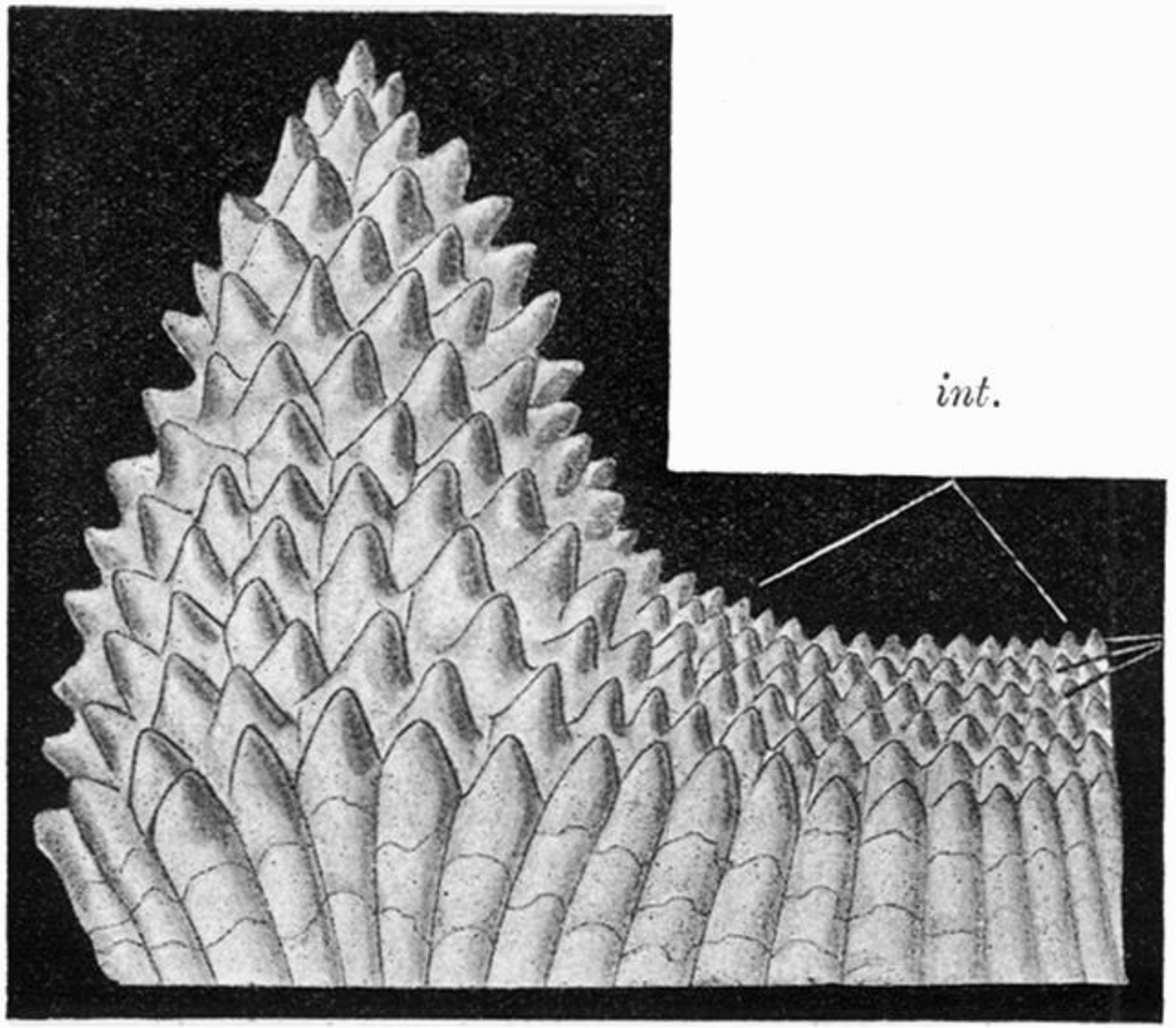
Transverse section through a thick spiniform tooth of the *Mussa* septum (low and high power); *c.c.* centre of calcification; *gr.* granulation; *g.l.* growth-lines, signifying successive growth-lamellæ (p. 125); *diss.* dissepiment.

Fig. 20A.



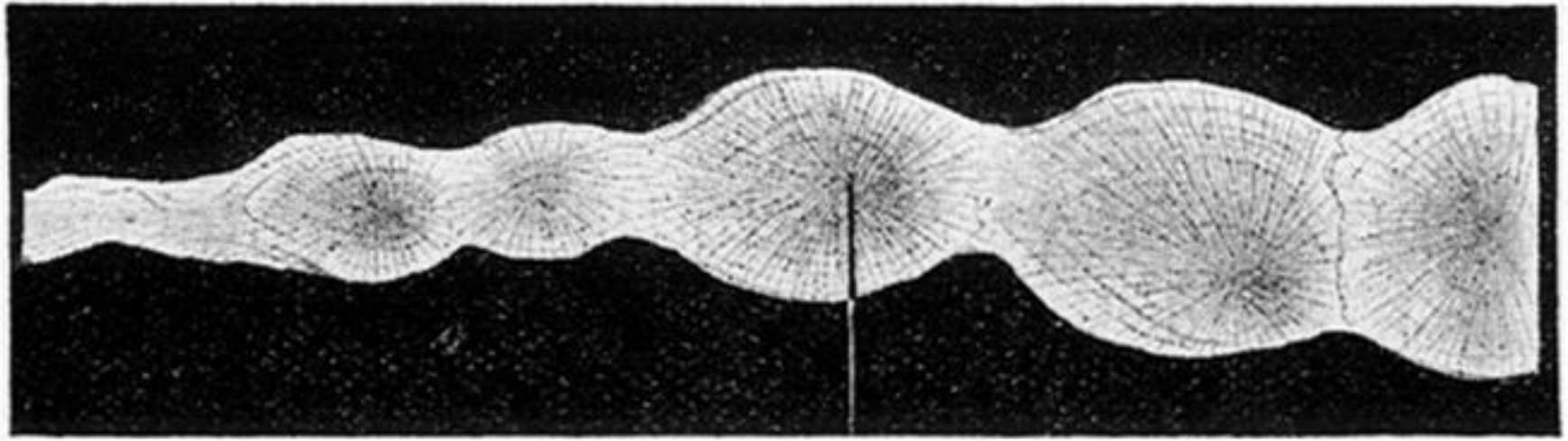
Transverse section through the *thin intermediate part* of a *Mussa* septum between two spiniform teeth. Several tiers of granulations are met on either side of the median plane.

Fig. 20B.



Diagrammatic drawing of a thick spiniform-toothed ridge and of the *thin intermediate part* (*int.*) with closely placed, small granulations.

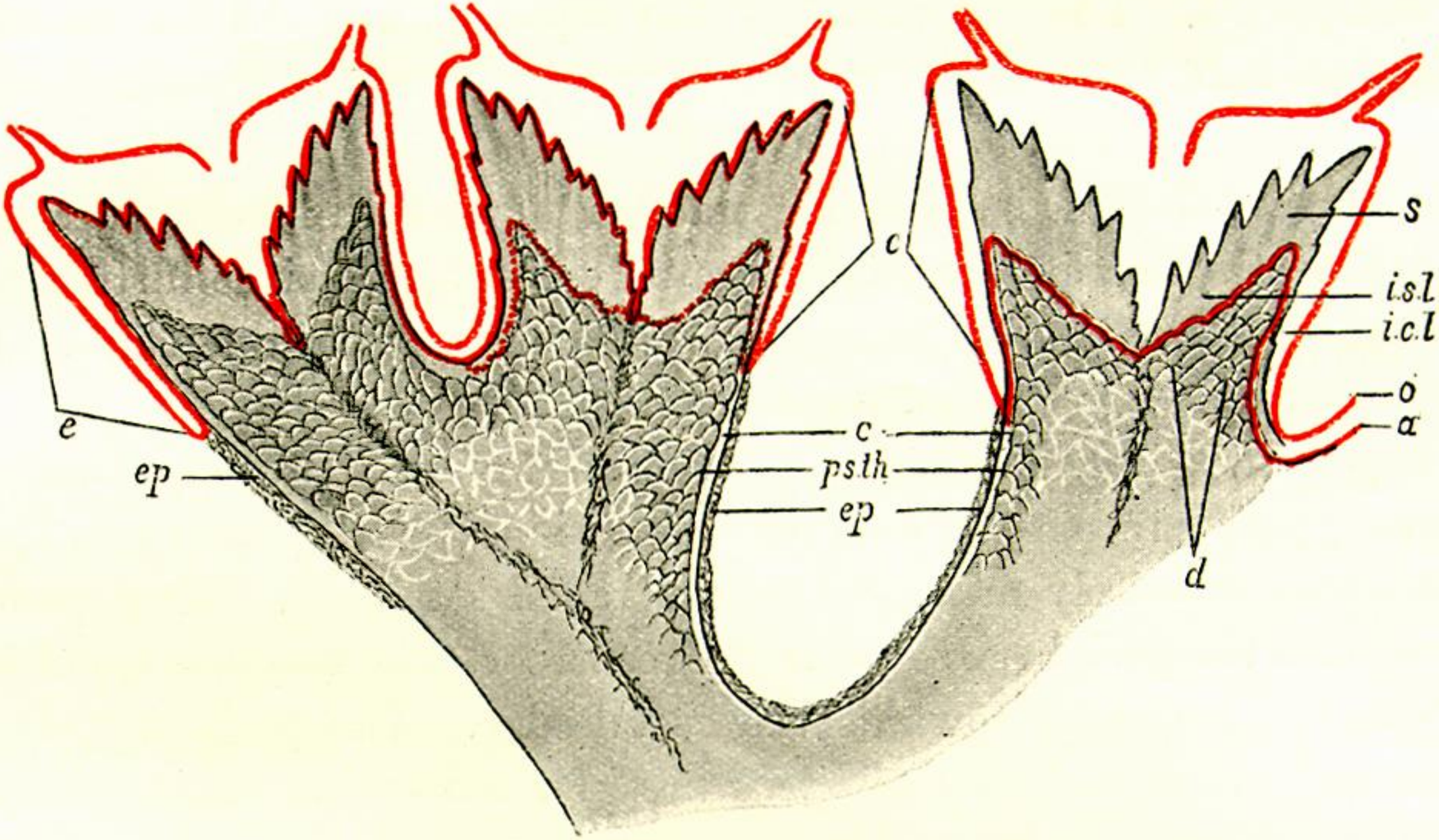
Fig. 21.



c.c.

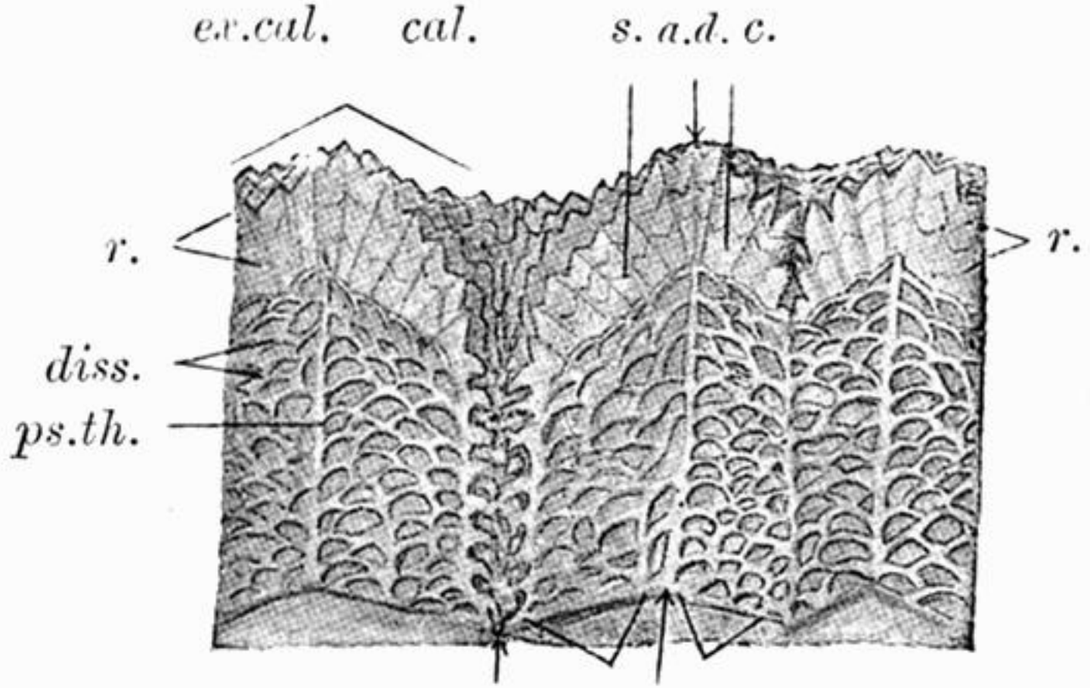
Transverse section of a very fine septum ·05 millim. thick (*cf.* fig. 19).

Fig. 22.



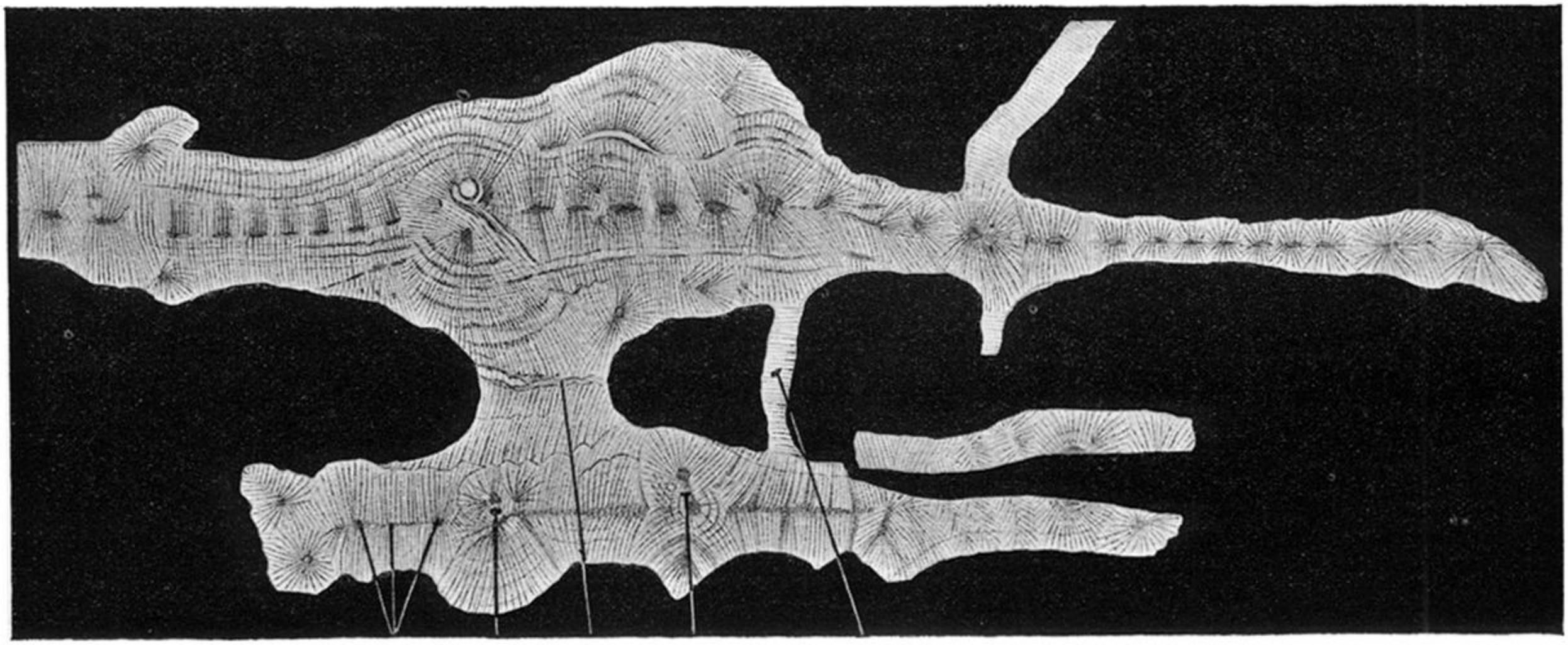
MUSSA.—Non-cœnenchymatous type ; *o.* = oral body-wall ; *a.* = aboral body-wall.
e. = edge-zone ; *s.* = septum ; *c.* = costa.
is.l. = interseptal loculus ; *ic.l.* = intercostal loculus.
ps.th. = pseudotheca ; *ep.* = epitheca ; *d.* = dissepiments.
(*cf.* also p. 156, and figs. 2, 35, 36, 56).

Fig. 23.



Skeletal parts of *Heliastræa*. *cal.*, calycinal parts; *ex.cal.*, extra calycinal parts; *s.*, septum; *a.d.* area of divergence of septal and costal ridges; *c.*, costa; *r.*, ridge; *d.*, dissepiment; *ps.th.*, pseudotheca; *ps.col.*, pseudocolumella.

Fig. 24A.



c.tr. *c.Tr.* *ps.th.* *c.Tr.* *d.*

Transverse section of two adjoining septa of *Heliastræa*, one of the septa having split along the median plane (containing the so-called "dark line") of the septum.

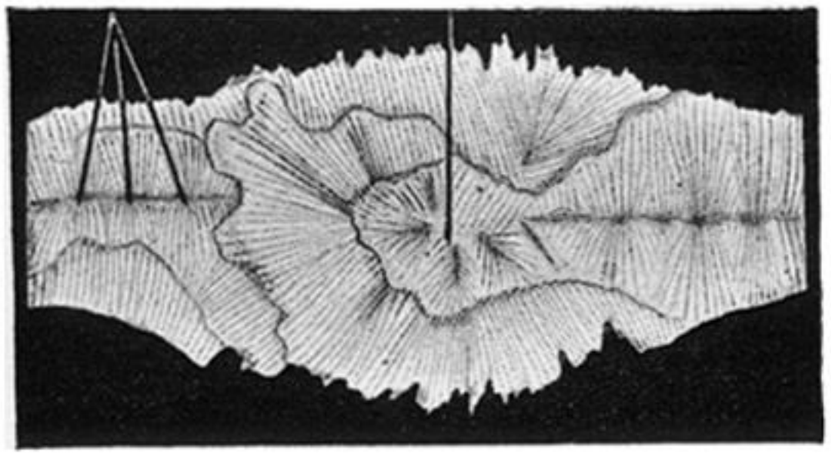
c.Tr. Centres of calcification in *compound* trabeculæ.

c.tr. „ „ „ *simple* trabeculæ.

ps.th. Pseudothecal, and *d.*, dissepimental deposit is shown to be *without* individual centres of calcification.

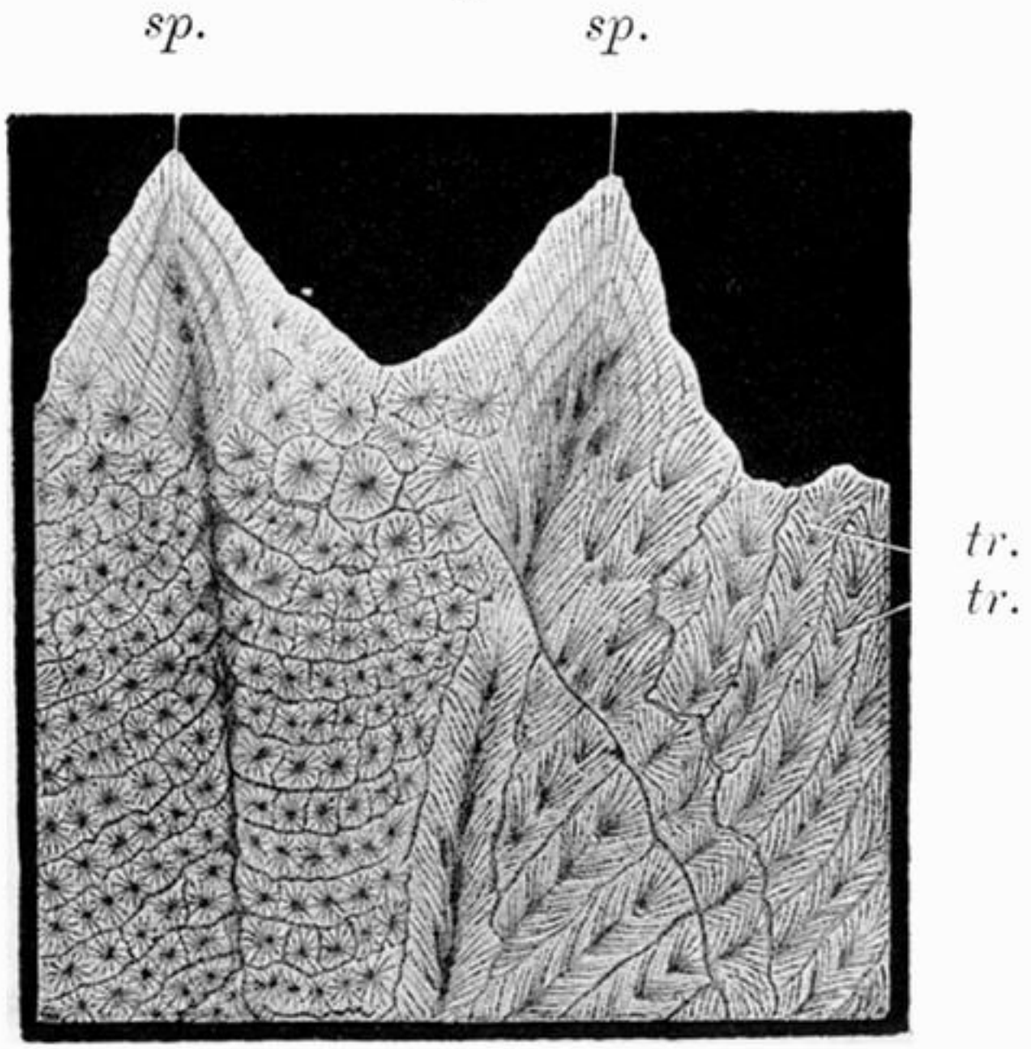
Fig. 24B.

tr. *Tr.*



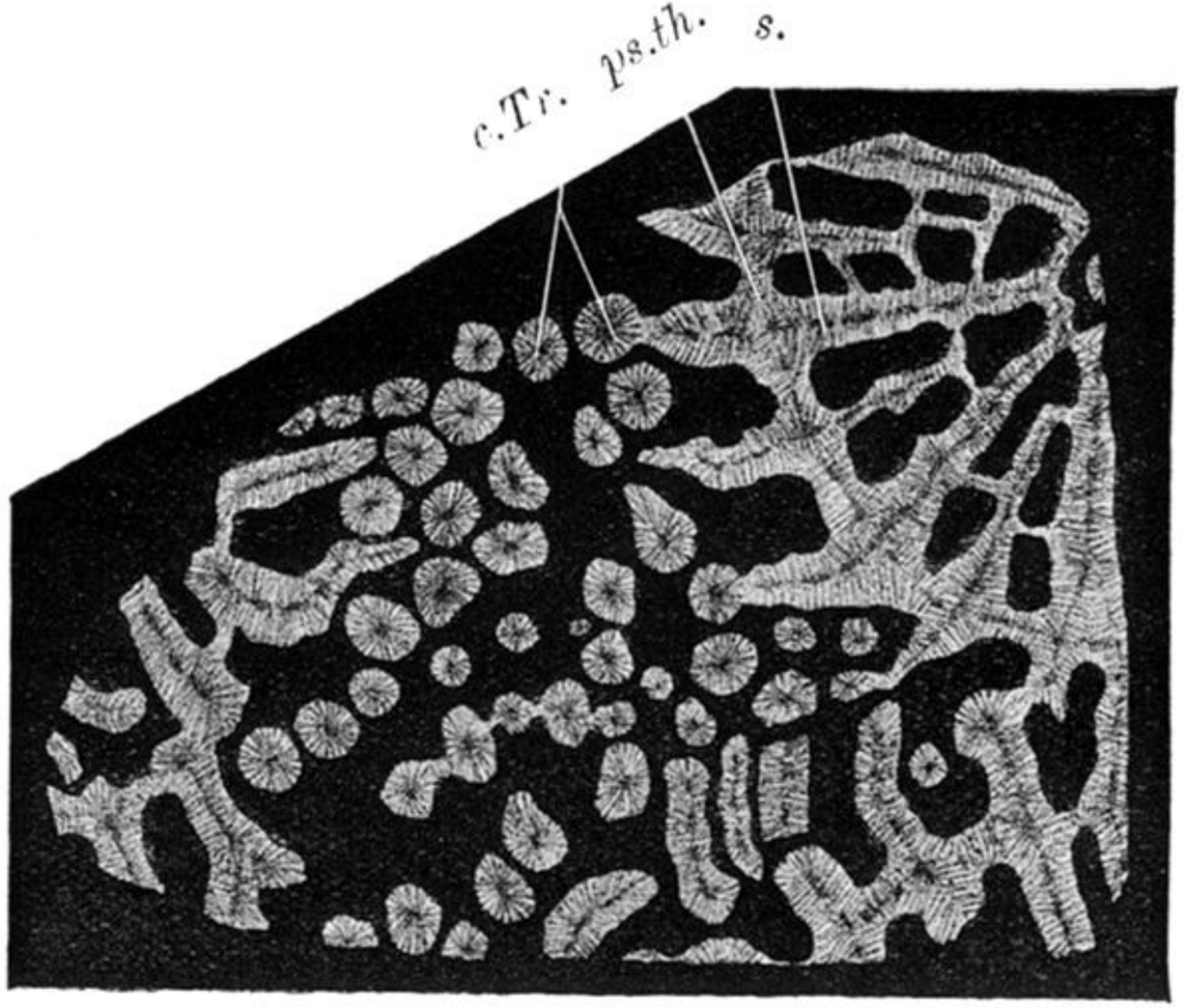
Thick central portion of a septal ridge formed by a "compound" trabecula (*Tr.*); and the thinner lateral wings of the same ridge passing into corresponding furrows—only "simple" trabeculæ (*tr.*) are present in these. (Magnified 70 times.)

Fig. 25.



Longitudinal section parallel with the septal plane; R_1 septal ridge met along the median plane; R_2 septal ridge met very obliquely; *tr.* trabeculæ; *sp.* spiniform teeth.

Fig. 26.



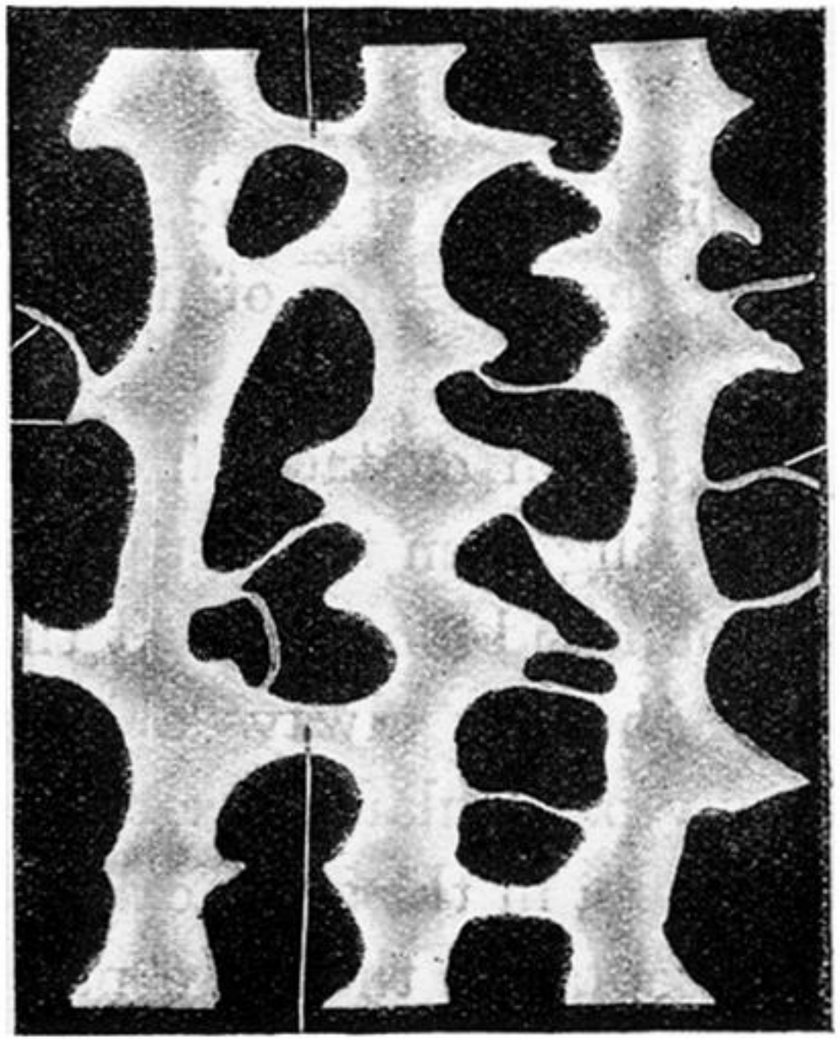
Transverse section showing the radial trabeculæ (comp.) in the intercalycinal portions of the *Heliastræa* skeleton; *c.Tr.* costal trabeculæ radial in structure; *ps.th.* pseudotheca; *s.* septum.

Fig. 27.

ps. syn.

d.

gr.

