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The Pelmatoporinae, an Essay on the Evolution of a Group of Cretaceous Polyzoa

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IV. *The Pelmatoporinæ, an Essay on the Evolution of a Group of Cretaceous Polyzoa.*

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A. INTRODUCTION.

Having spent many years in working through the Cretaceous Cribrimorph* material in the British Museum, and, consequently, the literature of the subject, I was forced to the conclusion that various Cribrimorph stocks had independently arisen over and over again from Membranimorph* ancestors, had run through a more or less similar evolution, and, finally, become extinct; so that the many forms described under *Cribrilina*, *Membraniporella*, and other Recent genera were really in no way closely related to these, and the Cretaceous Cribrimorph forms, in consequence, needed at least a generic nomenclature of their own.† These Cretaceous forms fell under ten main stocks, between which no direct relationship could be discovered, and whose