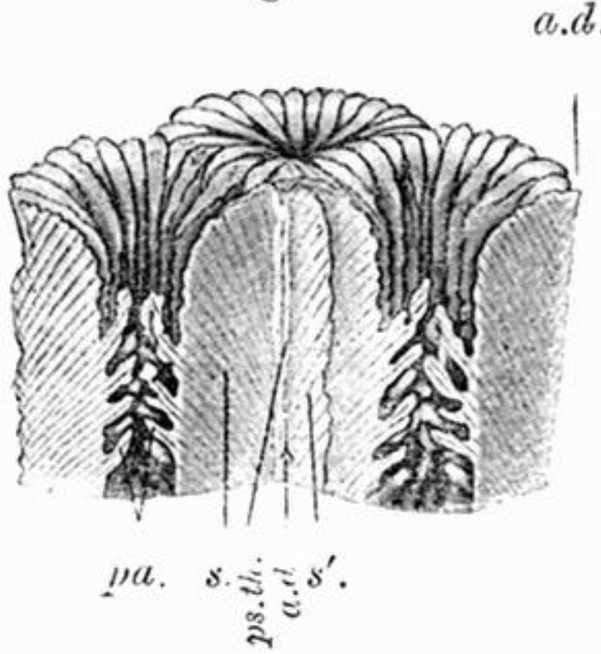


d.

s. *ps. syn.* *s.* *s.*

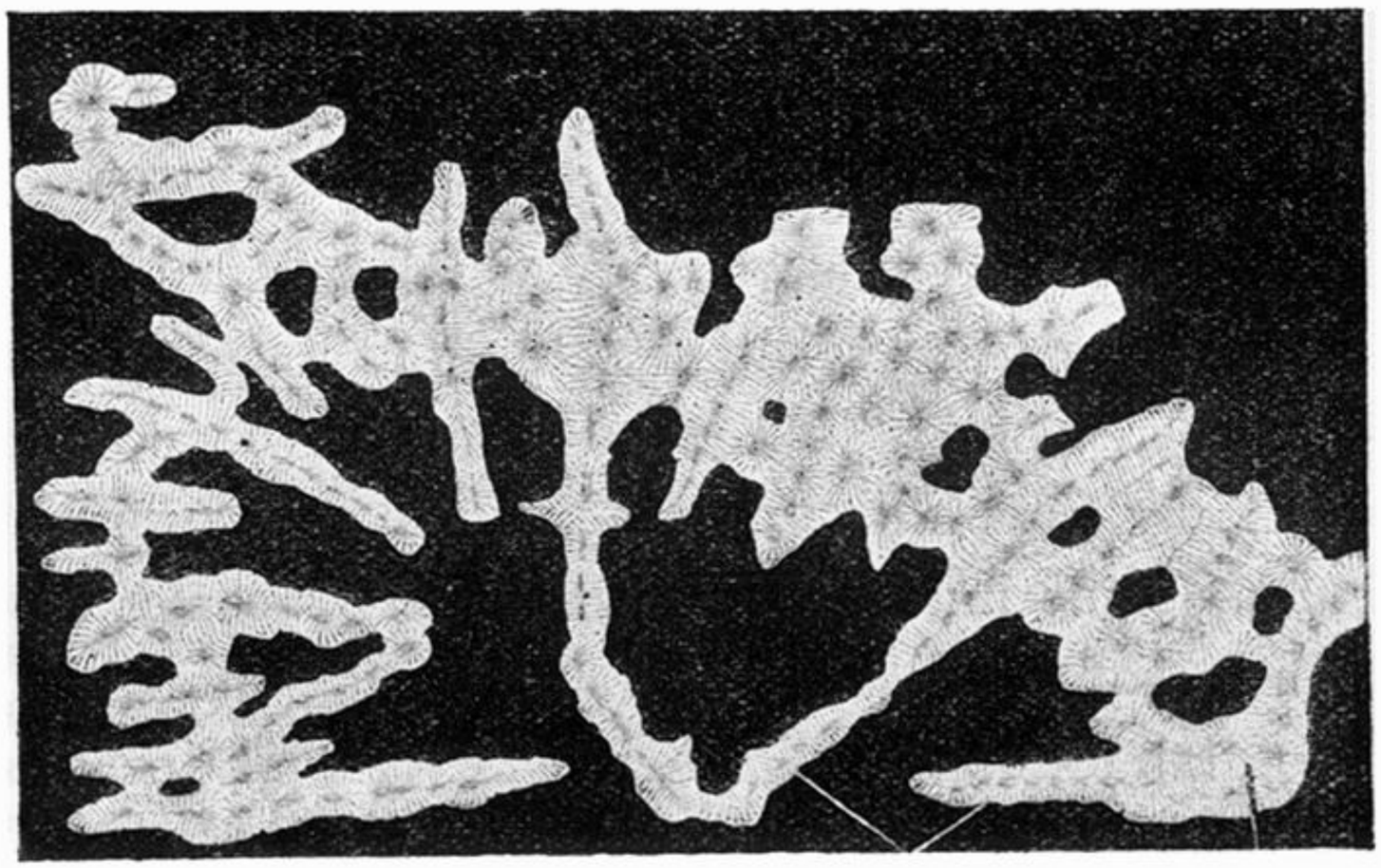
Longitudinal section (low power) through three adjacent septa, showing "pseudosynapticular" union between them, by means of the continued growth of granulations; *d.*, dissepiment; *gr.*, granulations; *ps. syn.*, pseudosynapticula; *s.*, septum.

Fig. 28.



Skeletal parts of *Goniastræa*. *s.*, large septum in one calyx; *s'.*, small septum in the adjoining calyx; *pa.*, pali; *ps.th.*, pseudotheca; *a.d.*, area of divergence.

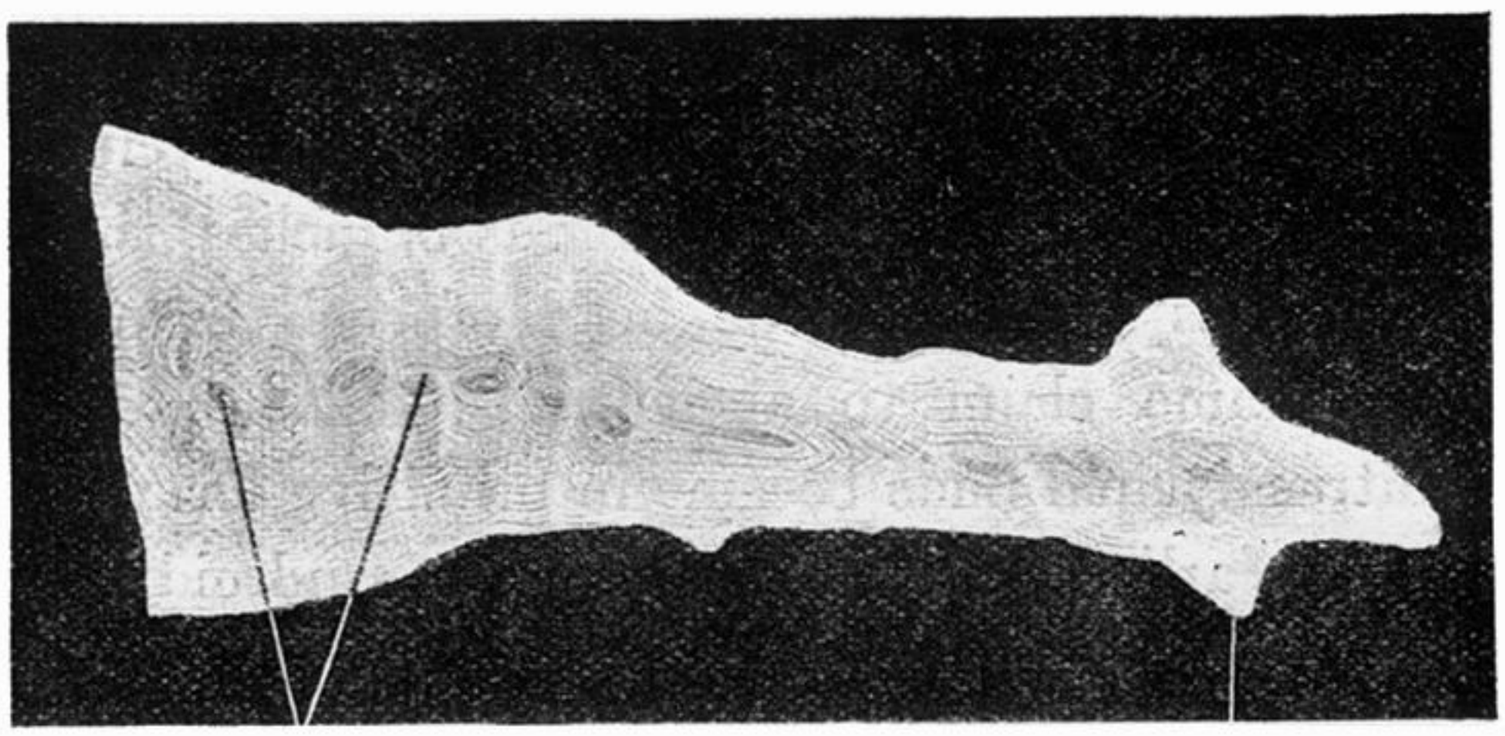
Fig. 29A.



s. *ps.th.*

Transverse section (20 times magnified). *s.*, septa; *ps.th.*, pseudotheca.

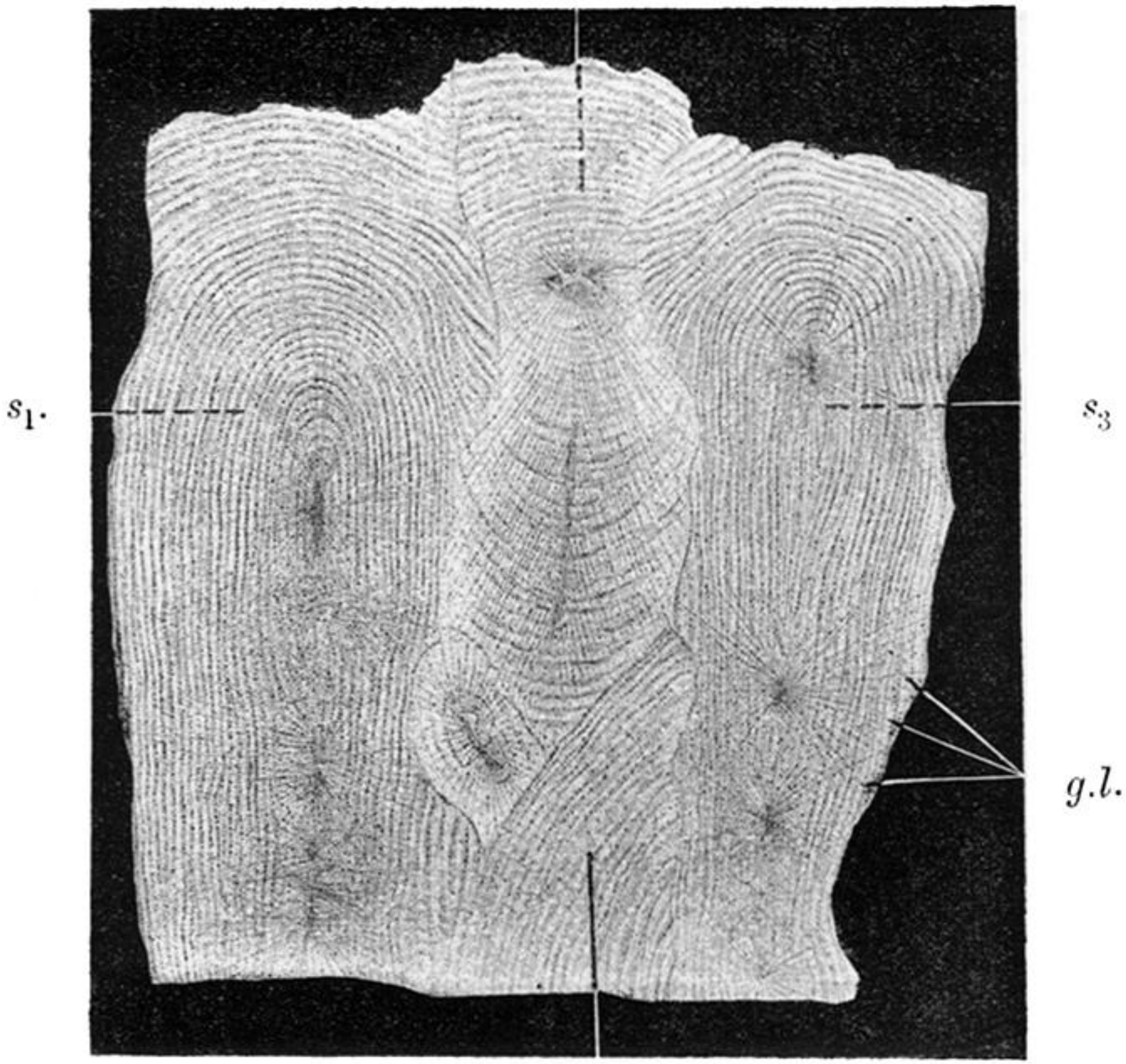
Fig. 29B.



c.c. *gr.*

Transverse section (70 times magnified) of a septum of *Goniastræa*, showing the curving lines of the growth-lamellæ crossed by the calcareous fibres. *c.c.*, centres of calcification; *gr.*, granulation.

Fig. 30A.

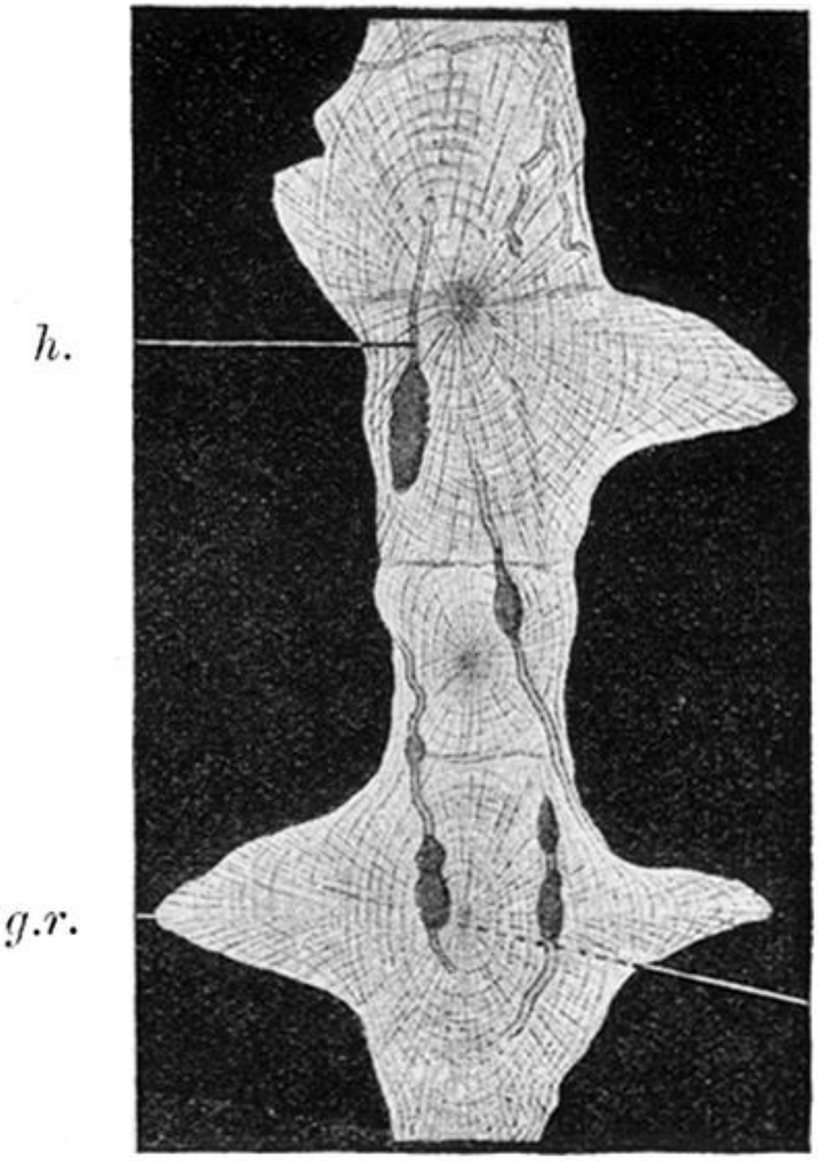


Transverse section of the wall area between two adjoining calyces of *Goniastræa*; large, compound trabeculæ are present in the septa ($s_1 s_2 s_3$), and thickened dissepiments (*d.*) add farther stability.

Fig. 30B.

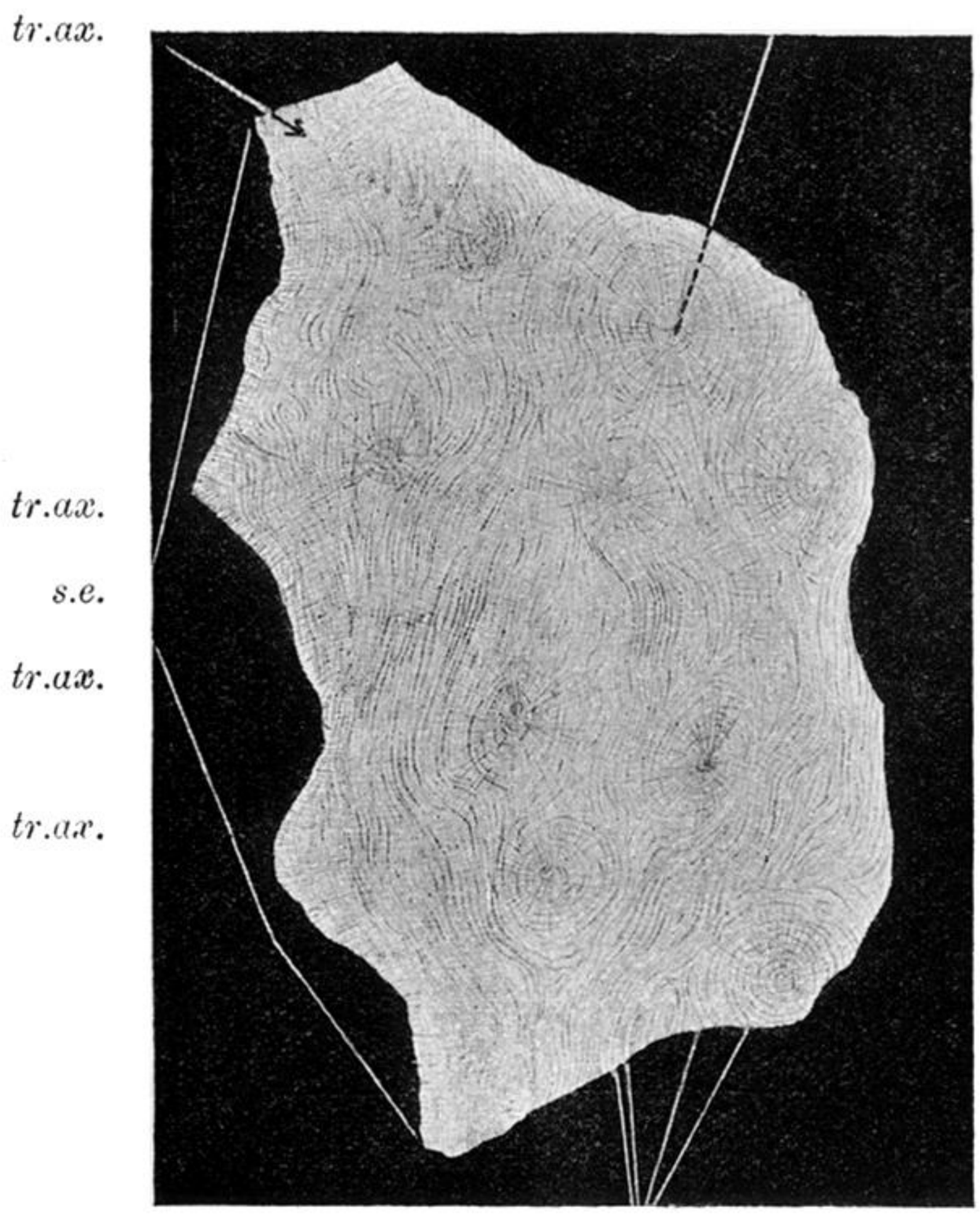
A small portion of fig. 30A seen under very high microscopic power. *c.c.*, centre of calcification; *g.l.*, growth lamellæ, edged by dark bands (*cf.* p. 125).

Fig. 31.



Septum cut lengthways. The septal ridge "*c*" shows an almost *transverse* section of the ridge trabecula with granulations on opposite surfaces. *tr.ax.*, trabecular centre or axis; *h*, hypha of a fungal growth.

Fig. 32.



Longitudinal section parallel with the septal plane. Four trabecular axes (*tr.ax.*) run from their apices at the septal edge (*s.e.*) obliquely downwards through the section, and the latter thus meets four different "ridge" series of granulations (*gr.*); growth-lamellæ (*g.l.*).

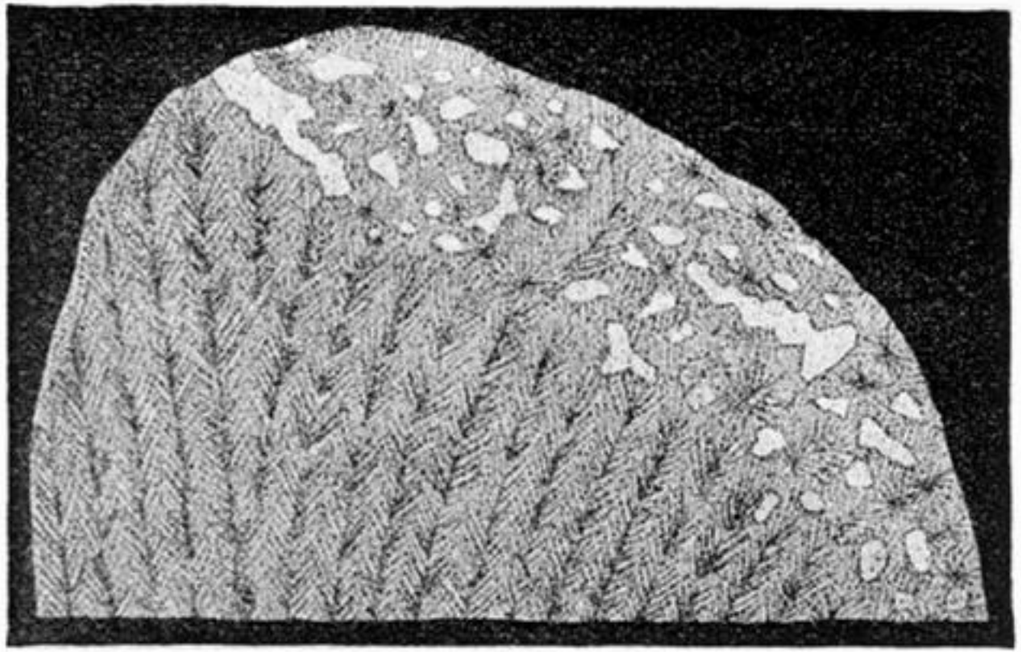
Fig. 33A.

Vertical section of septum penetrated with fungal growth.

Fig. 33B.

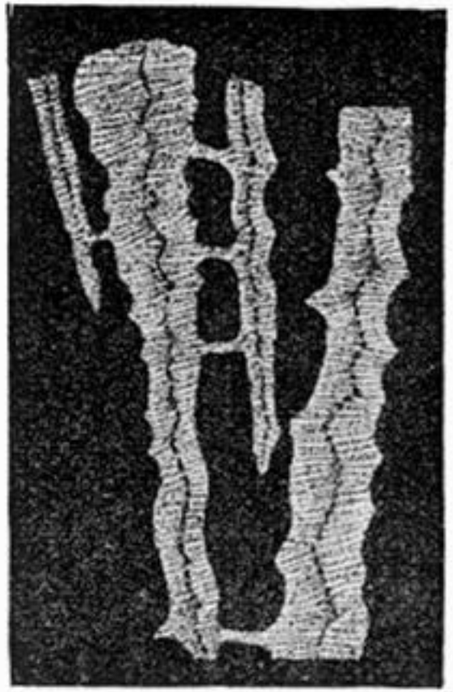
Section parallel with septal plane. *d.* dissepiment; *h.* fungal hyphæ; *s.e.* septal edge.

Fig. 34A.



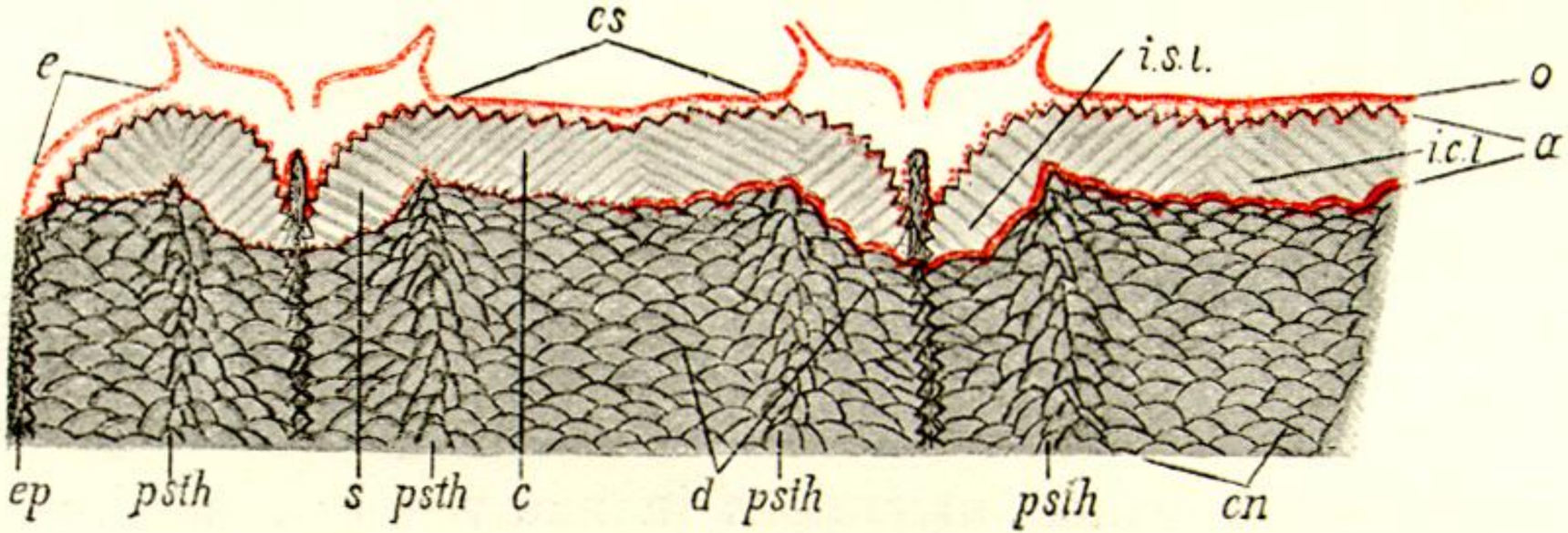
Longitudinal section parallel with the septal plane. Each trabecula is seen to be a series of fascicles (*cf.* figs. 10, 17B, 25).

Fig. 34B.



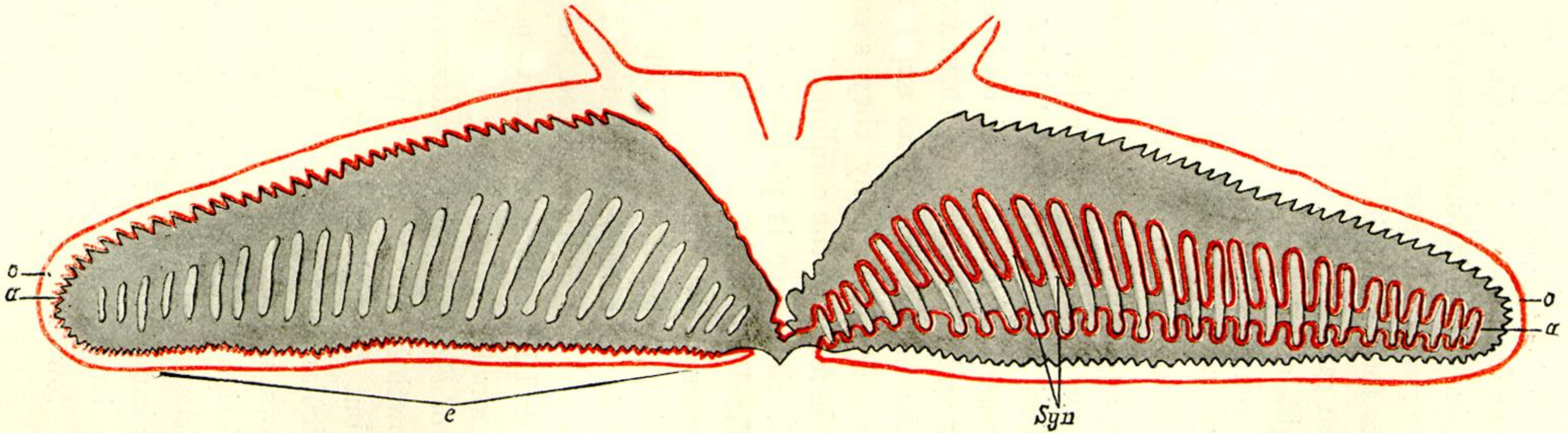
Transverse section of alternating thick and thin septa. Zig-zag appearance of median "dark line" (*antea*, pp. 116, 117).

Fig. 35.



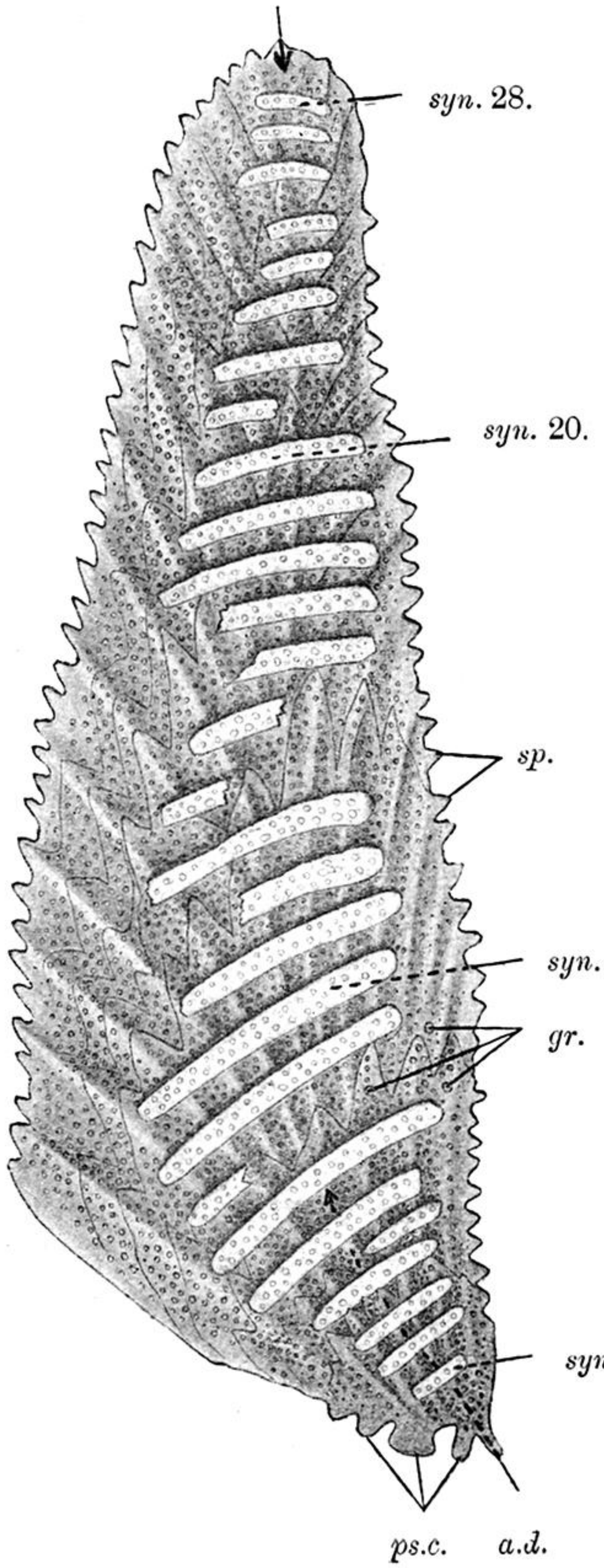
Typical *Stylinid* colony; letters as in fig. 2, p. 107; a columella is present in the middle of the calyx; the edge-zone extends horizontally—it is lettered "*cs.*" cœnosarc, for comparison with *Turbinaria*, fig. 56, and *Galaxea; psth.* pseudotheca; *ic. l.* intercostal loculus.

Fig. 36.



FUNGIA. The oral (*o.*) and aboral (*a.*) body-wall are doubled round, so that the part corresponding to the edge-zone (*e.*) of *Mussa* is here found on the basal surface *syn.* synapticulæ (*cf.* pp. 168–171). This diagram is to be compared especially with fig. 22. Two *non-cœnenchymatous* types, *Mussa* and *Fungia*, are represented in this way for the sake of comparison with *cœnenchymatous* types, *e.g.*, *Galaxea*, fig. 2, and Turbinaria, fig. 56.

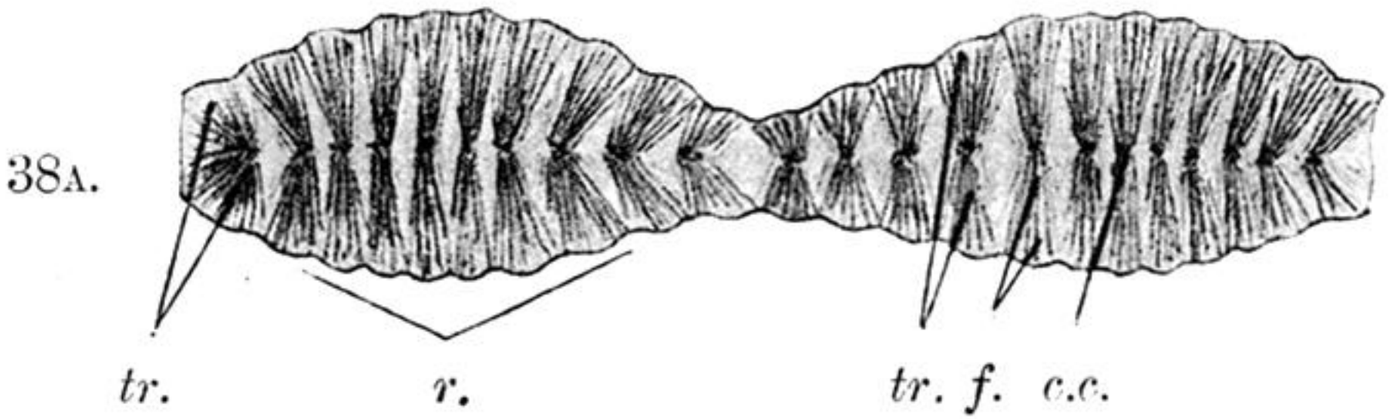
Fig. 37.

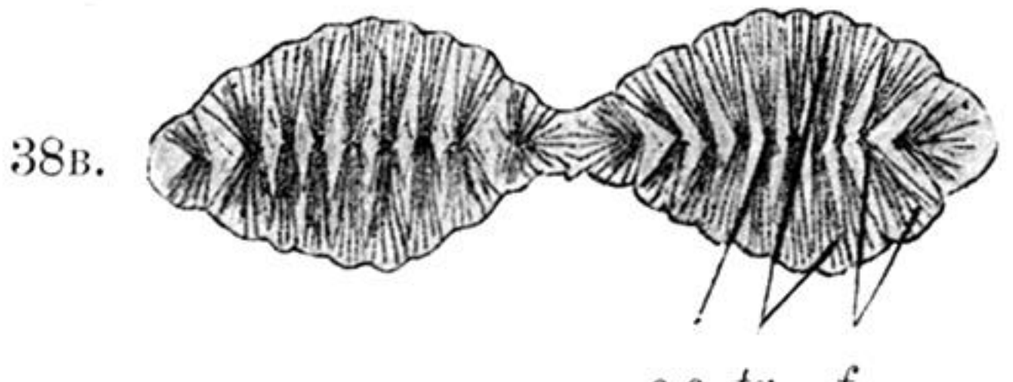


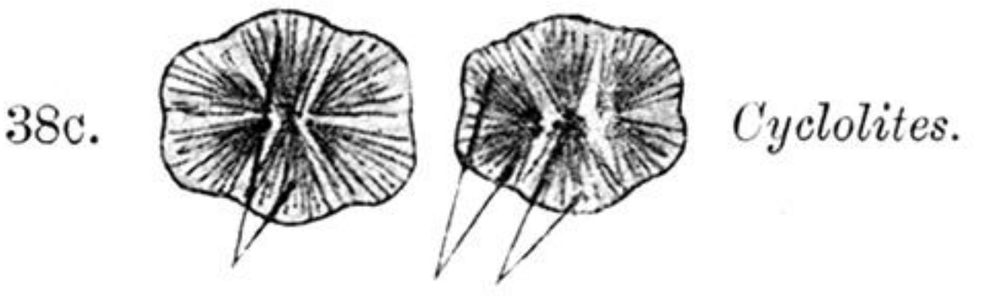
Septum of *Fungia* represented in a vertical position instead of the horizontal position assumed in nature. The area of divergence (*a.d.*) of the trabecular ridges is thus seen to follow a line in the septal plane rather nearer the outer or "costal" edge than the inner or "septal" edge of the septum (*cf.* fig. 15).

sp. = spiniform teeth of the costal edge.
syn. = synapticulæ in ascending series.
gr. = granulations.
ps.c. = pseudo-columellar teeth.

Fig. 38.

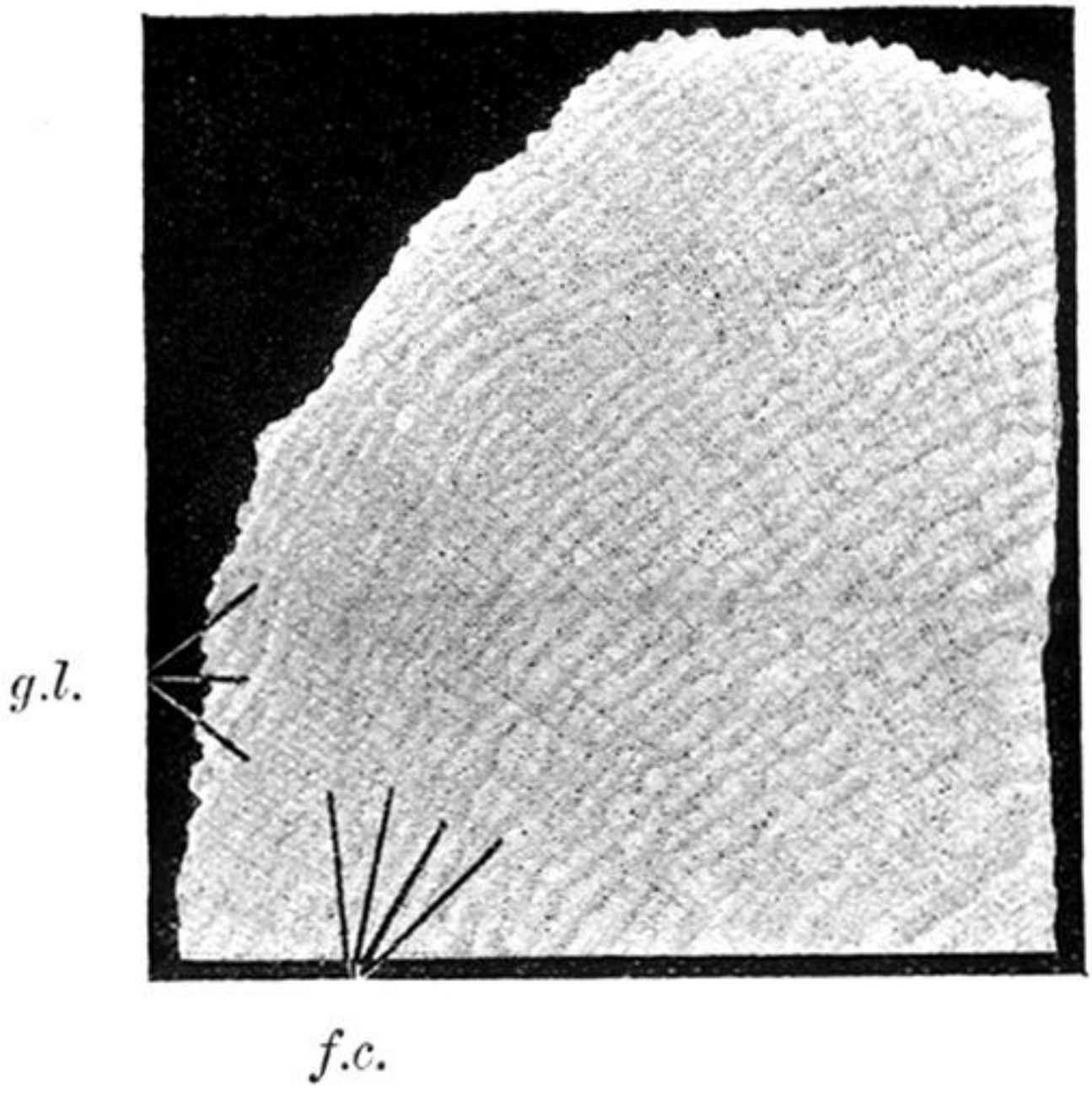






Comparison of transverse sections (diagrammatic, *cf.* fig. 18) through three characteristic septal types; *Mussa*, the septal ridges (*r.*) are elongate, and the centres of calcification (*c.c.*) widely spaced; *Fungia*, ridges more elliptical in outline, and the centres (*c.c.*) more closely packed; *Cyclolites*, ridges rounded, centres (*c.c.*) in one group, so that six fascicles (*f.*) form here a "compound trabecula."

Fig. 39.



Section horizontal with the septal surface.

g.l., wavy "dark bands" of the growth-lamellæ.

f.c., fibro-crystals of the lamellæ crossing the "bands" in direction.

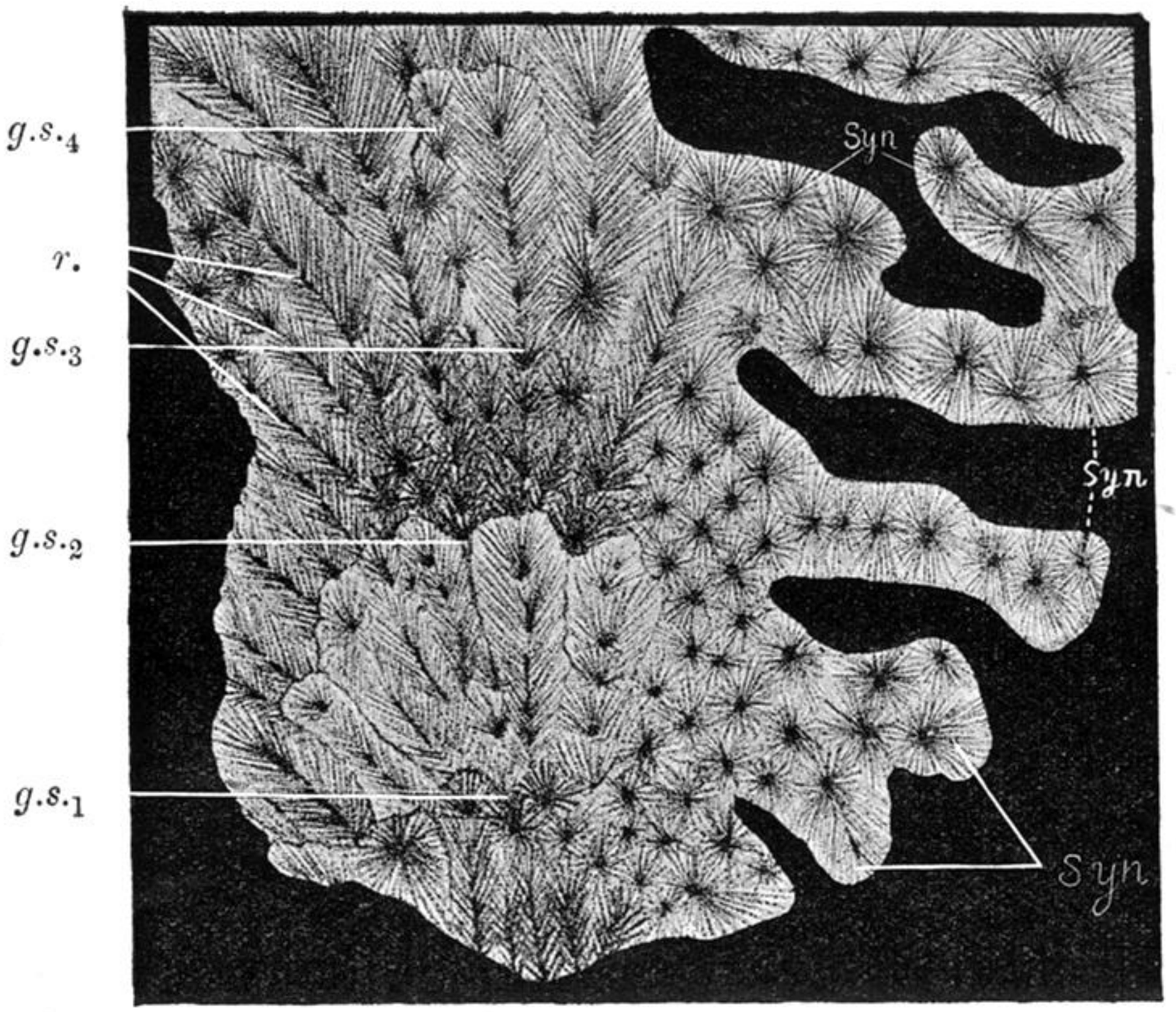
Fig. 40A.

Small drawing to show the positions of the sections represented in fig. 40c ("*x*" in drawing) and fig. 40D (= "*y*").

Fig. 40B.

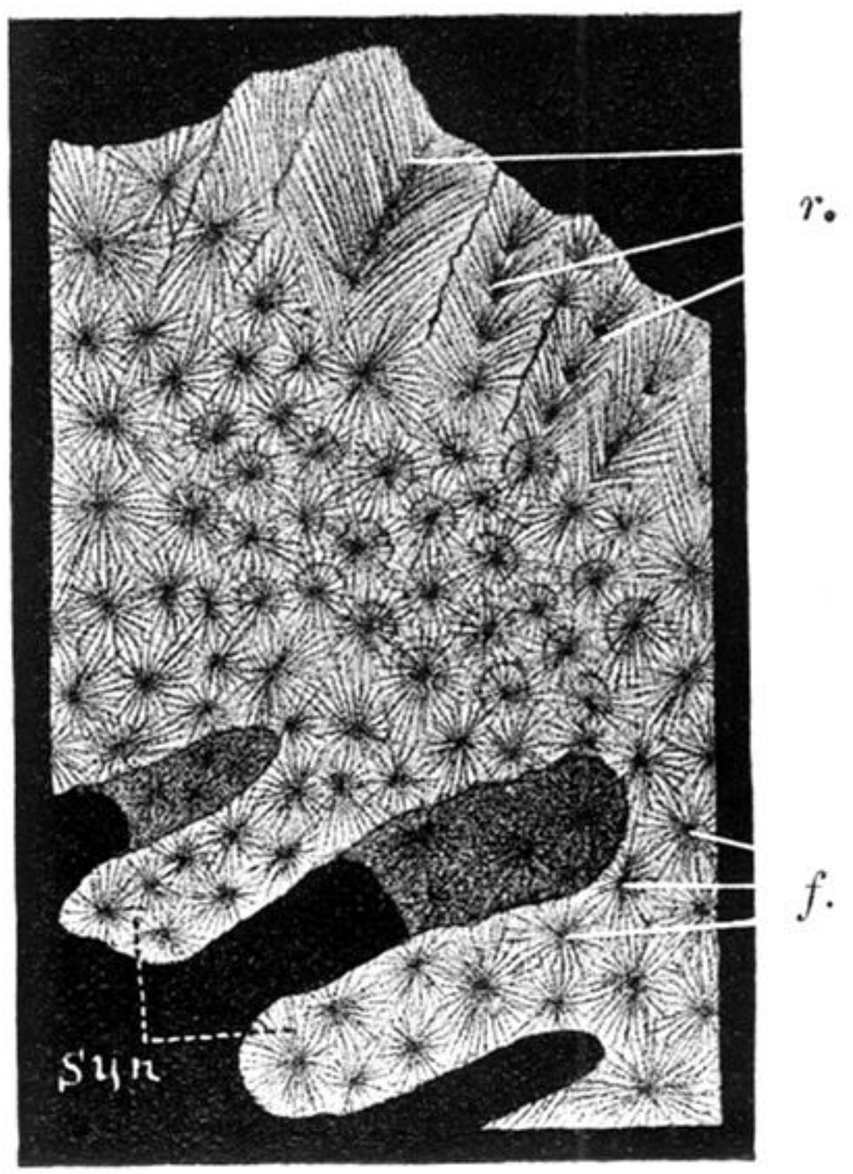
Small diagrammatic drawing to show how the plane of polishing in fig. 40A passed through two adjoining septa and the synapticulæ between.

Fig. 40C.



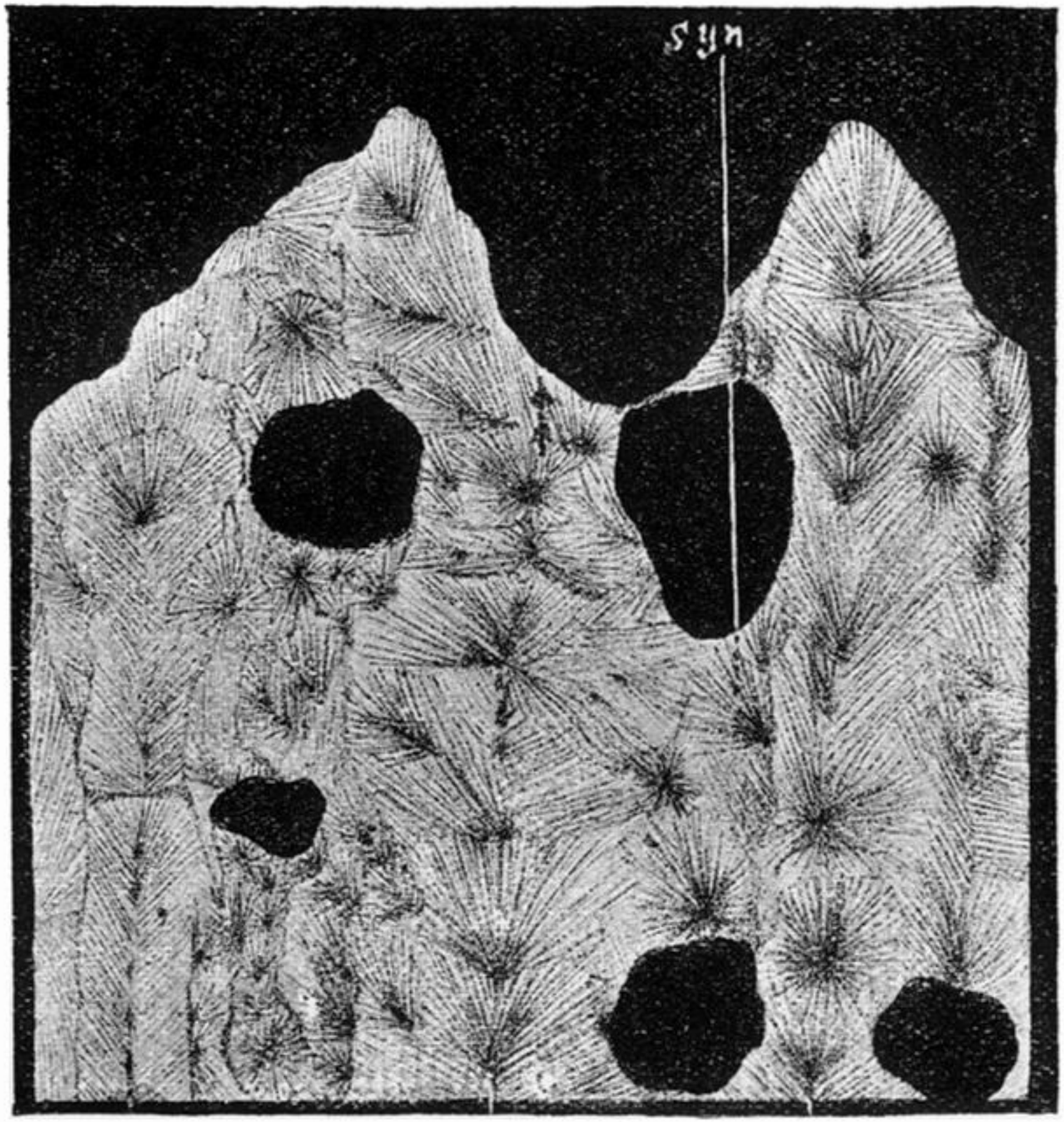
Section passing obliquely through a septum into the interseptal loculus with synapticular bars (*syn.*). Four growth-segments (*g.s.*) are indicated by fans of diverging trabecular ridges (*r.*), a single "syn." corresponding to each.

Fig. 40D.



Same section continued through the interseptal loculus to the adjacent septum *f.* = fascicles cut across.

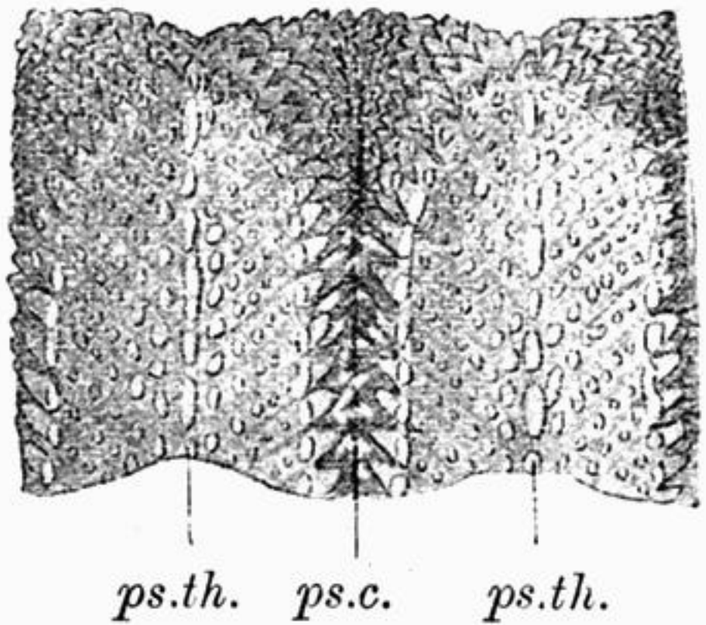
Fig. 41.



s. *syn.* *s.* *syn.* *s.*

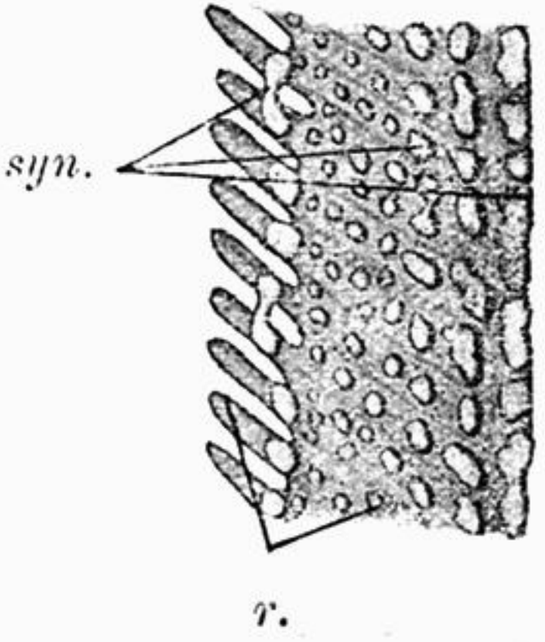
Tangential section of Fungia. *s.* = septa ; *syn.* = synapticulæ. Independent centres of calcification are present in the synapticulæ.

Fig. 42A.



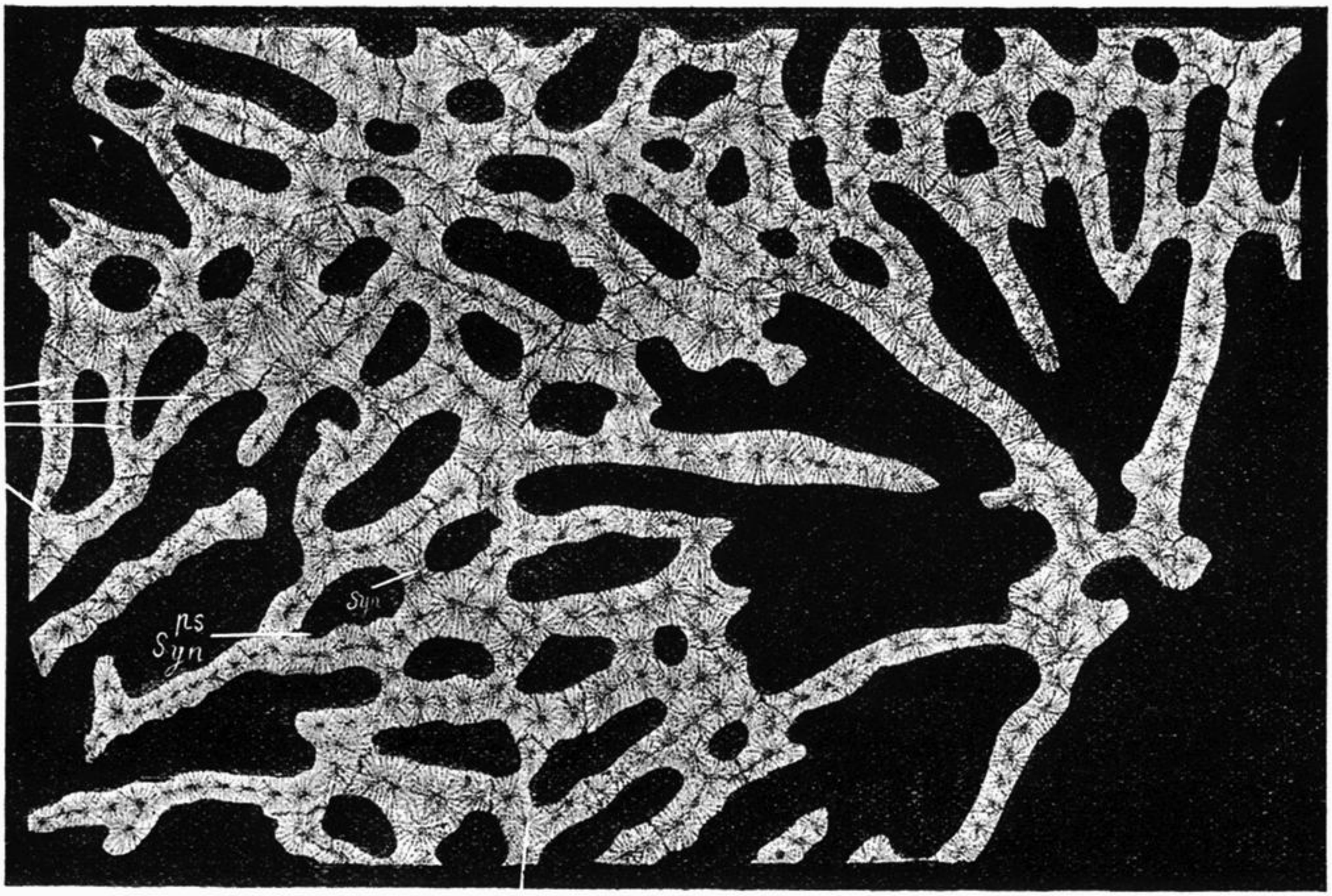
Skeletal parts of *Siderastræa ps.c.*, pseudocolumella of calyx, *ps.th.*, pseudotheca between calyces.

Fig. 42B.



Septal surface showing the direction of the ridges (*r*), and the position of the large synapticular granulations (*syn.*).

Fig. 43A.

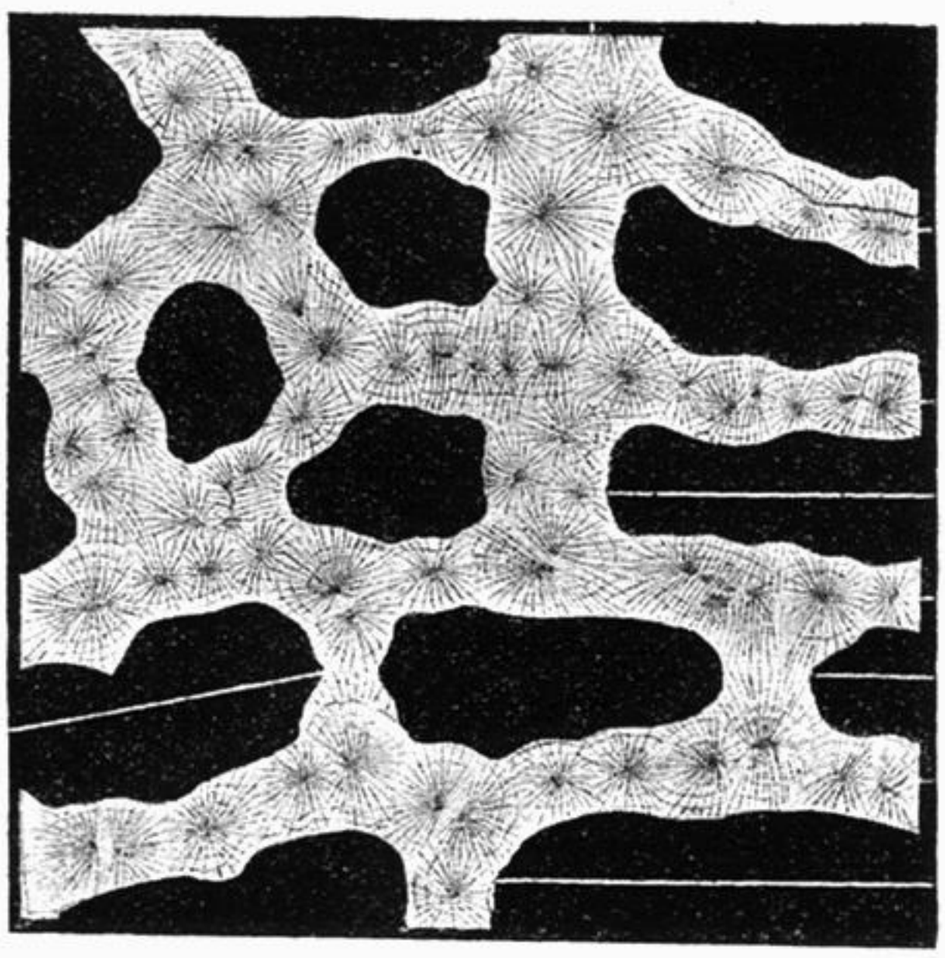


syn.

Transverse section through calyces of *Siderastræa*. The synapticular "wall," or pseudotheca (*ps.th.*) is seen between three adjacent calyces: *syn.* synapticula; *ps.syn.* pseudosynapticula; *co.se.* lateral coalescence of septa, *s.* septa.

Fig. 43B.

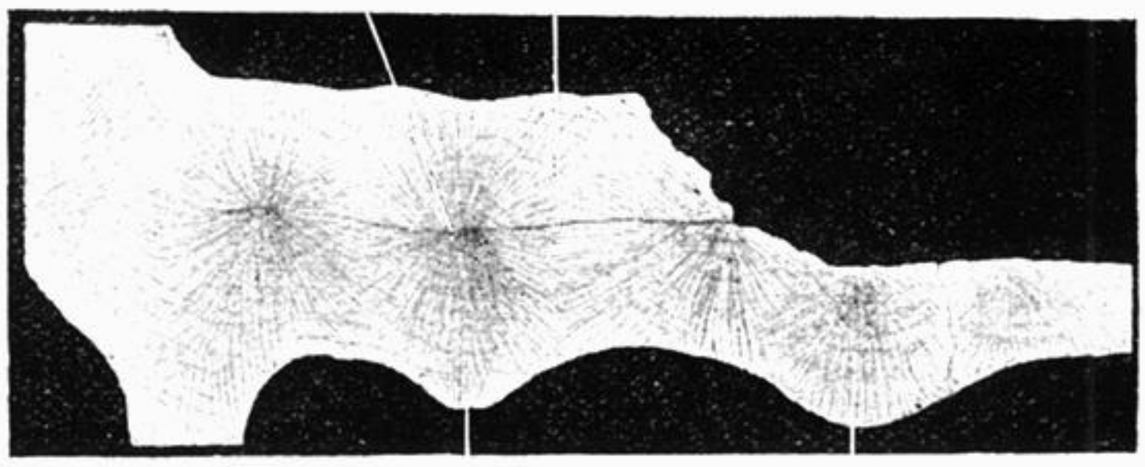
ps.th.



Transverse section; enlarged drawing of a pseudothecal part of the same section as fig. 43A.

Fig. 43C.

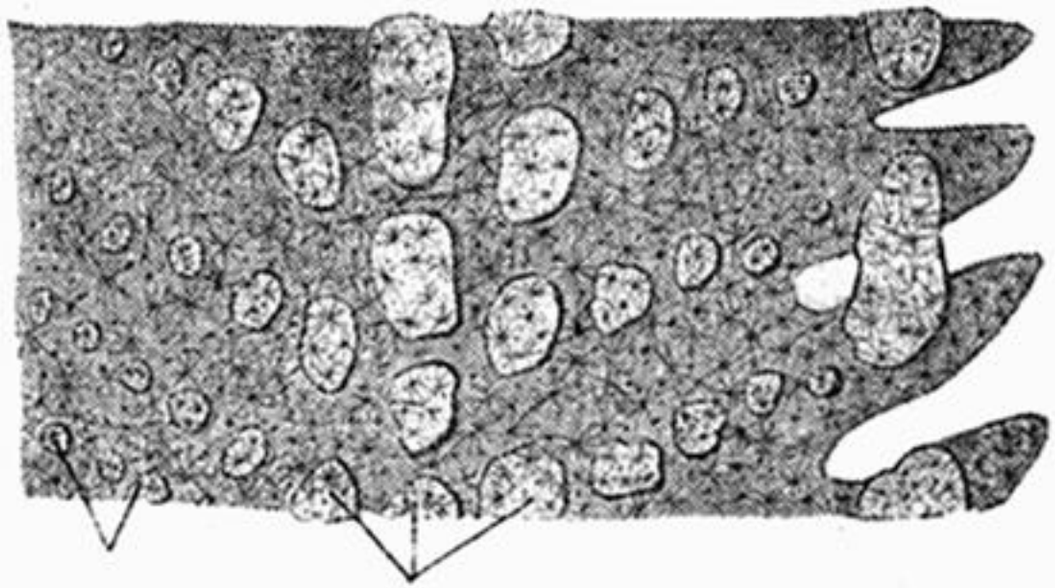
cr. *cr.*



gr. *gr.*

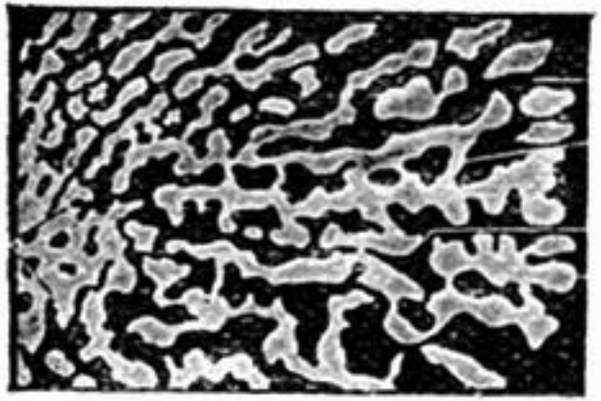
One septum (high power). *gr.* granulations; *cr.* a crack in the section along the median plane.

Fig. 44.



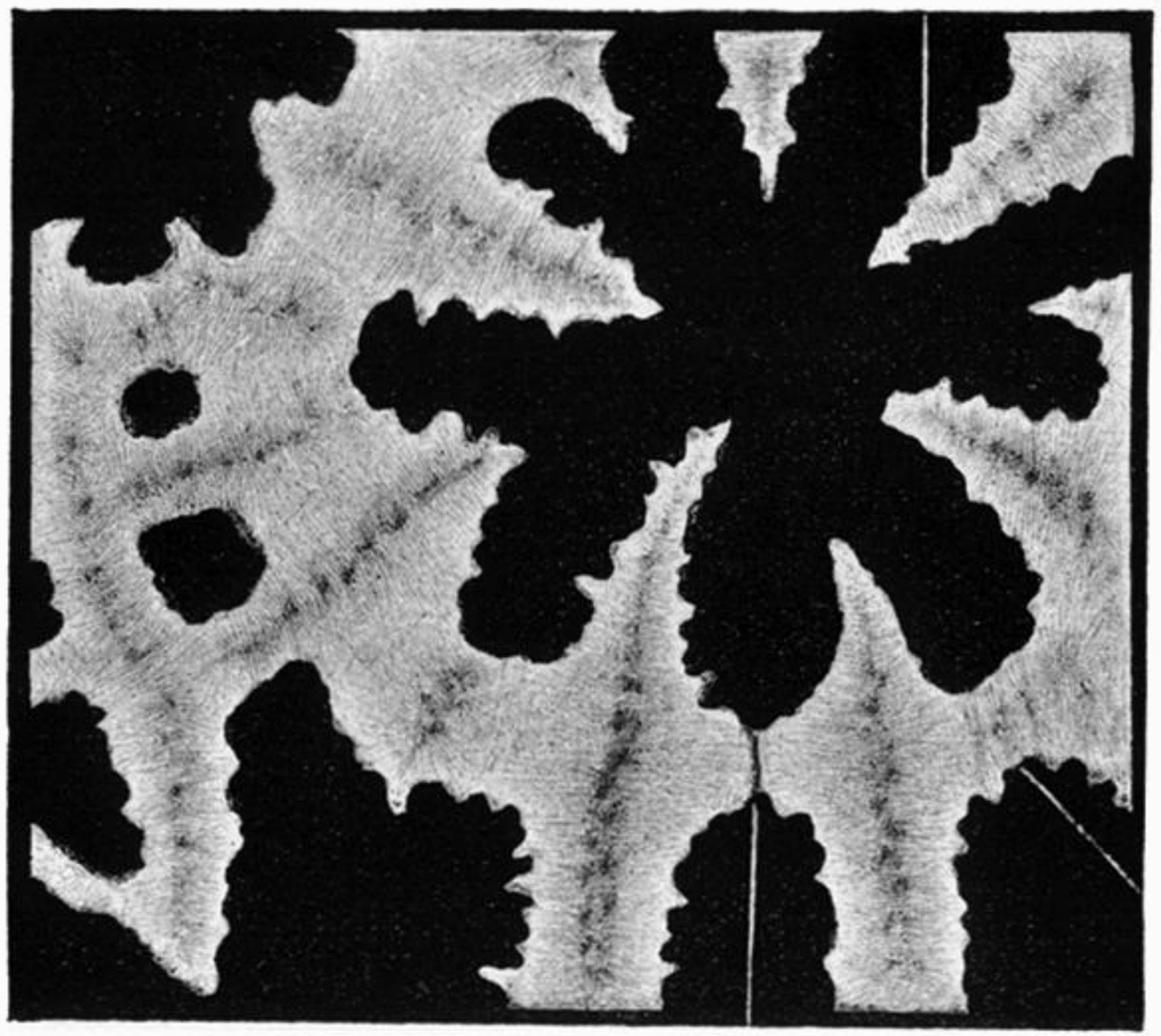
Longitudinal section parallel with the septal plane; pseudosynapticulæ (*ps.syn.*), an enlarged form of granulation (*gr.*).

Fig. 45.



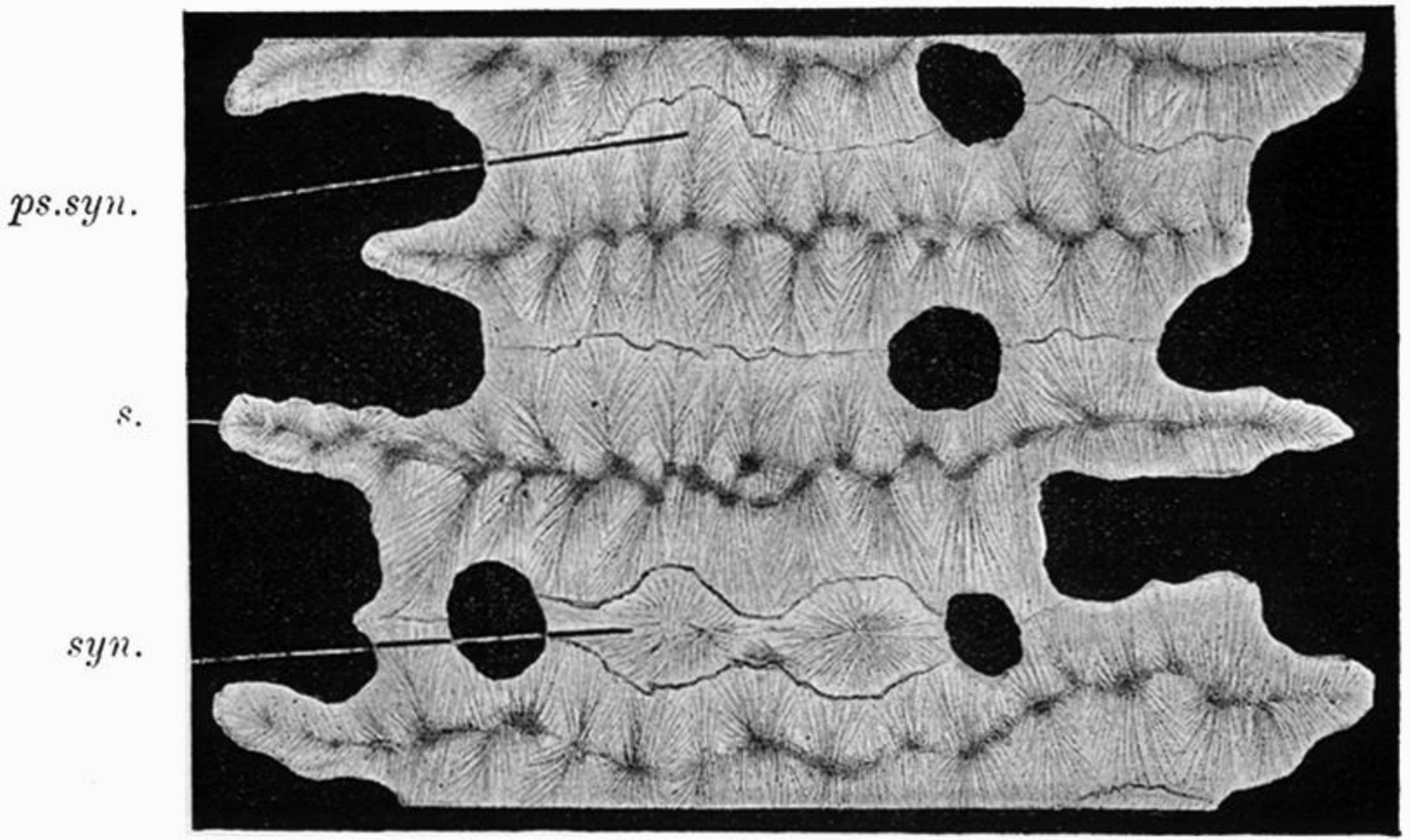
Transverse section of *Haplarœa*, showing spongiose columella, septa with pores (*p.*) and united laterally by true synapticulæ (*syn.*), also a pseudothecal wall with pores (*ps. th.*).

Fig. 46.



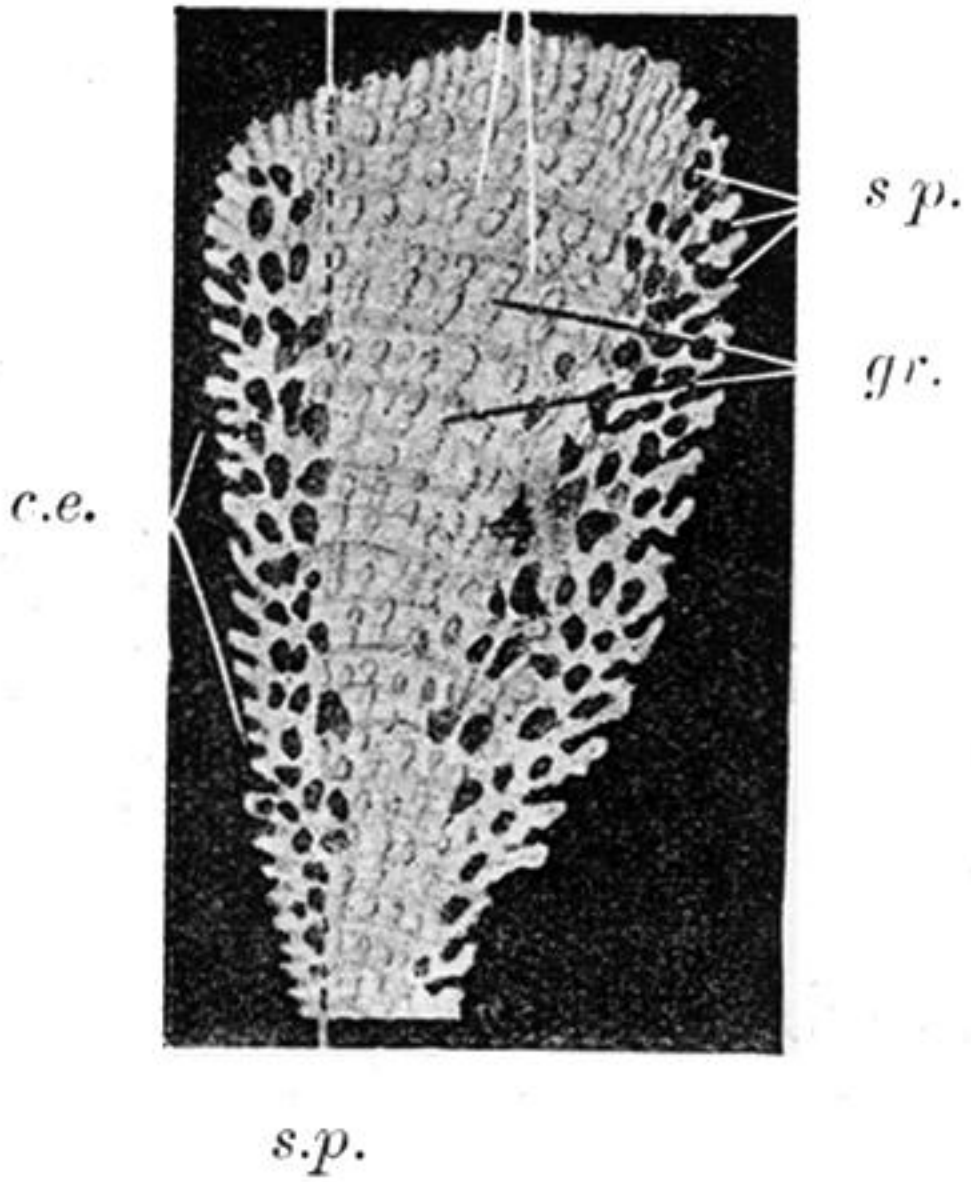
Transvesre section of a calyx of Lophoseris—true synapticulæ (*syn.*), and pseudosynapticulæ (*ps.syn.*). form the pseudotheca;—septal granulations (*gr.*) correspond with the "centres of calcification."

Fig. 47.



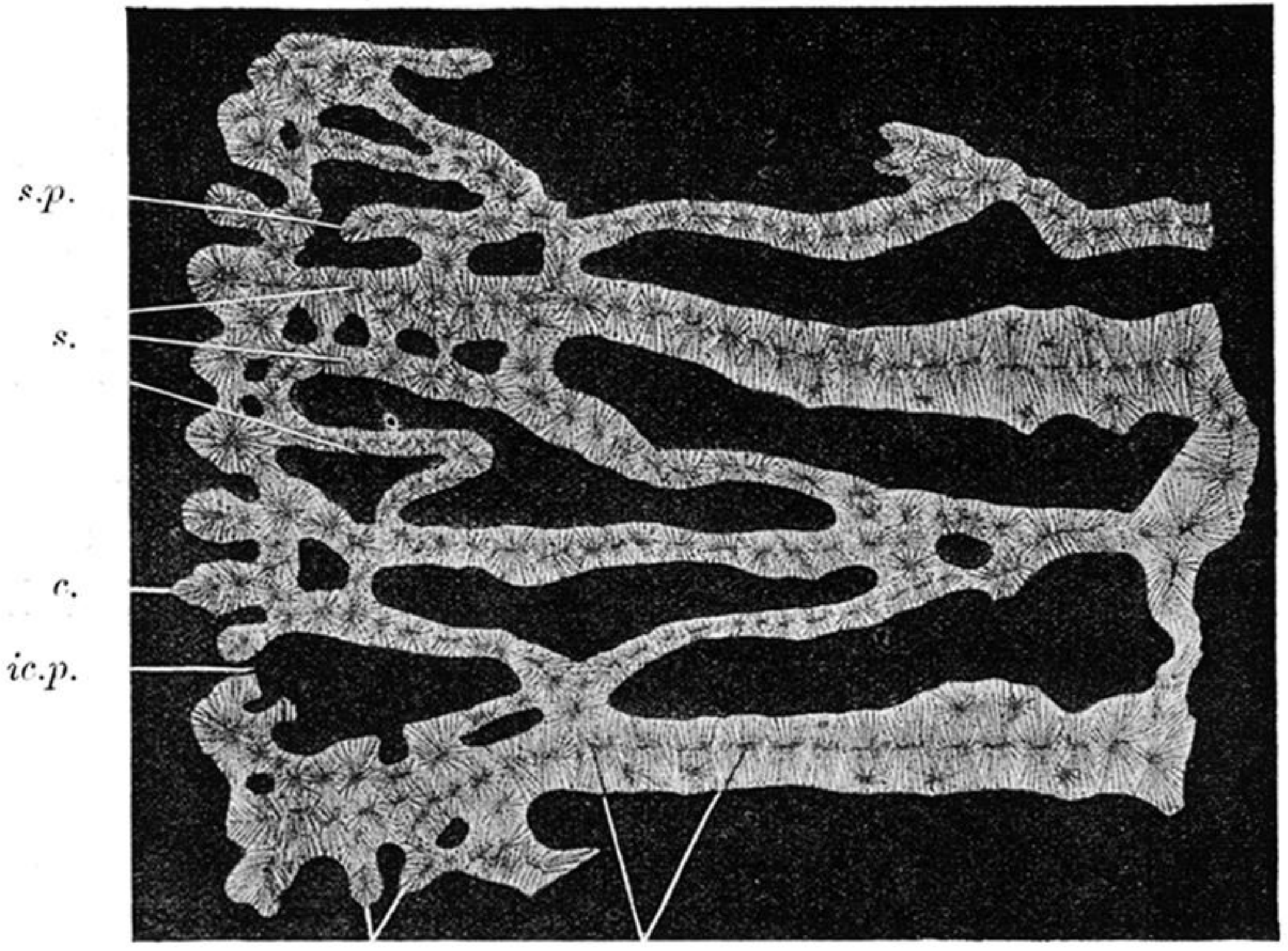
Transverse section through a much thickened pseudotheca, continued growth of the synapticulæ and pseudosynapticular granulations having blocked up a large part of the interseptal loculi.

Fig. 48.



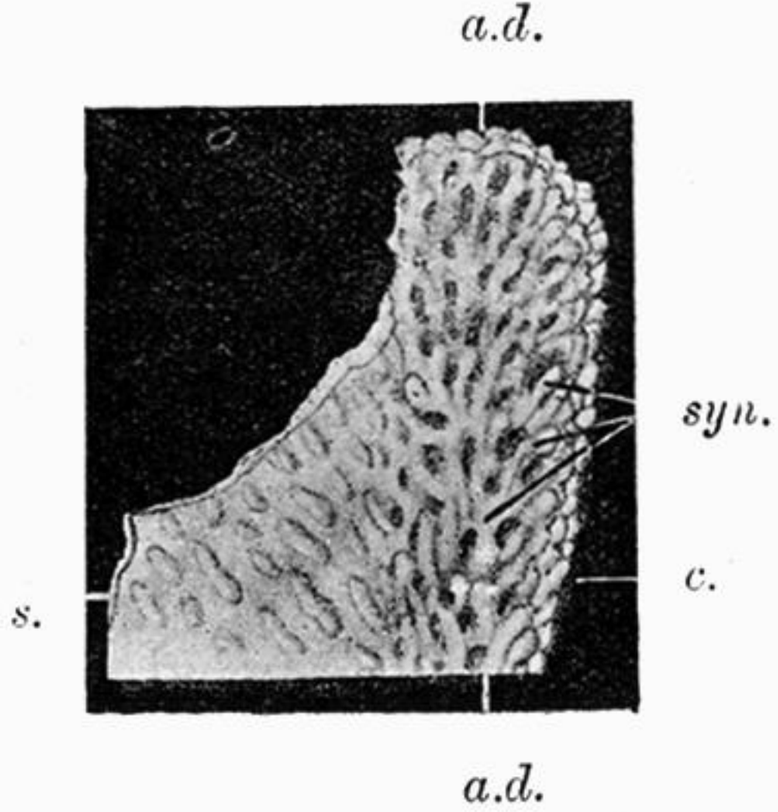
Septum of *Eupsammia trochiformis*, E.H.; *s.p.*, septal pores at the inner (columellar) and outer (pseudothecal) regions; *c.e.*, costal edge of septum; *g.s.*, a growth-segment of septum with its curving series of granulations; *gr.*, granulations in other growth-segments.

Fig. 49.



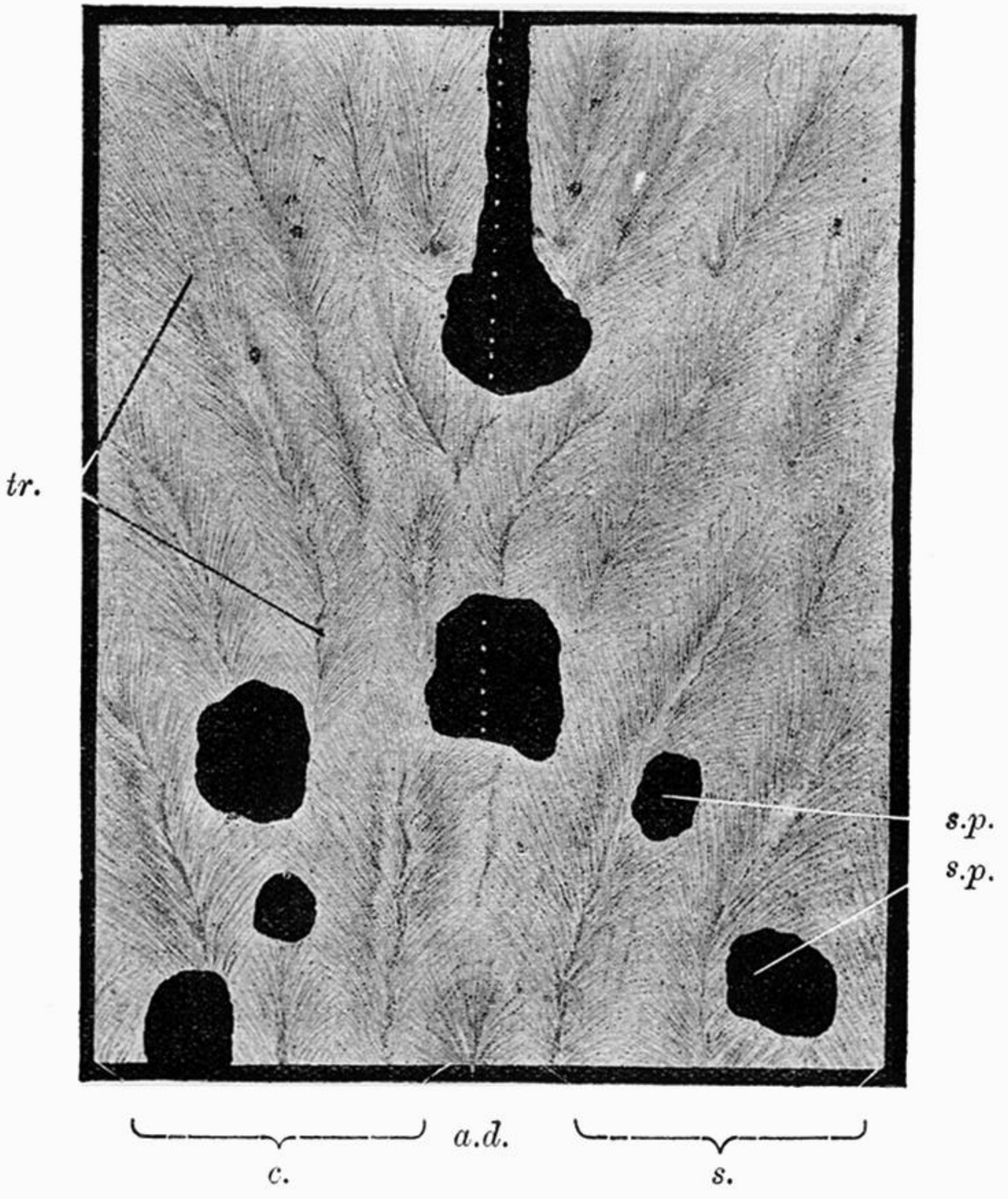
Transverse section *Eupsammia*; *s.*, septa united by the synapticular network; *s.p.*, septal pore near the periphery; *c.*, costa; *ic.p.*, intercostal pore; *c.c.*, centres of calcification.

Fig. 50.



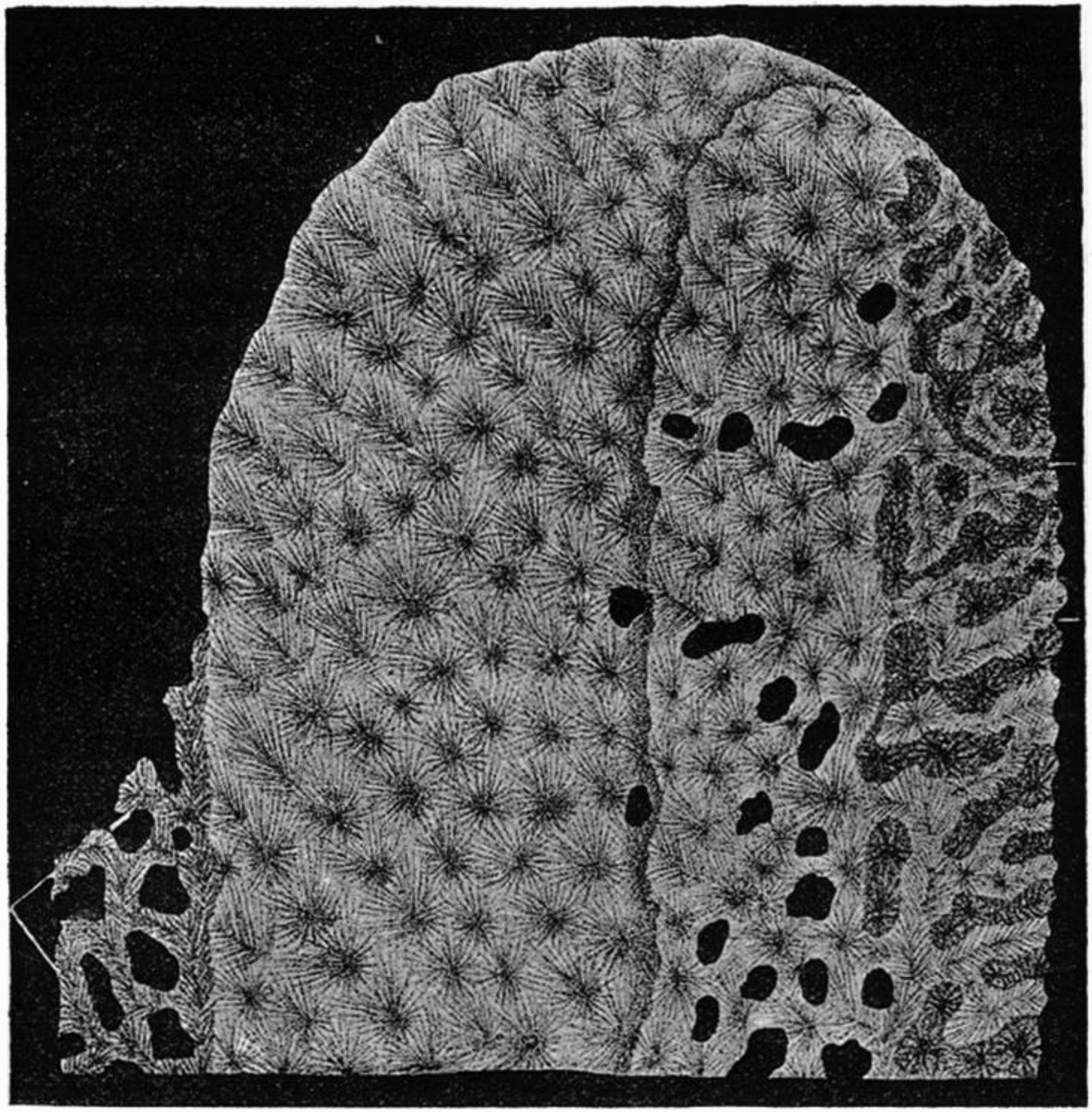
Enlarged drawing of septal surface (broken at left-hand side), showing the branching synapticulæ (*syn.*), and its part in the formation of rows of tubercles between the costal continuations of septa; *s.* septum; *c.* costa; *a.d.* area of divergence.

Fig. 51A.



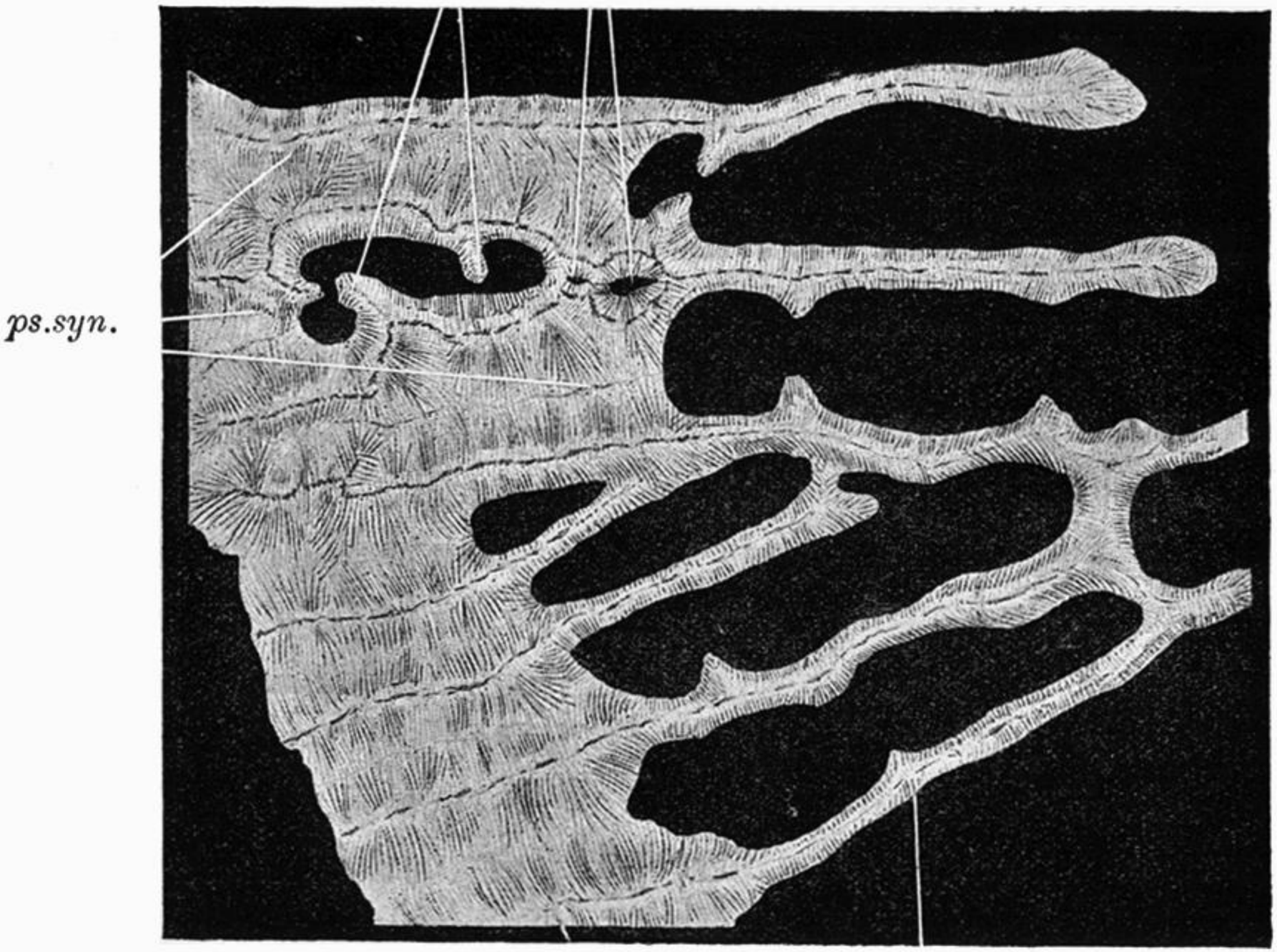
Eupsammia: section parallel with the septal plane, meeting trabeculæ only at part of their length, the tips of the trabeculæ bend outwards from the plane of section; *a.d.* area of divergence; *s.* septum; *c.* costa; *s.p.* septal pores—*two* of a curve of *four* pores indicating the limit of one growth-segment at this peripheral region.

Fig. 51B.



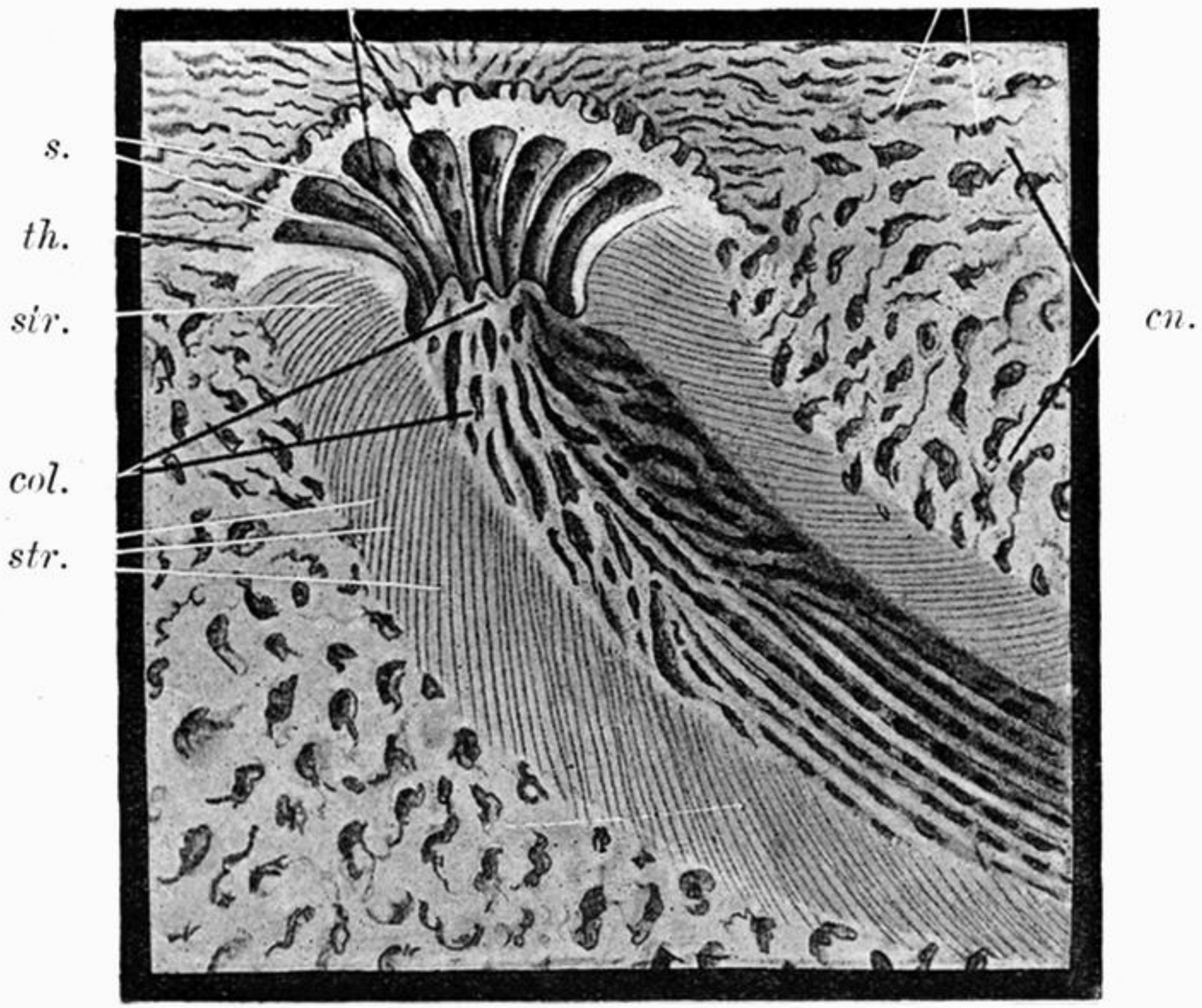
Section parallel with the septal plane, but cut nearer the surface than 51A—hence the outward-bent tips of trabeculæ are met almost rectangularly. *col.*, columella; *syn.*, synapticular network, seen as if projected against the darker-looking septum behind (*s.*).

Fig. 52.



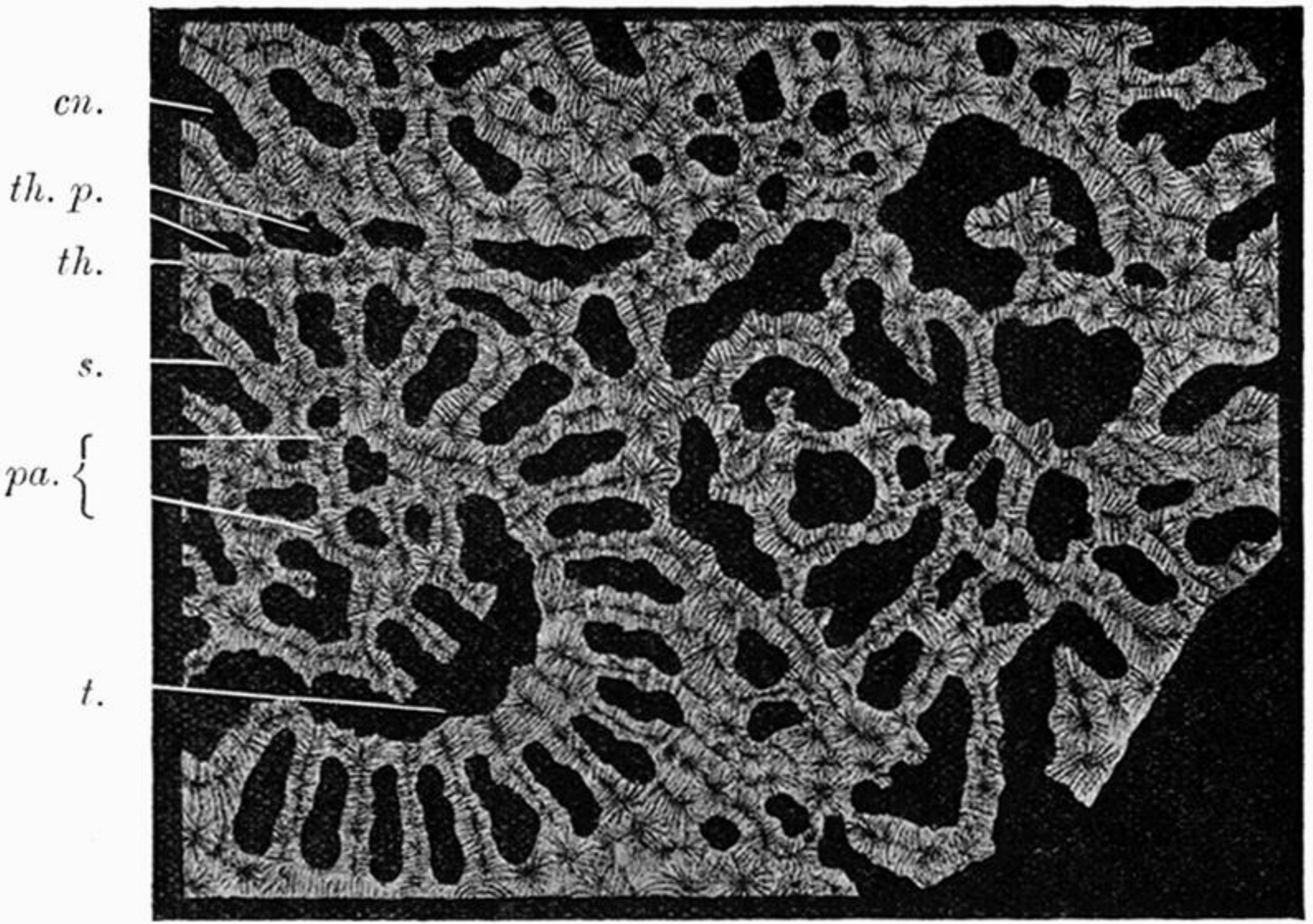
Transverse section *Eupsammia*, showing secondary thickening filling up the interseptal loculi. *s.*, septum; *syn.*, synapticula; *ps.syn.*, pseudosynapticula; *sp.*, interseptal space.

Fig. 53.



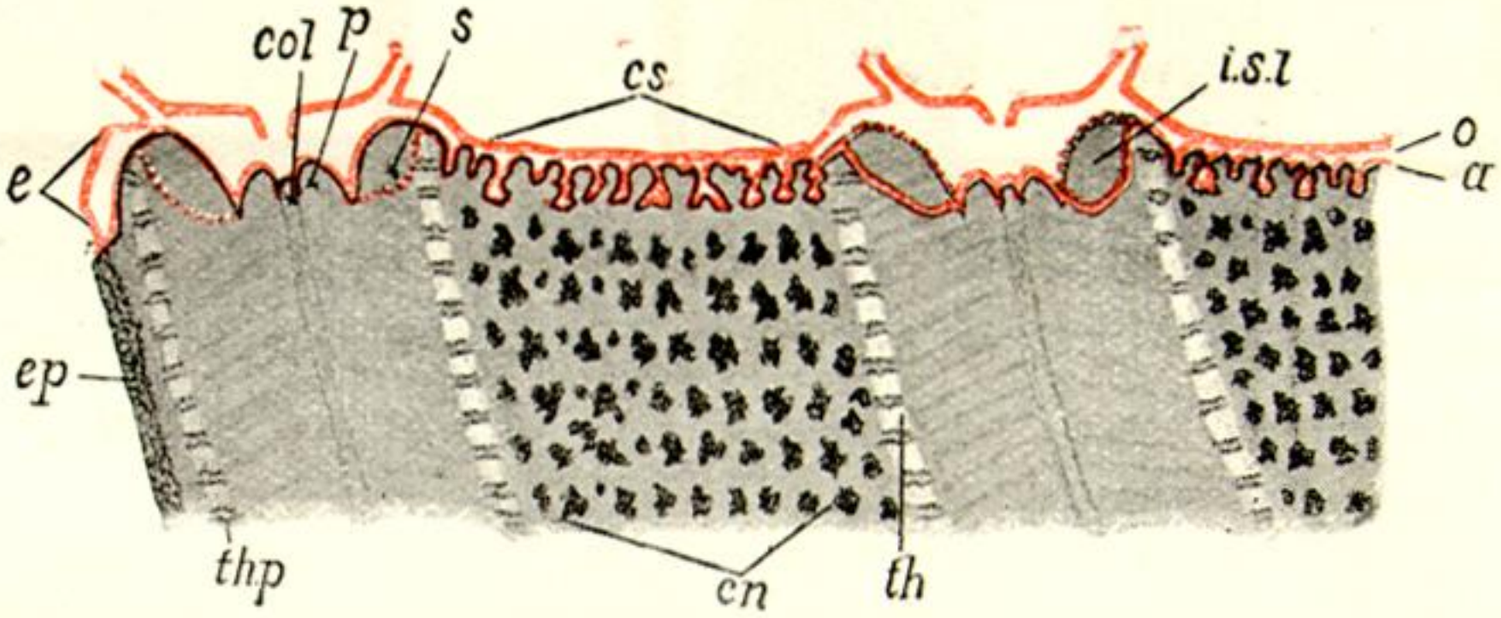
Enlarged drawing of *Turbinaria mesenterina*, LAM.; *col.*, columellar pali; *th. p.*, thecal pores; *cn. p.*, cœnenchymal pores; *s.*, septa; *str.* striæ (septal trabeculæ).

Fig. 54.



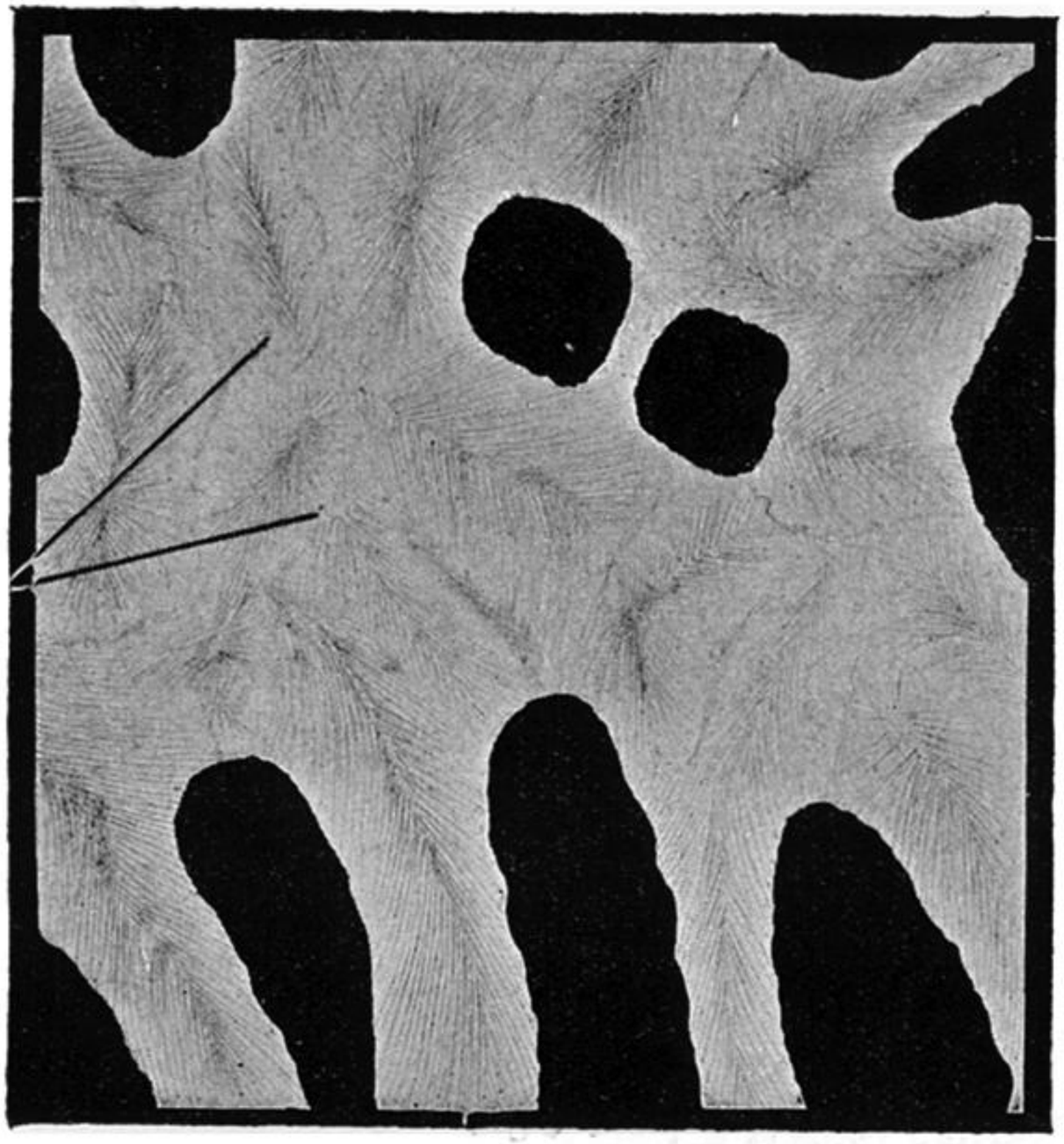
Turbinaria: transverse section showing the microscopic structure of septa (*s.*), their prolongations as pali (*pa.*) surrounding the columella, the theca (*th*), thecal pores (*th. p.*), and cœnenchymal interspaces (*cn.*), radial in direction; *t.*, an accidental tear in the section.

Fig. 56.



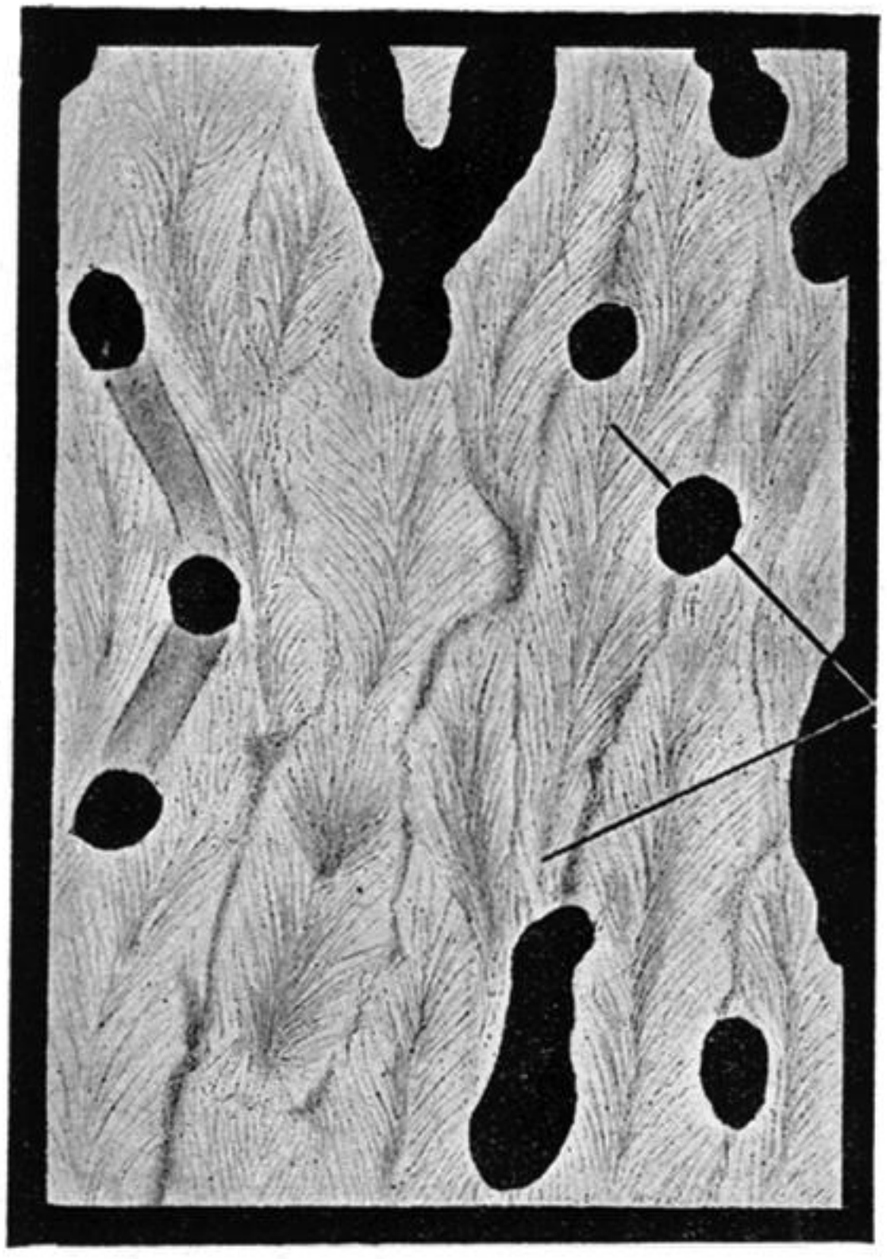
TURBINARIA.--Cœnenchymatous type; letters as in fig. 2, p. 107; a columella (*col.*), and pali (*p.*), are present; *th.p.* thecal pores, which open into those (black in the figure) of the cœnenchyme (*cn.*) (*cf.* p. 203). This diagram is given for comparison with the similarly-treated figs. 2, 22, 35, and 36.

Fig. 57A.



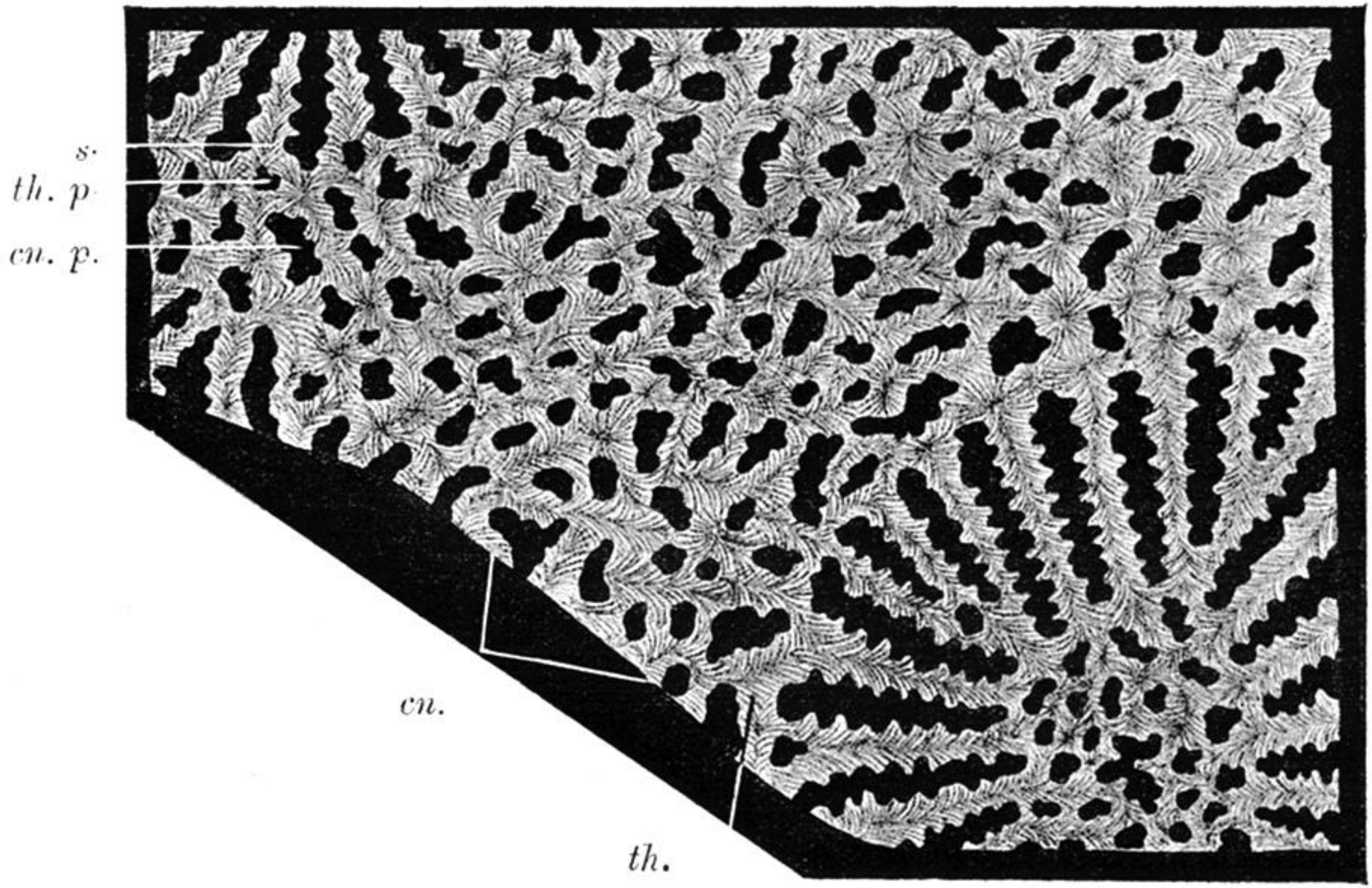
Transverse section through cœnenchyme between two adjacent calyces of *Turbinaria*. Median "darker line" (calcification centres) seen in the septa (*s.*) and also in the several trabeculæ of the cœnenchyme (*cn.*).

Fig. 57B.



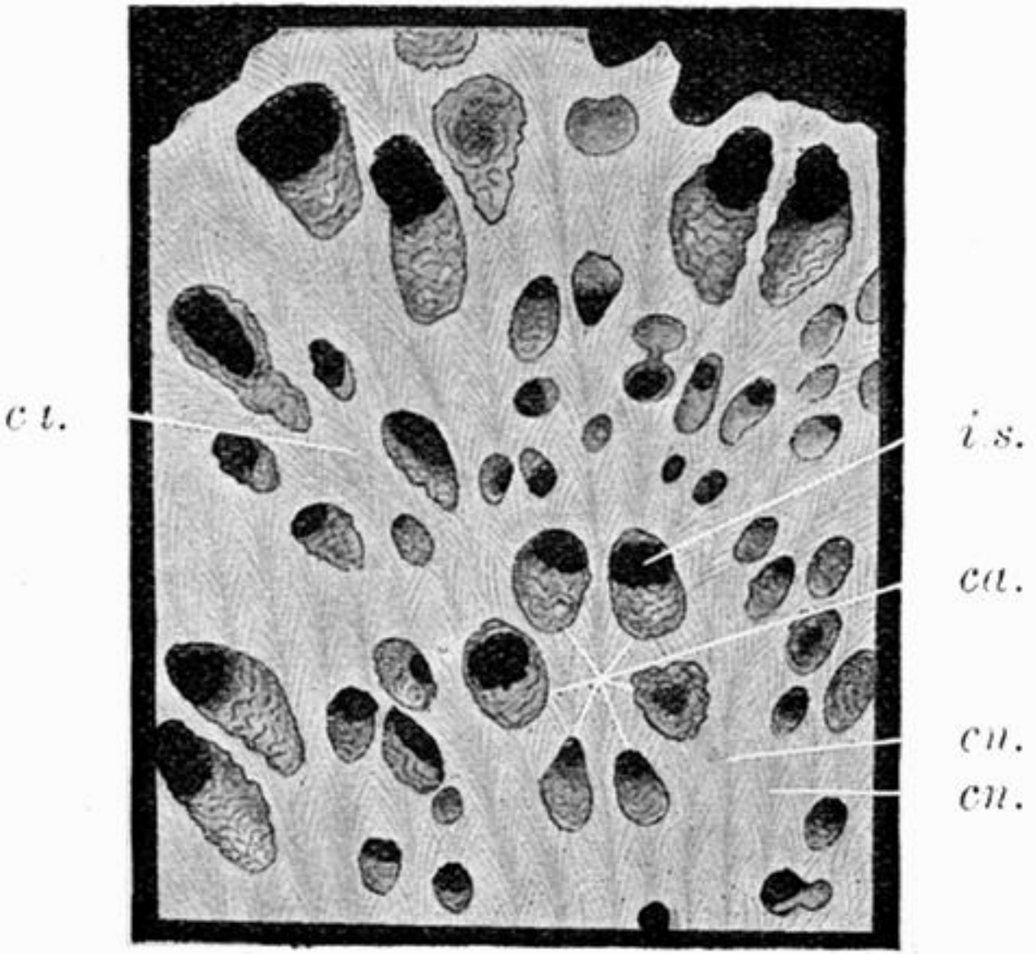
Section longitudinally cut through cœnenchyme, showing the varying direction of trabeculæ (*tr.*) and the occurrence of pores.

Fig. 58.



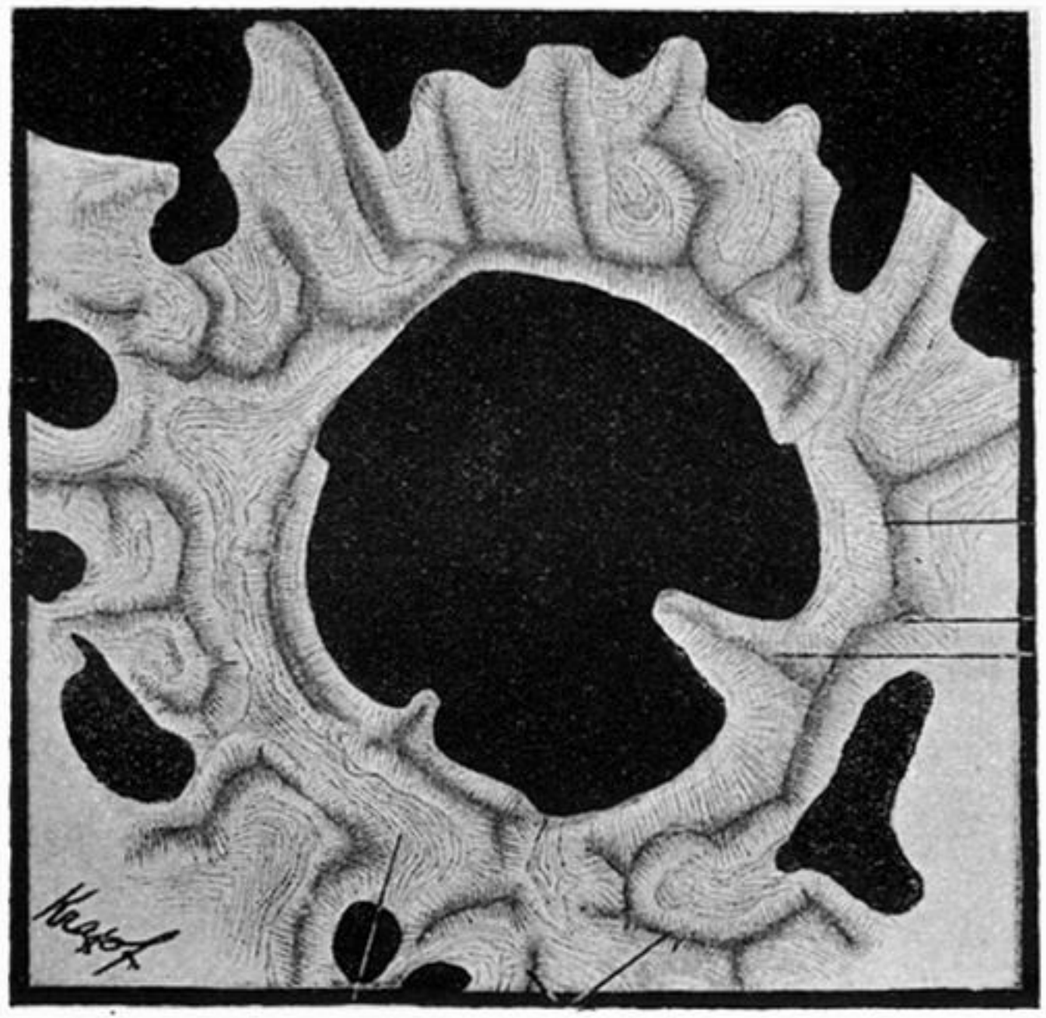
Transverse section Actinacis; *s*, septa; *th. p.*, thecal pore, where a septum splits into two, to form mural bars; *cn. p.*, cœnenchymal pore in a line with the thecal pore.

Fig. 59.



Longitudinal section passing obliquely through a branch of *Madrepora*; *ca.*, the six-septate calyces distorted by section; *i.s.*, an interseptal loculus; *cn.*, cœnenchymal trabeculæ.

Fig. 60.



Transverse section (partly injured inside the calyx). The fibro-crystals close to the centres of calcification are met obliquely by the section.

Those of the secondary deposit (*sec.*) are met almost perpendicularly.

Fig. 61.

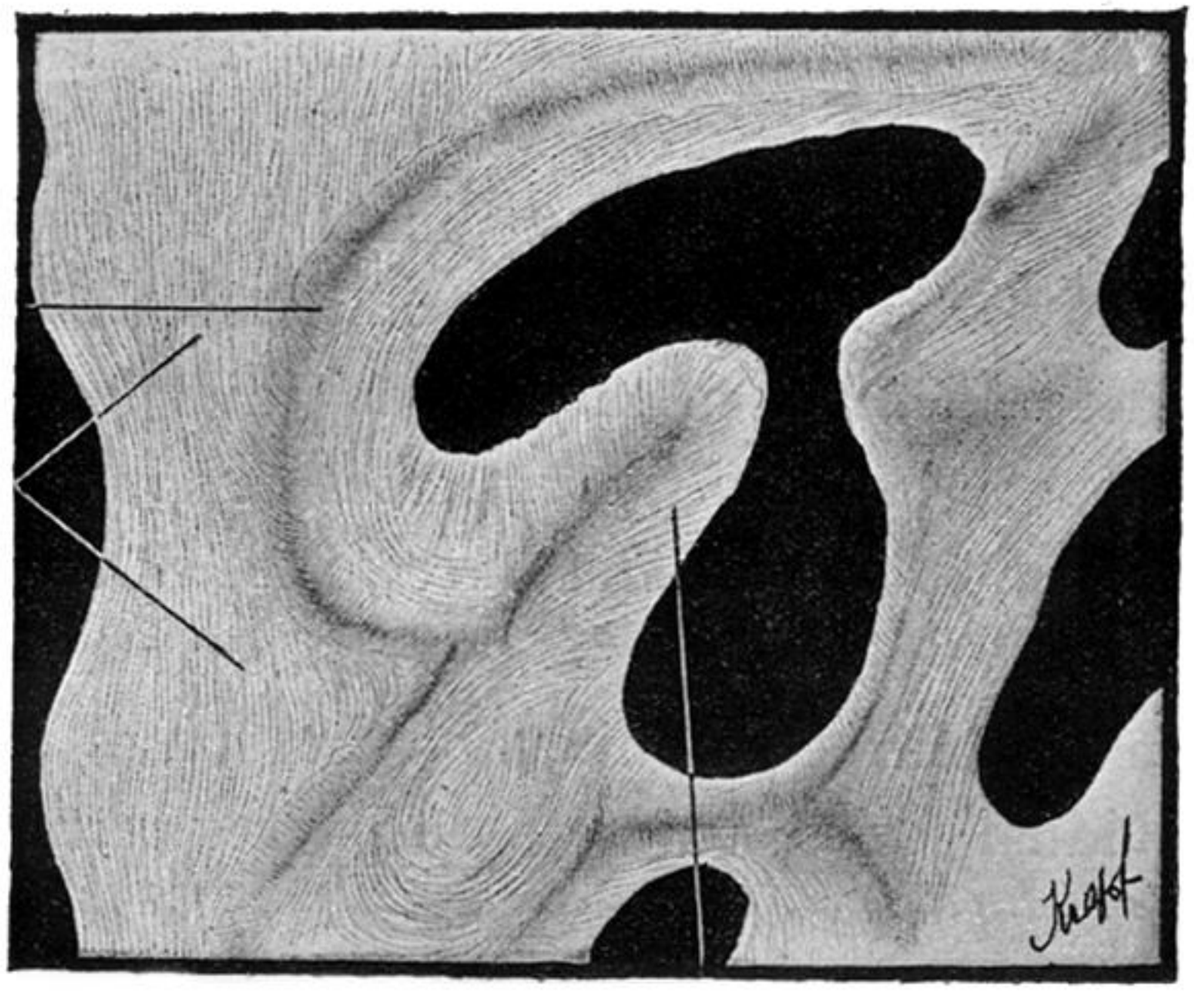
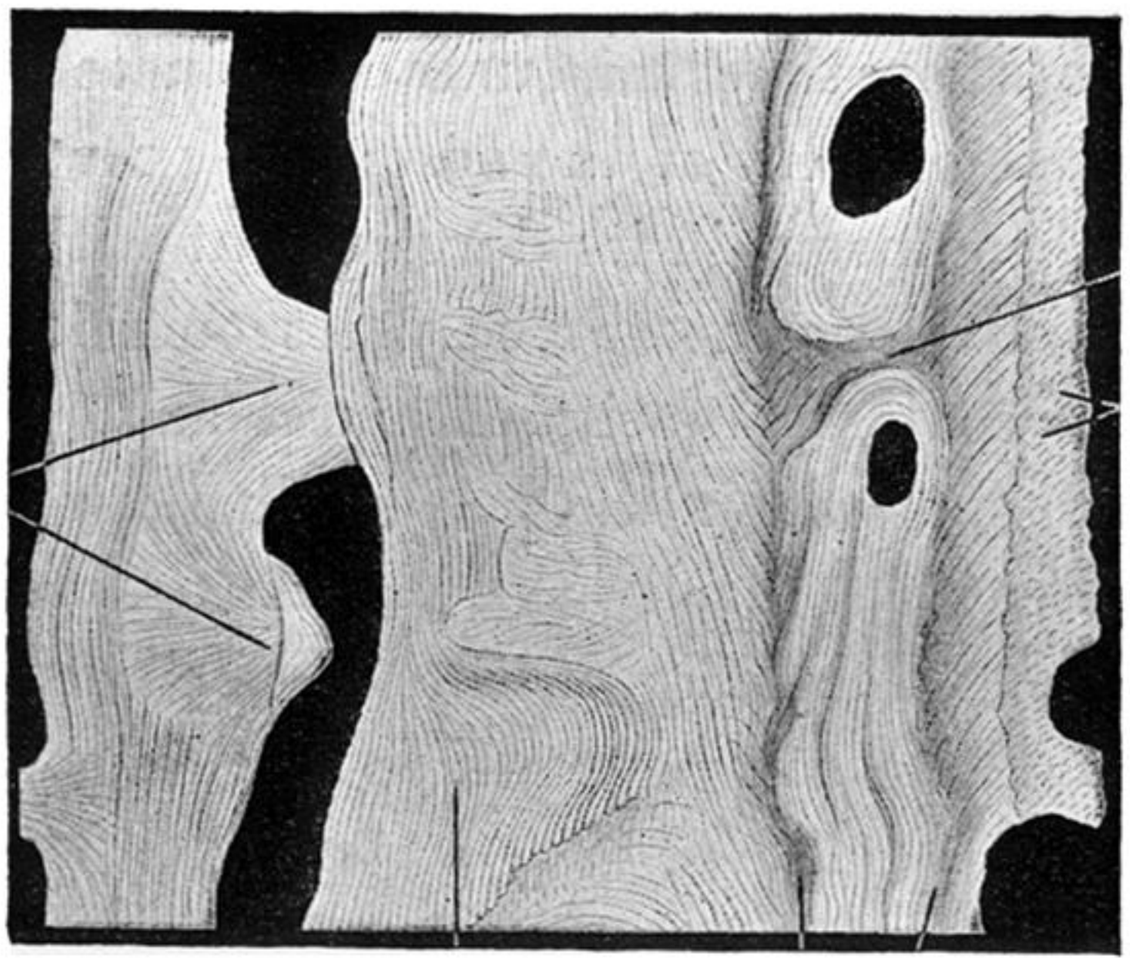
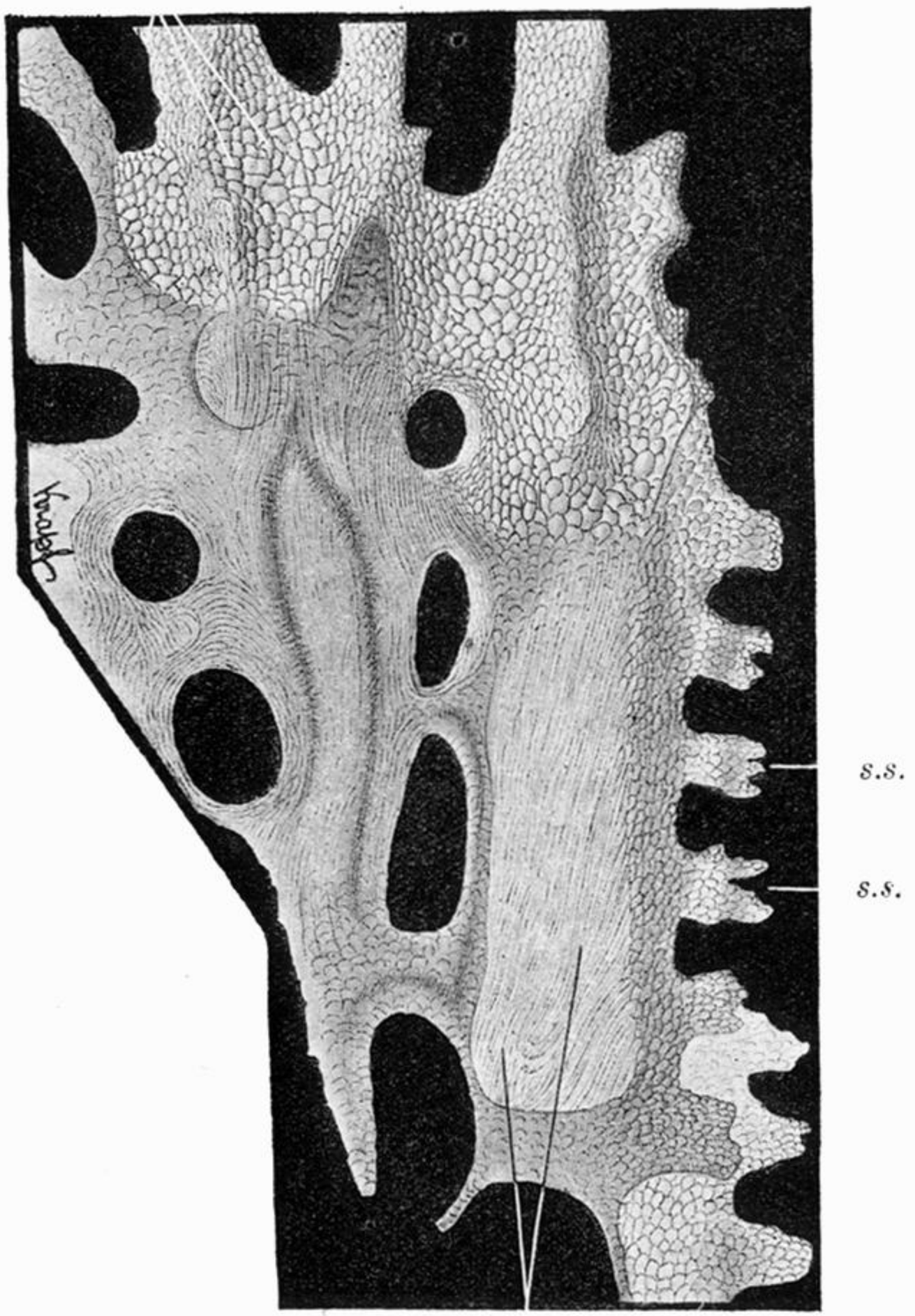


Fig. 62.



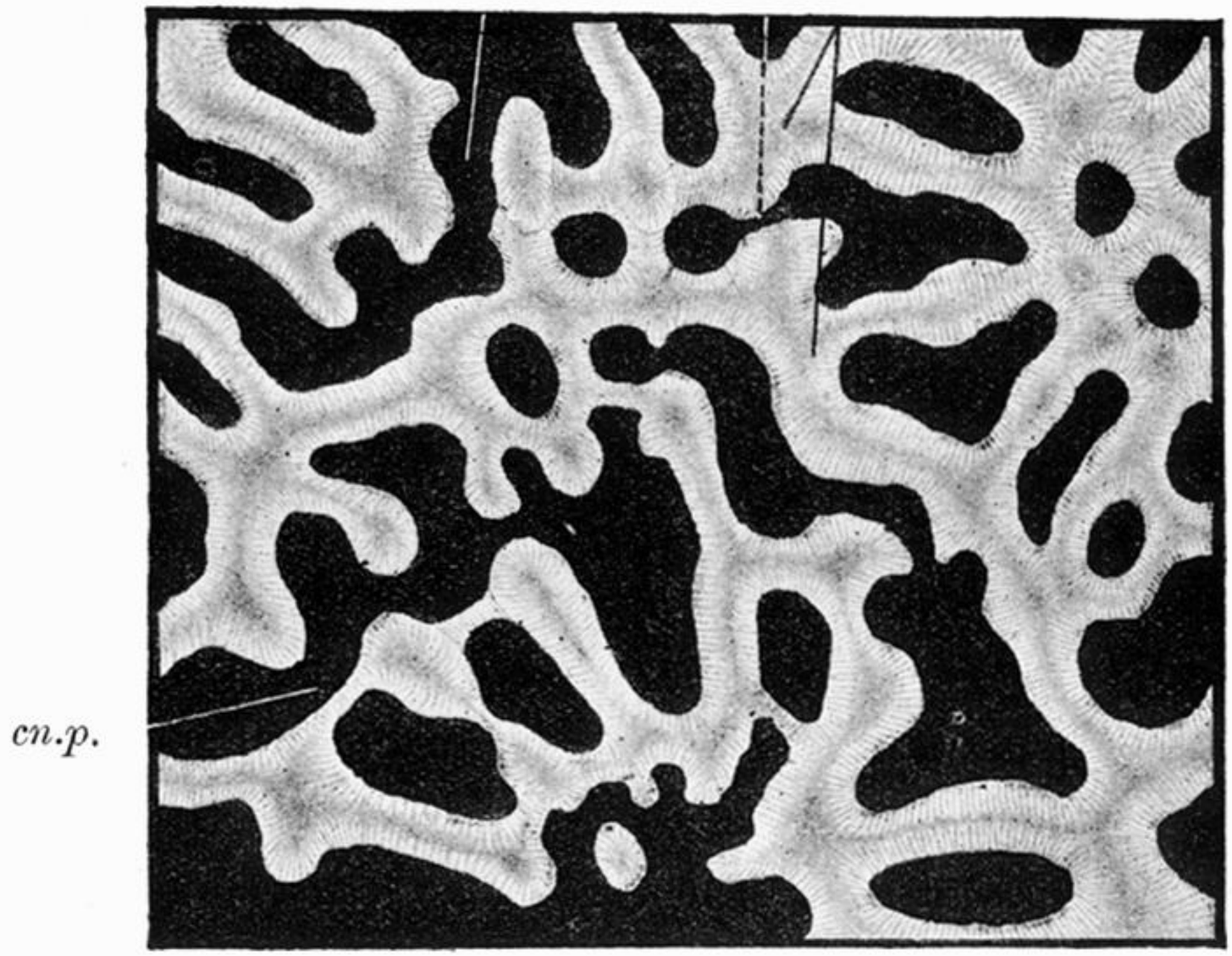
Longitudinal sections—fig. 61 obliquely cut, fig. 62 vertically cut: *m.s.*, main septum of calyx; *th.*, thecal centres of calcification; *sec.*, secondary deposit; *f.c.*, fibro-crystals of secondary deposit met across their axes; *c.c.*, centres of calcification in costæ; *syn.*, synapticulæ.

Fig. 63.



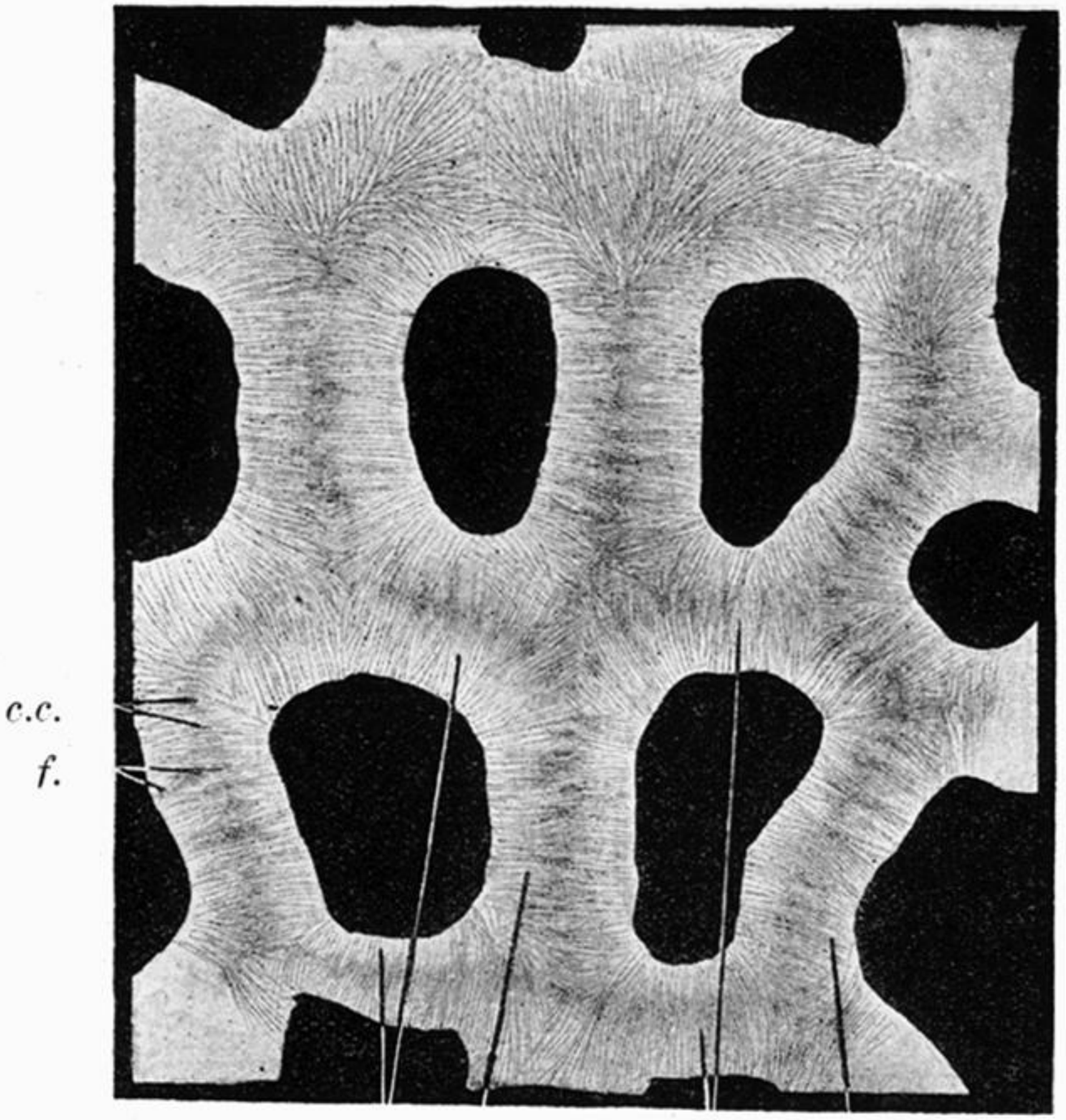
Longitudinal section of *Madrepora* (partly decalcified); *c.s.*, calicoblast scales in decalcified portion; *c.f.*, calcareous fibres; *s.s.*, septal spines covered by the constituent scales of the growth-lamellæ.

Fig. 65.



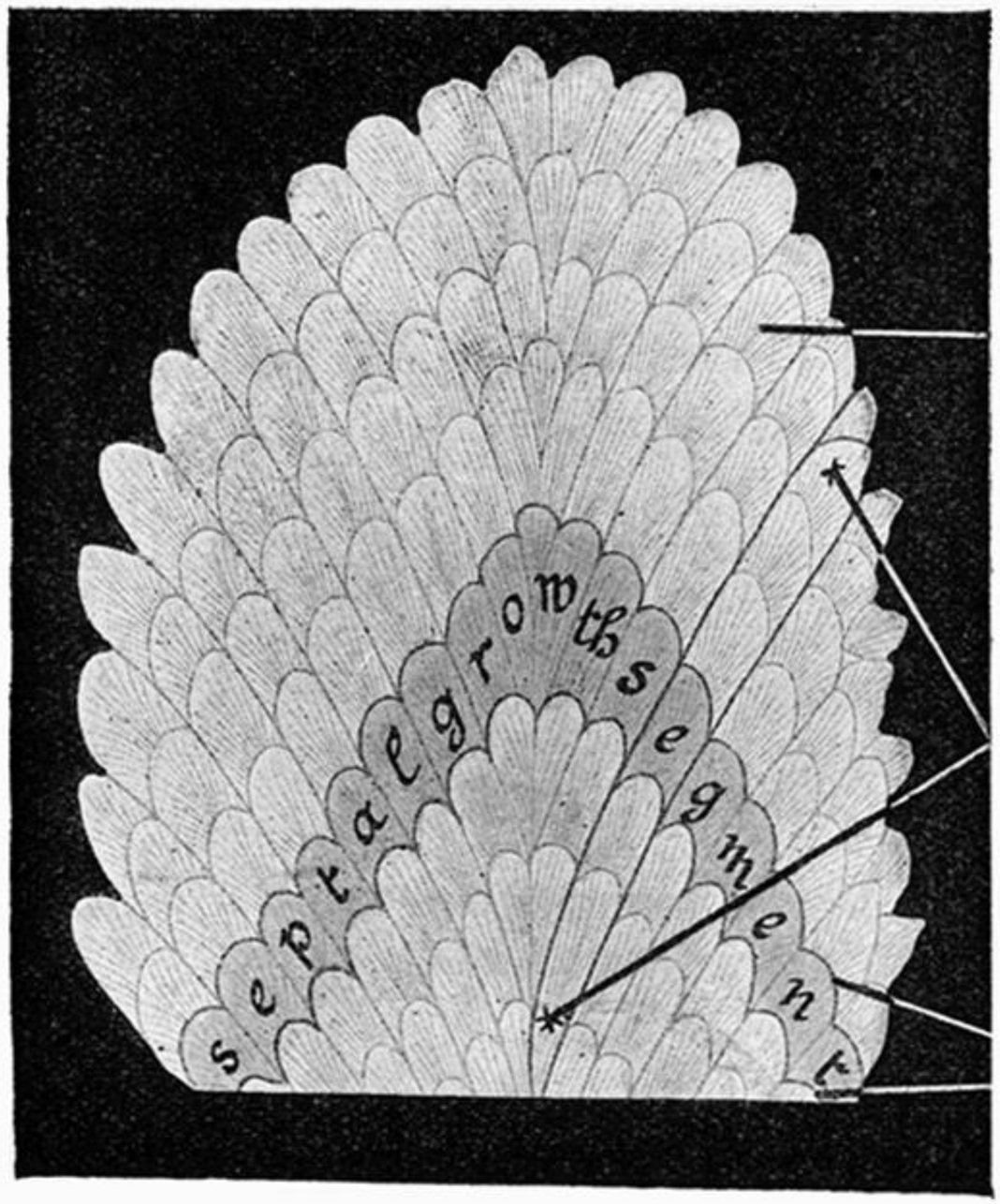
Transverse section Porites incrustans. *th.*, theca; *th.p.*, thecal pore; *cn.p.*, cœnenchymal pore. Pali are seen in front of septa, or in various stages of fusion.

Fig. 66.



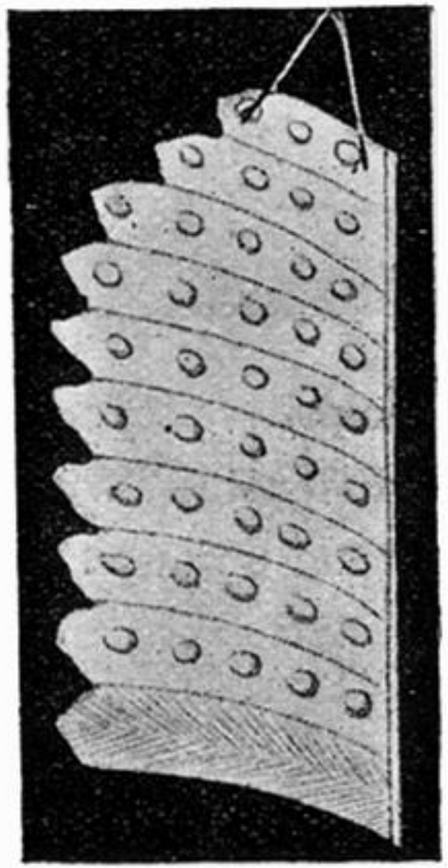
Longitudinal section, showing the precise similarity of structure in septa (*s.*), and synapticulæ (*syn.*). In both, the fascicles (*f.*) bush out circularly around the calcification centres (*c.c.*).

Fig. 67.



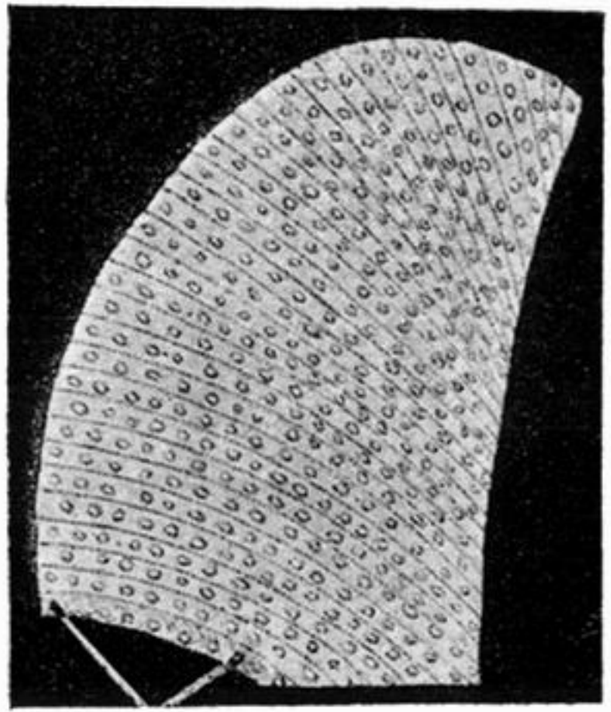
Radial structure (equiv. whole *septum* of primitive types) marked out in types with exsert septa, *e.g.*, Astræids, into so-called "septal" and "costal" wings to left and right of the *area of divergence*, at which the trabeculæ take their origin and diverge. The trabecula (*tr.*) signified in the figure, is composed of seven *trabecular parts* (*tr.p.*), and represents, therefore, seven successive gowth-periods. The trabecular parts between two *growth-curves* (*g.c.*) form a *septal growth-segment*, and represent *one growth-period.*

Fig. 68A.



Diagrammatic drawing of a compact septum composed of monaxial septal segments.
Tr. = trabecula from wall to centre of calyx. The lowest trabecula is shown in section; those above are drawn with their surface granulæ.

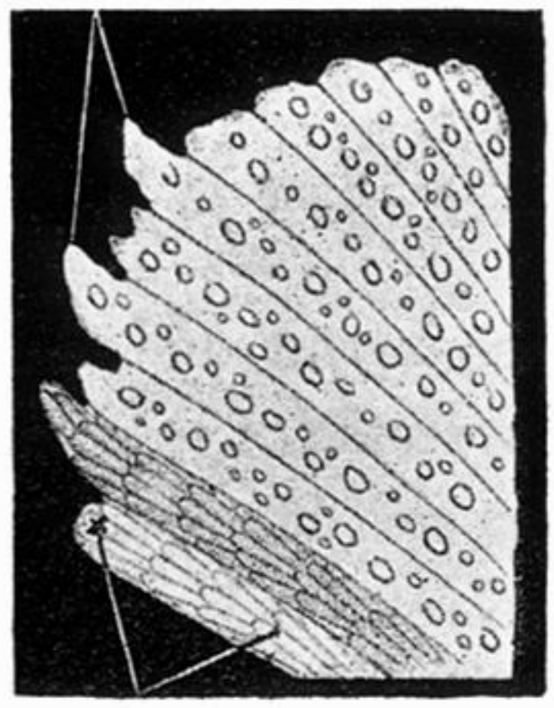
Fig. 68B.



tr.

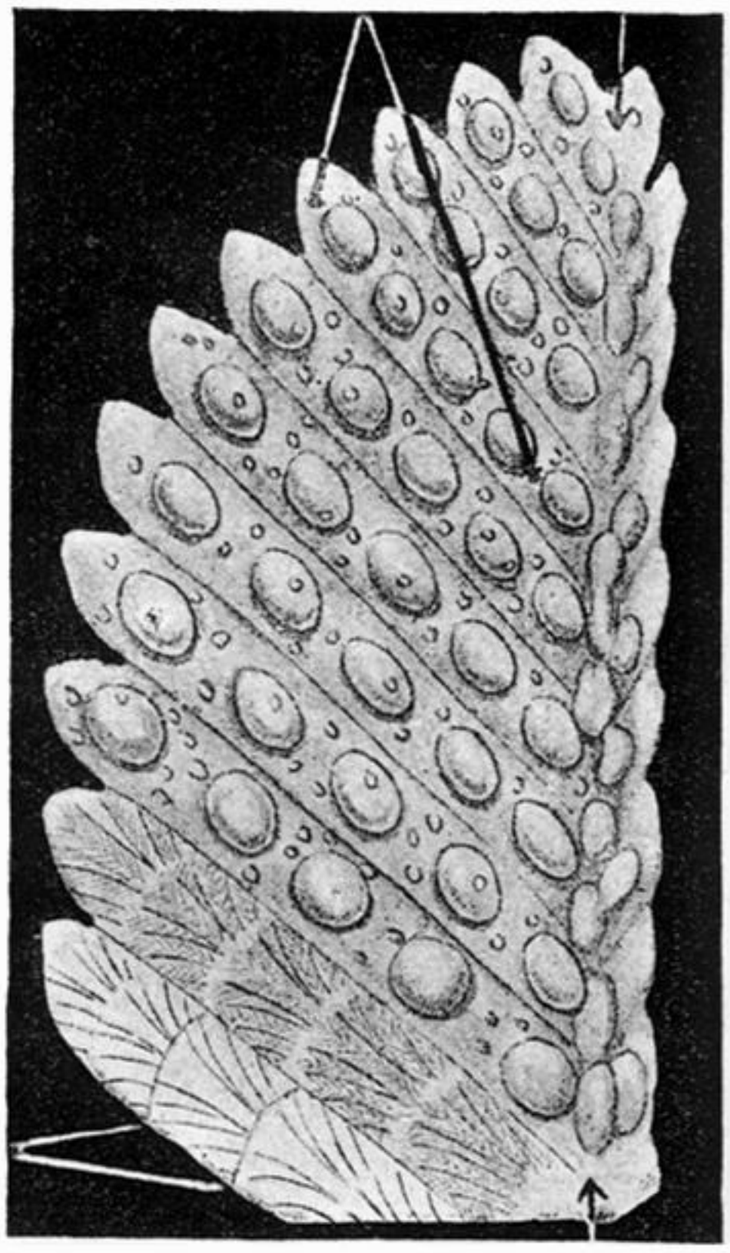
Type of septum in a Turbinolid coral; the striæ on the surface correspond to "simple" trabeculæ, whose elliptical axes give rise to a "median dark line" in transverse sections.

Fig. 68c.



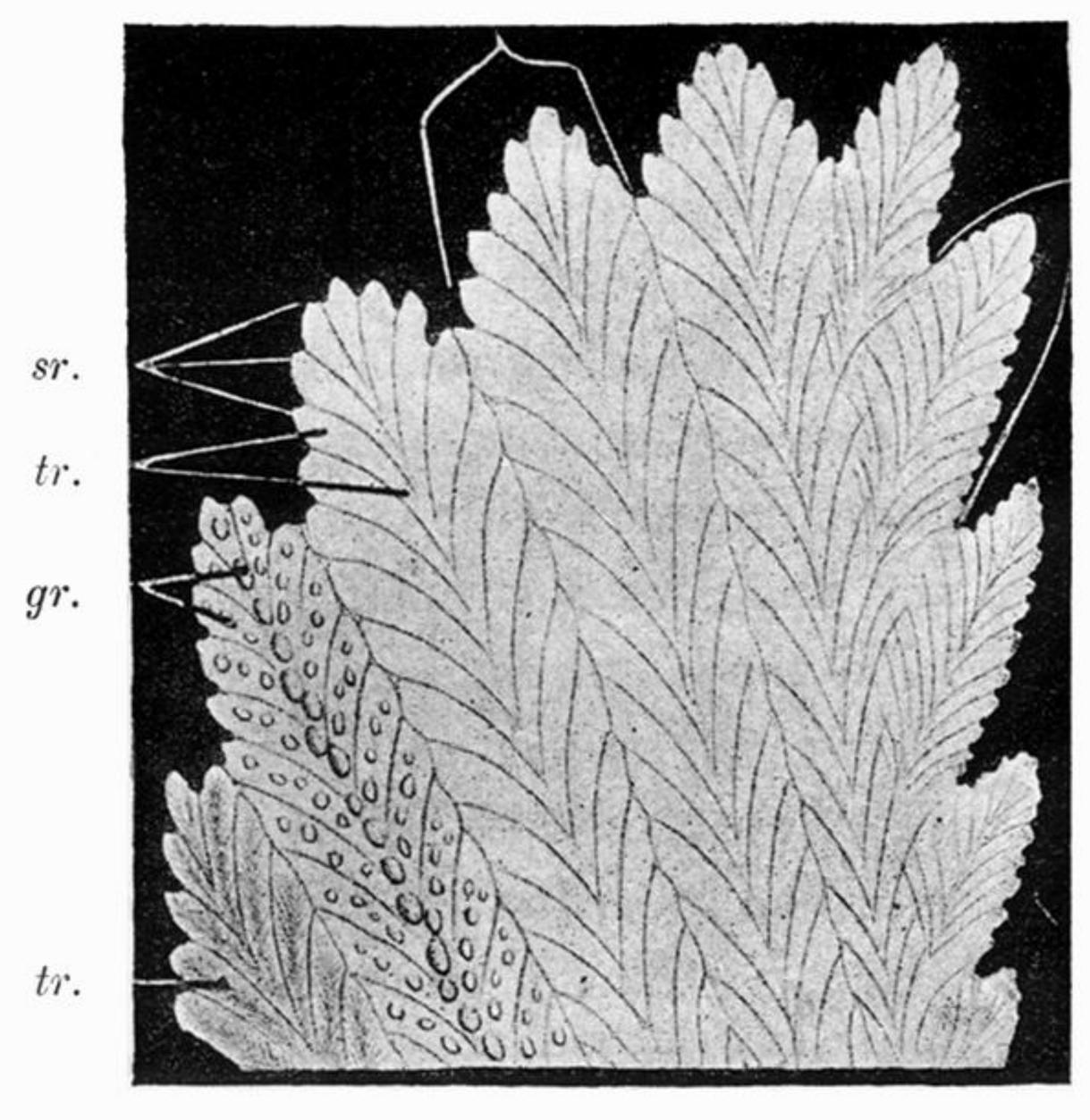
Septum with fine granulations. The trabecula (*tr.*) shows four successive fan-groups of fascicles = four "trabecular parts." Any trabecula may be elongated as a palus (*pa.*), or to form part of a "spongiose" columella. (The two lowest trabeculæ are drawn in section to elucidate the microscopic structure.)

Fig. 68d.



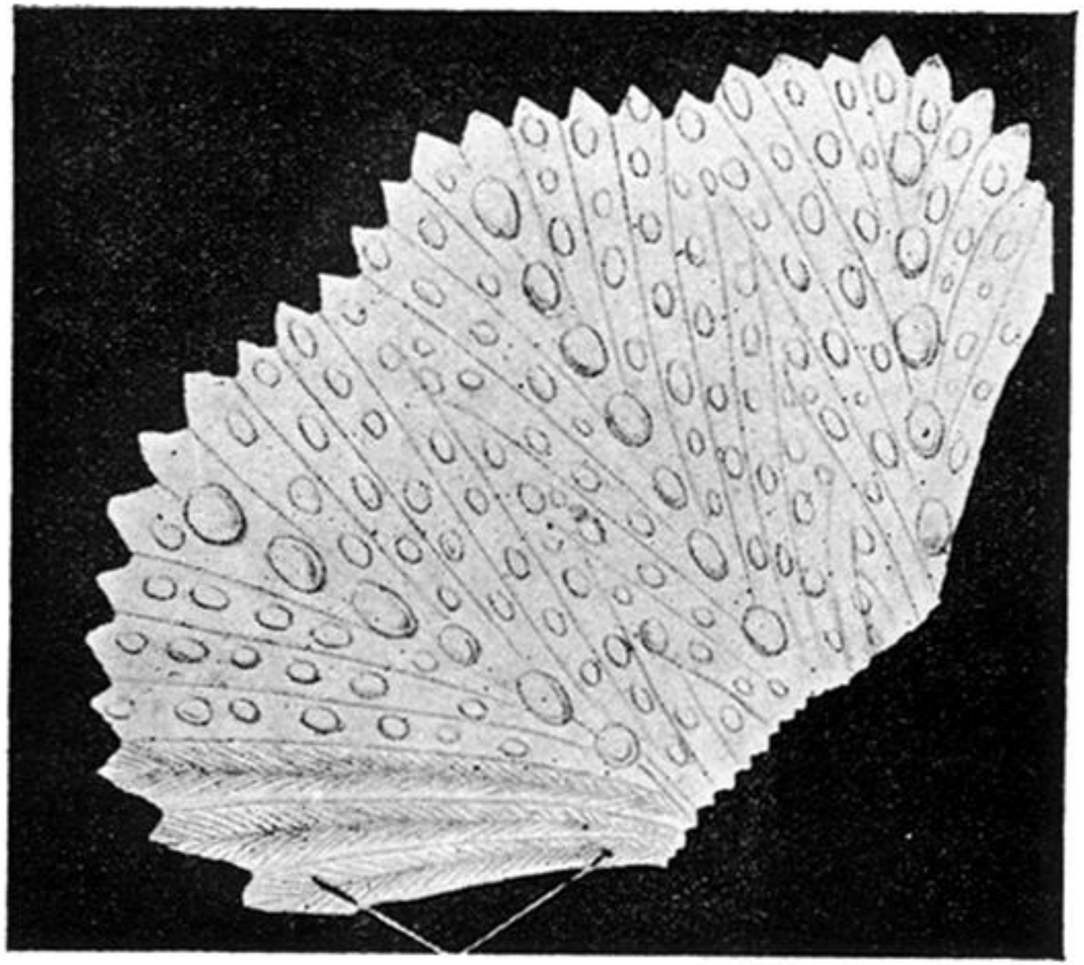
Septum with regularly placed, large granulations marking successive "trabecular parts" (*tr. p.*) on the septal ridges. At the "area of divergence" (*a. d.*) the granulations coalesce and help to form the pseudotheca between septum and costa.

Fig. 68e.



Septum with broad ridges studded with granulations (*gr.*); *s. r.*, septal ridge; *c. r.*, costal ridge; *s.r.*, serræ at the tips of the trabeculæ (*tr.*).

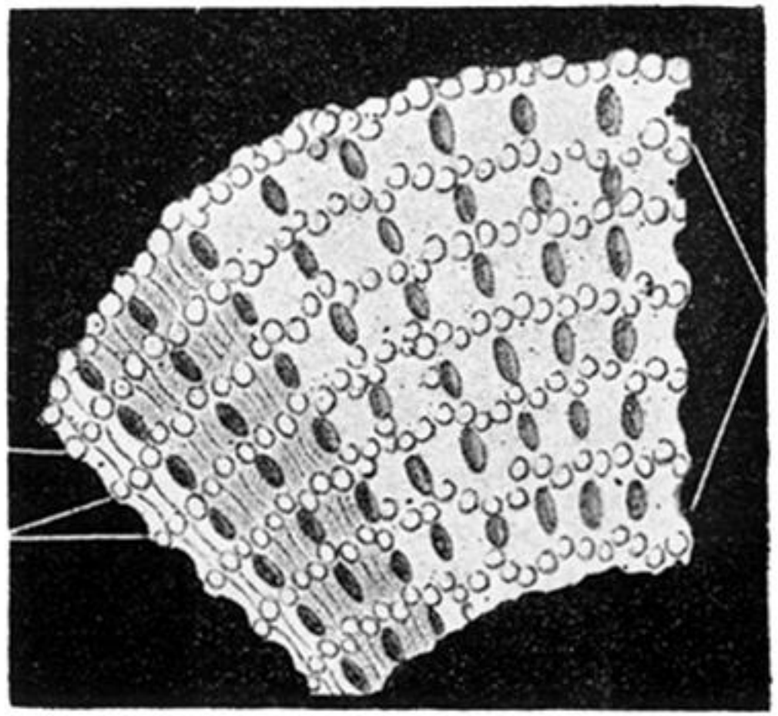
Fig. 68F.



tr.

Septum compact, composed of three main "fans" of trabeculæ (*tr.*) shown in section at the lower part of figure. Synapticulate granulations mark trabecular growth-parts.

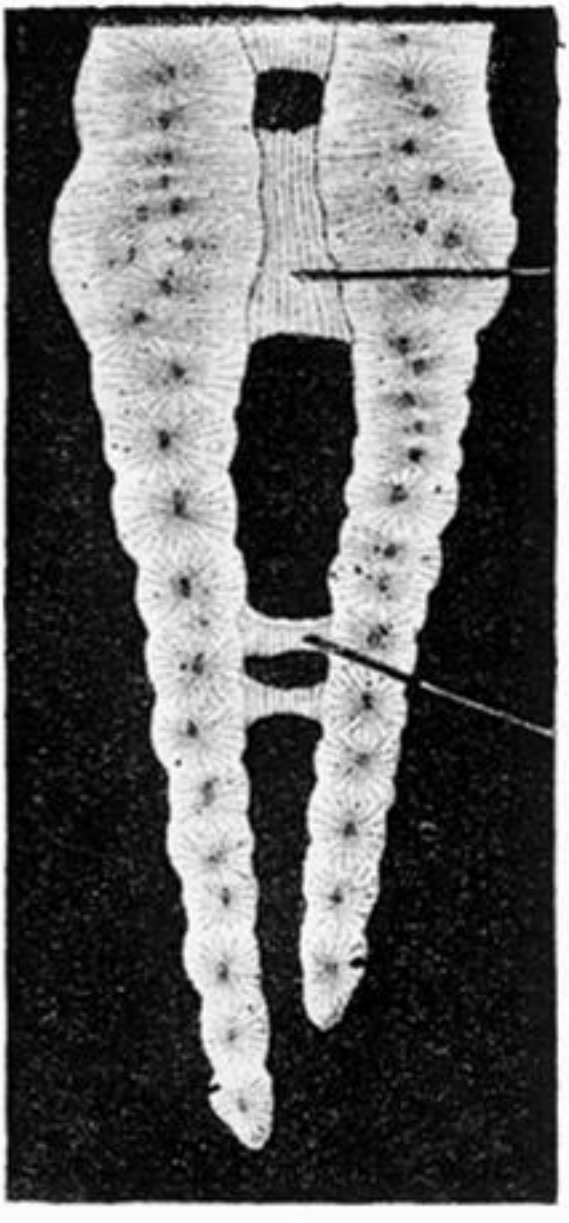
Fig. 69.



Septum porous; adapted from a drawing by PRATZ ('Palæontographica,' *loc. cit.*, Taf. 14); *tr.* trabecula; *tr. p.*, a trabecular growth-part; *gr.*, synapticulate granulations coalescing in parallel lines between the pores.

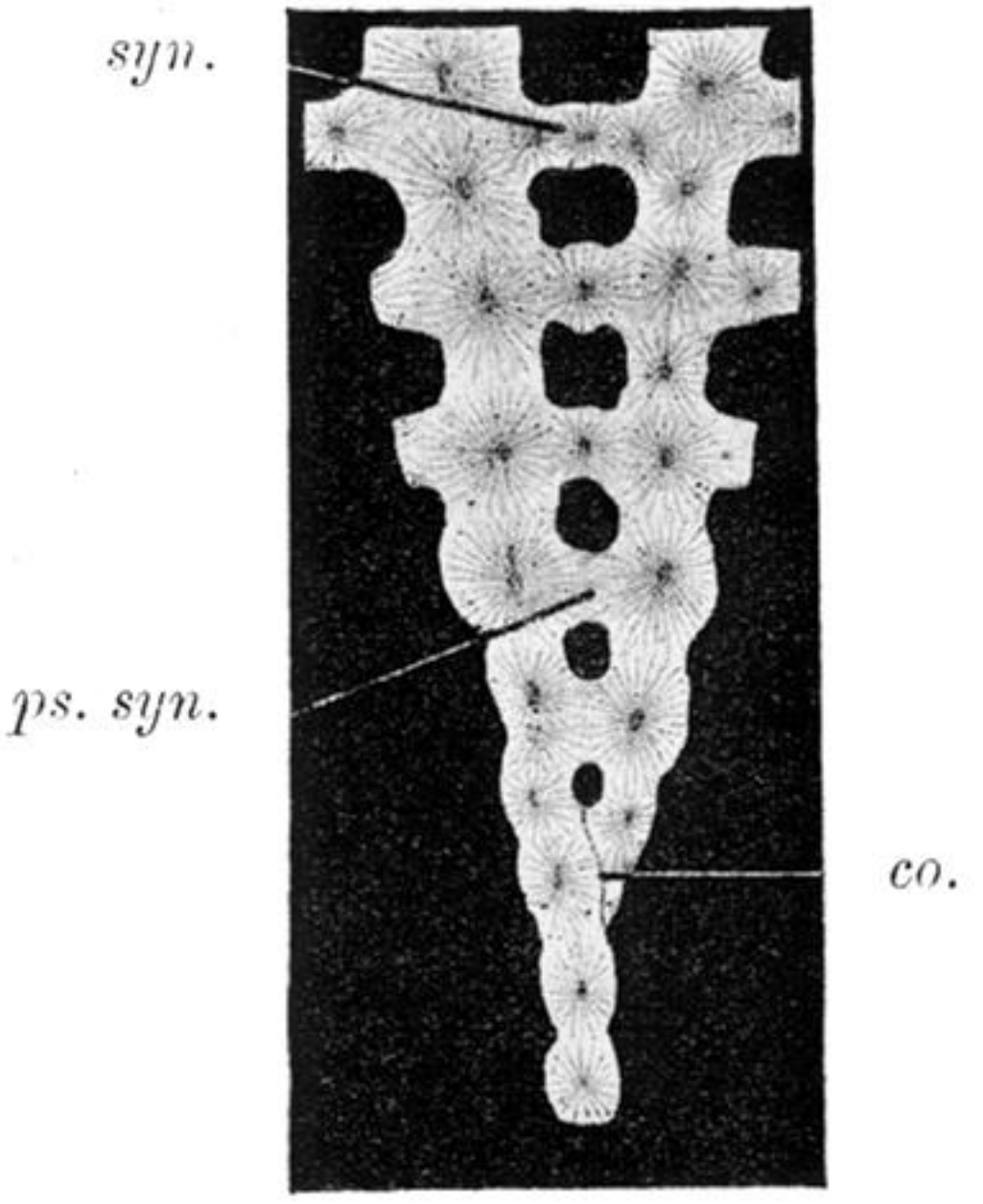
Types of Fungid Septa.

Fig. 70.



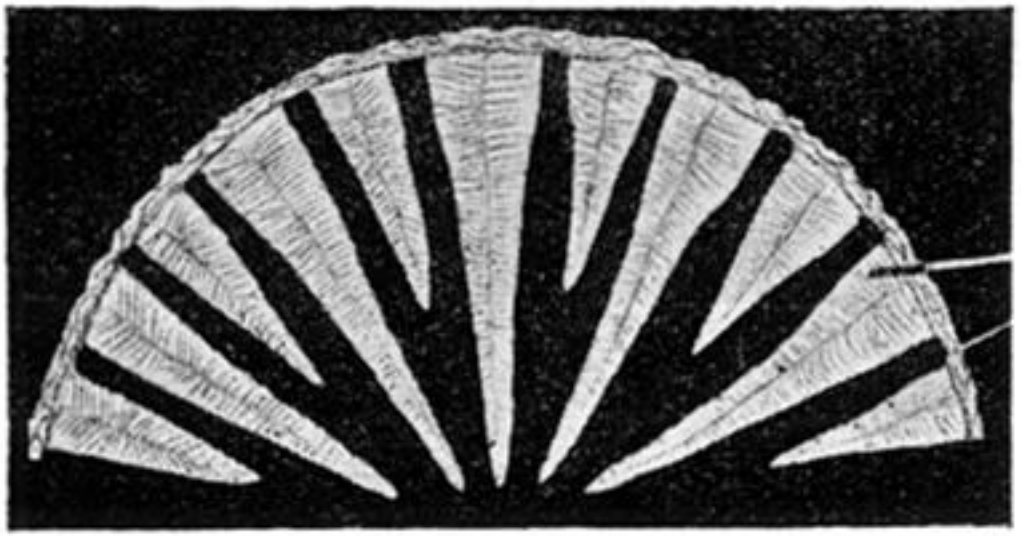
Dissepiments belonging to different "floors" between two septa, and met obliquely in a transverse section.

Fig. 71.



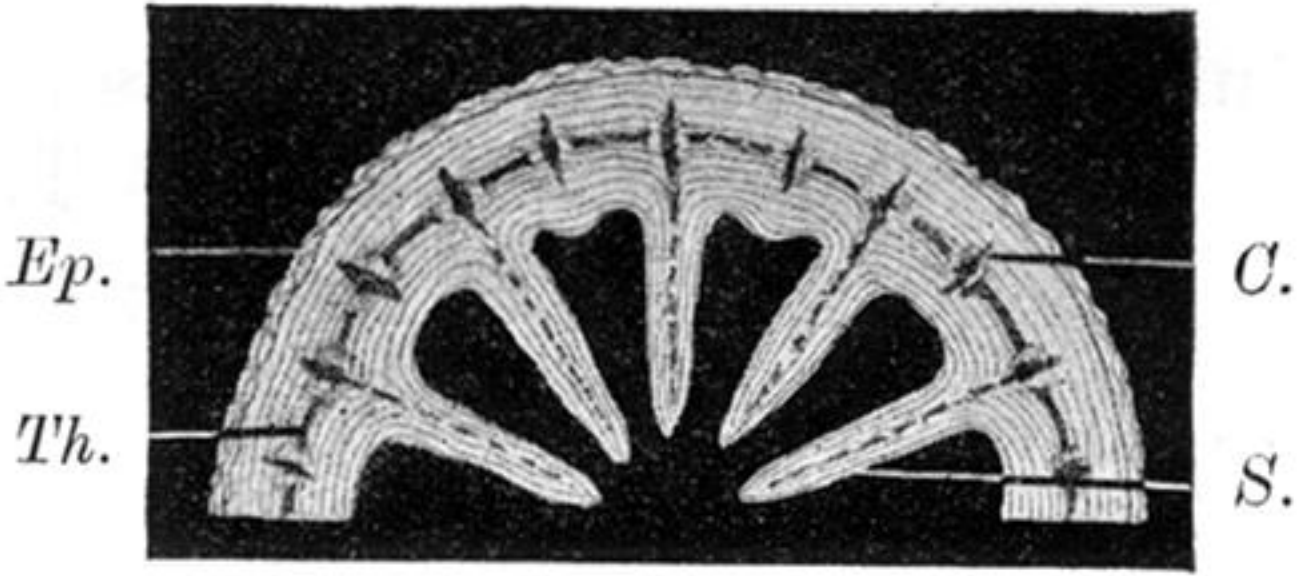
True synapticulæ, "*syn.*," pseudosynapticulæ, "*ps. syn.*," and synapticular coalescence of septa, "*co.*," seen in transverse section (p. 240 and *cf.* p. 176).

Fig. 72.



Transverse section showing the relation of Epitheca to Septa, where neither Theca nor Pseudotheca is present. The interseptal loculi are filled by basal supports, omitted for clearness in the figure (tabulæ, dissepiments, or synapticulæ), which coalesce directly with the epitheca at their external edges.

Fig. 73.



Transverse section showing the structural relation of "S." = Septa, "C." = Costa, "Th." = Theca, and "Ep." = Epitheca in a typical Turbinolid.

Fig. 74A.

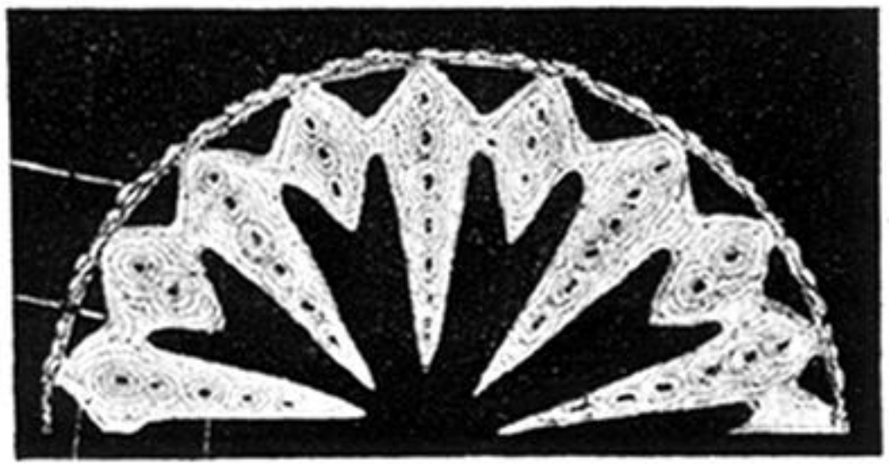
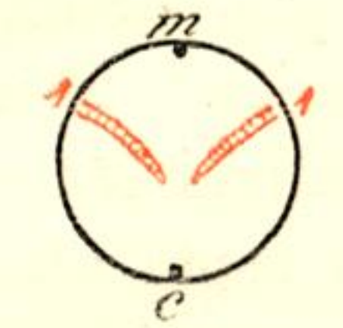


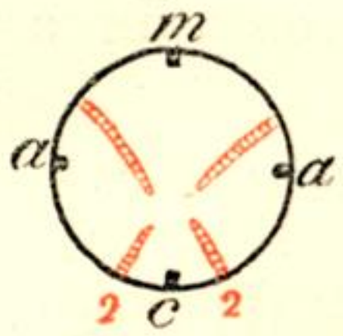
Fig. 74B.

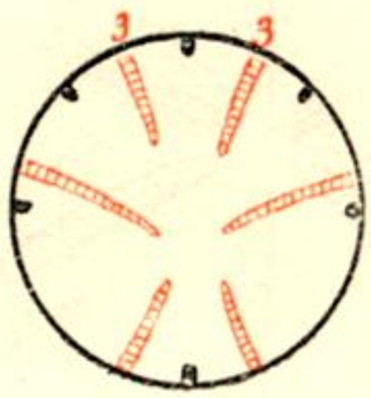
Transverse sections showing the structural relations between "*s.*" = septum, "*c.*" = costa, "*ps.th*" = pseudotheca, and "*ep.*" = epitheca. The pseudotheca is shown rather nearer the centre of the calyx in fig. 74B than in fig. 74A; all grades occur between a position of the pseudotheca very near the centre and very remote from it, until it may be almost coalescent with the epitheca; the costa is respectively longer or shorter.

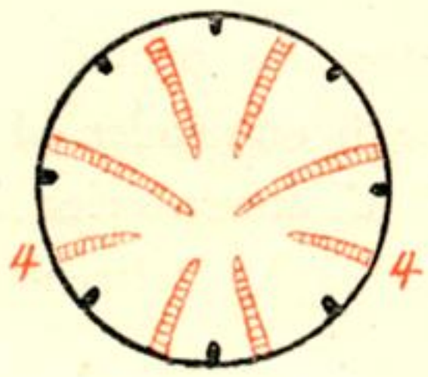
Radial structures (septa, costæ, pali).							
Centres of Calcification, with especial reference to the arrangement of the microscopic calcareous fibres and the appearance of a so-called "dark line."	Compactness or porosity.		Direction of the trabeculæ or trabecular ridges in the radial structure.	FAMILIES.	Relation of the *radial structures* (septa and costæ) to the wall.	*Interradial and axio-polypal basal supports*:—(Tabulæ, dissepiments, synapticulæ, pseudo-synapticulæ, lateral septal coalescence, terminal septal coalescence, columella.	*Wall.* (1) Compact or porous. (2) The "centres of calcification," their relation to septal "centres."
	Successive growth-parts in individual trabeculæ.	Contemporaneously-formed growth-parts of adjacent trabeculæ (the septal segment).					
Several centres of calcification are gathered in groups corresponding to the individual trabecular ridges. Each group is clearly distinguishable in transverse section from neighbouring groups, and as the trabeculæ meet the septal edge at a high angle, no appearance of a continuous "dark line" in the median plane of the septum is presented. The calcareous fibres pass upwards and outwards from the axes of the trabeculæ to the surface of the septum. Fascicles of longer fibres emerge as septal granulations.	The individual trabeculæ consist of a continuous, *compact*, vertical series of trabecular growth-parts.	A *compact* tier of trabecular growth-parts is formed at the edge of the radial structures during each successive growth-period.	The trabeculæ or ridges diverge obliquely upwards, in *regular* fan-like form, to right and left, from one or more areas of divergence in the radial structure.	FUNGIDÆ: ASTRÆIDÆ.	*The radial structures pass through the pseudotheca* and the interradial loculi correspond in the adjacent polyps of colony-building forms. All costæ are represented by septa within the calyx.	*Dissepiments.* Rare occurrence of pseudo-synapticulæ. Terminal septal coalescence produces very often a pseudo-columella.	The theca is compact.
				FUNGIDÆ: THAMNASTRÆINÆ.		*Pseudo-synapticulæ* in vertical series. Dissepiments also present. Occasional occurrence of a pseudo-columella.	Outer (true) theca very rarely present; a pseudotheca is formed by a thickening of the lateral surfaces of the septa at the peripheral area, together with a modification of the interseptal basal supports.
	The individual trabeculæ are *not primitively compact*; the series of growth-parts are not joined up end to end, successive parts may sometimes alternate in position.	The tier of trabecular growth-parts at the edges of septa and costæ are *often not compacted* within one period of growth. Apertures may remain unfilled between the neighbouring growth-parts or they may be subsequently filled up.		FUNGIDÆ: FUNGINÆ.		*Synapticulæ* (both true, and pseudo-synapticulæ) in vertical series. Dissepiments also present except in the genus *Fungia*, where the synapticulæ form continuous bars. Lateral septal coalescence characteristic; terminal septal coalescence also present.	The theca is seldom compact throughout, it is usually partly porous, partly compact.
				FUNGIDÆ: LOPHOSERINÆ.			
The first-formed fibrous deposit is more horizontal in position than the latter. The groups of "centres" are again present, but always in close contiguity with one another, and in a straight median row, so as to give the effect of a continuous median line of calcification.			The trabeculæ diverge in irregular fan-shaped figures in the radial structure.	EUPSAMMIDÆ.	*The radial structures pass through the pseudotheca*, but the interradial loculi do not always correspond in adjacent polyps of colonies. All costæ are represented by septa within the calyx.	*Idem*, but the synapticulæ are not placed in regular vertical series, they are mostly limited to the wall area and form an irregular network.	The theca is irregularly porous.
Characteristic wheel-like arrangement of *fascicles of fibres directed horizontally outwards* from one common axis or centre in each trabecula. No appearance of a "dark line" in the median septal plane.	Successive growth-parts are always directly above each other in position, but *pores are sometimes* left in the trabecula, opposite synapticulæ.	*Usually porous.* The individual trabeculæ are very distinct, and their parts at the edge completely enveloped in polypal flesh during any one period of deposit.	The trabeculæ are directed almost vertically upwards, more or less parallel with one another.	MADREPORIDÆ: PORITIDÆ.	*The radial structures may or may not pass through the theca*; the interradial loculi never correspond in adjacent polyps of colonies. Alternate costæ occur in the wall which are not represented by septa within the calyx.	*Synapticulæ* (only true synapticulæ) in vertical series. *Dissepiments* also present. *Columella* frequent. *Lateral coalescence of septal pairs* to form pali.	The theca is regularly porous; in form zigzagged.
Strongly-marked "dark line" in the median plane of the septum, owing to the almost horizontal position of the trabecula or spine. The fibres pass obliquely upwards and outwards.	*Compact septa.* The individual trabeculæ are compacted (*Turbinaria* and *Madrepora*, (pp. 213, 214) or remain free from one another as septal spines.	*Compact.* Since the trabecula or spine is *horizontal* with the growing septal edge, *one growth-part represents the whole septal segment.*	The trabeculæ are directed almost horizontally inwards from the theca towards the centre of the calyx, and outwards towards the cœnenchyme.	MADREPORIDÆ: MADREPORINÆ.		*Extremely variable nature of basal deposit*, representing an irregular combination of tabulate and synapticulate structures; *it is almost absent in the calyces, richly developed in the cœnenchyme.* A main septum is often continued as columella.	The theca is regularly porous; in form perfectly circular.
				MADREPORIDÆ: TURBINARINÆ.			
The fibres vary, horizontal or oblique. Strongly-marked "dark line" here, owing usually to the very close setting (in serial line) of the centres of calcification.	The individual trabeculæ consist of a continuous, *compact*, vertical series of trabecular growth-parts.	*Compact.* The trabeculæ are extremely narrow and adjoining growth-parts in any one septal segment are intimately compacted.	The trabeculæ vary greatly in direction. At the very *base* of a septum an area of divergence is usually present, afterwards *the trabeculæ grow inwards from the wall as* in the Madreporidæ.	TURBINOLIDÆ.		*Interradial deposit almost absent*; represented at the base of the calyces by a solid tabulate deposit. Lateral septal coalescence may occur. *Columella* usually present either as an independent structure or connected with a main septum or with pali.	Outer (true) theca is the only one present. It has its own centres of calcareous deposit, independent of those in the radial structures. The thecal deposit usually seen to bend tangentially round and form continuity between adjacent septa.
							The theca is compact, either zigzagged or circular in shape.

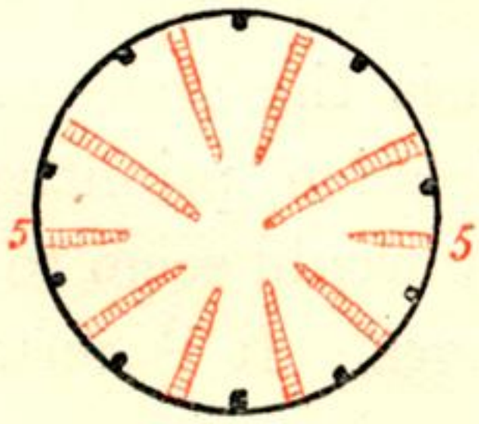
Diagram A.











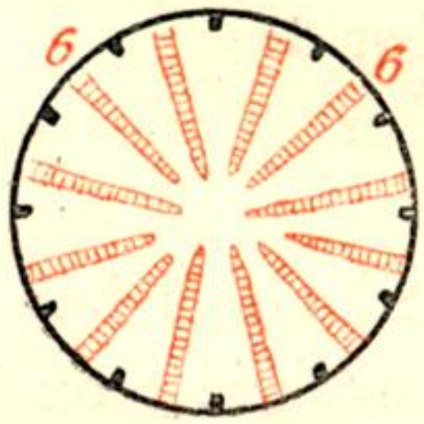
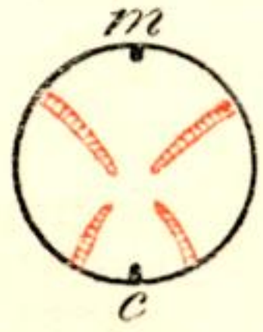
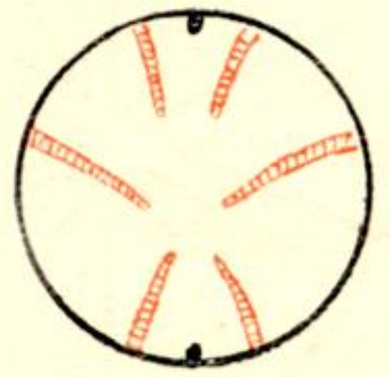
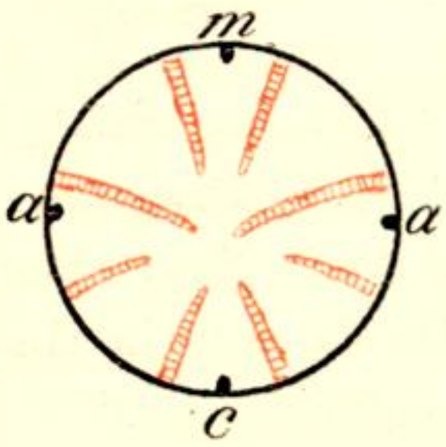
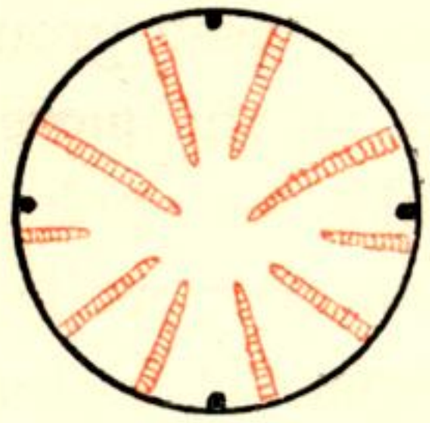


Diagram B.









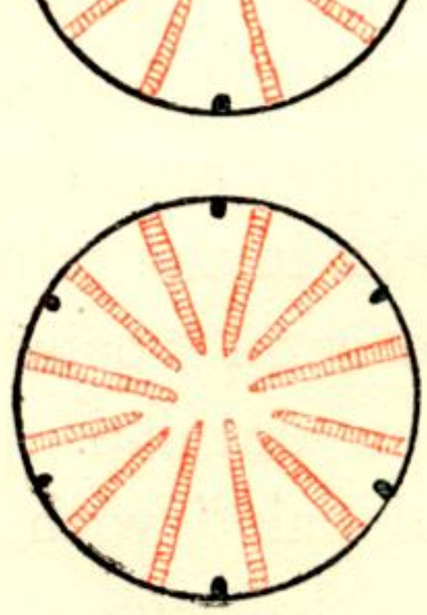


Diagram A.—Insertion of a pair of septa after each pair of mesenteries (hypothetic) would result in the *ectocœlic and entocœlic* position of septa (*primary cycle* 12).

Diagram B.—Insertion of a pair of septa after every two pairs of mesenteries ("pause" of LACAZE DUTHIERS) would result in the *entocœlic position only* of the septa (primary cycle 6). *m.* main septum; *c.* counterseptum; *a.* alar septa; (mesenteries after LACAZE DUTHIERS).

Diagram C.

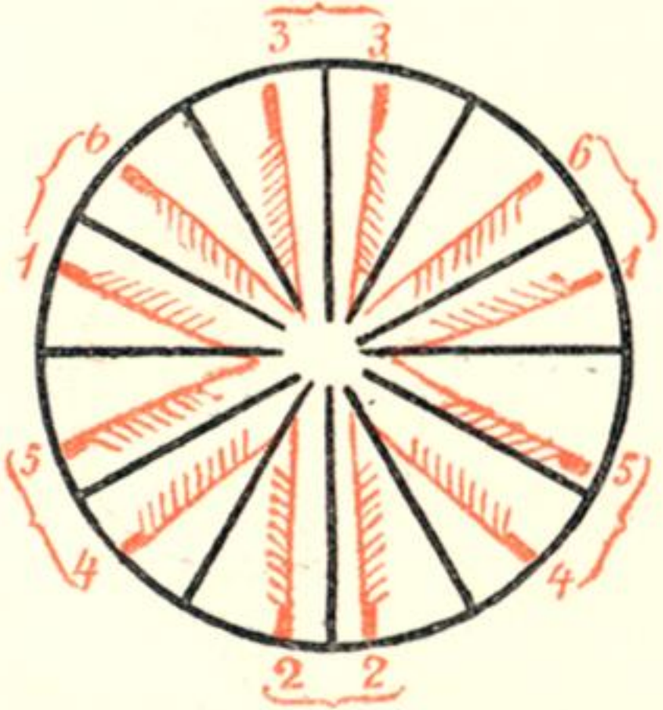


Diagram D.

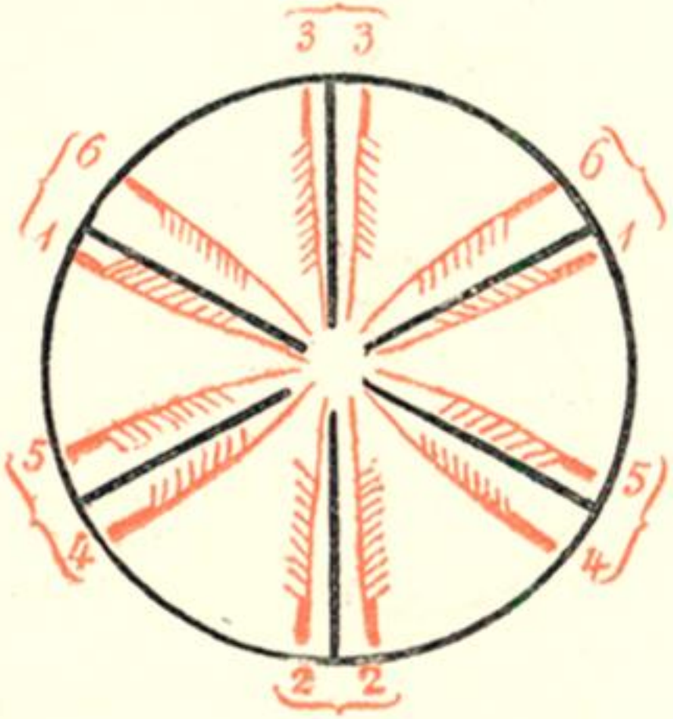
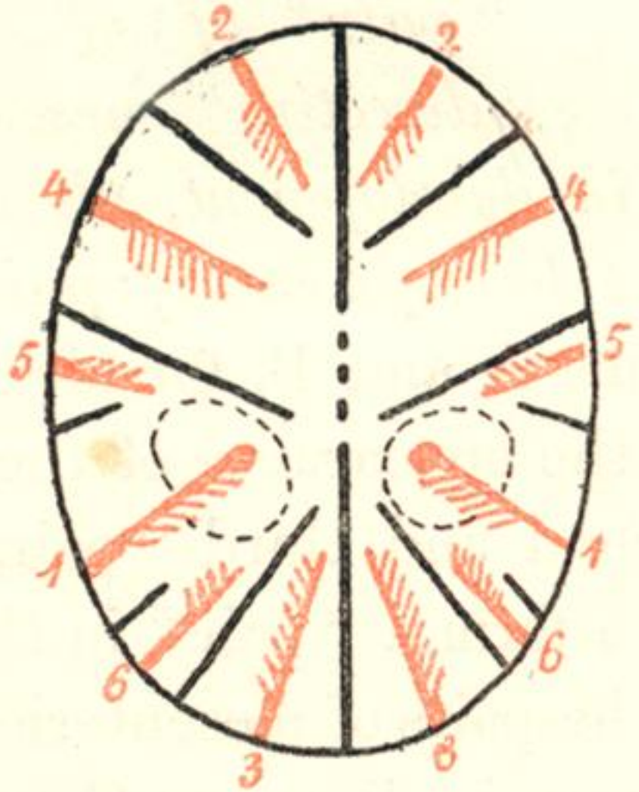


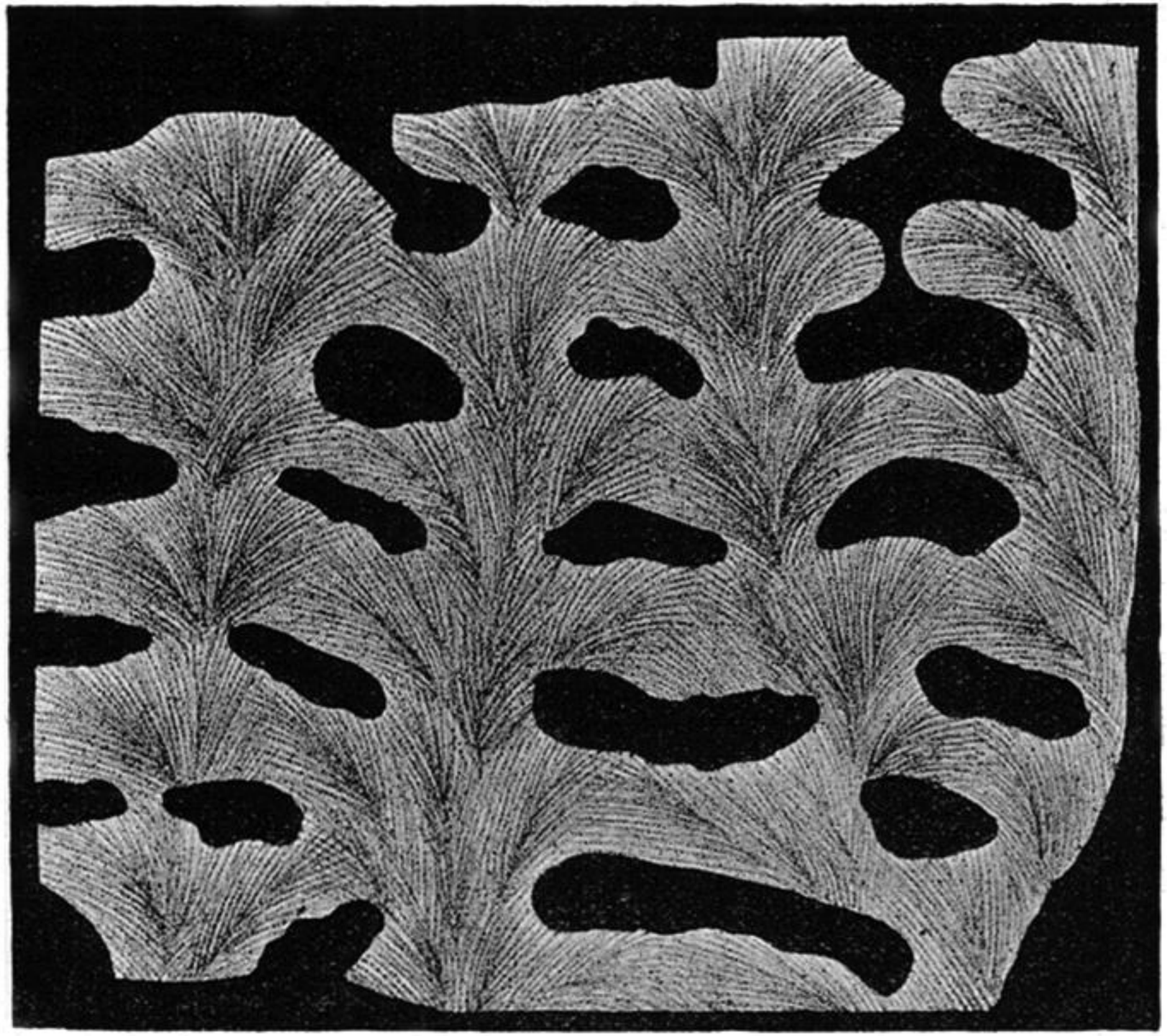
Diagram C shows 12 septa occupying the 6 ectocœles and the 6 entocœles formed by the mesenteries (*cf.* diagram A). Diagram D shows 6 septa occupying the 6 entocœles of the mesenteries (*cf.* diagram B). Note also that the *developmental* "pairs" of mesenteries indicated by the numerals coincide only in the cases of the 2nd and 3rd "pairs" (the "directive mesenteries") with the *muscular* "pairs."

Diagram E.



Plan of the septa and mesenterial "pits" in *Seriatopora* (after MOSELEY). The pair of mesenteries numbered 1, are specialized for reproduction, and occupy the lateral (alar) "pits" or "fossulæ" (*cf.* pp. 279, 280).

Fig. 75.



Heptastylis. Longitudinal section, showing the erect trabeculæ and horizontal synapticulæ. Fascicles of fibres are seen here and there in the section.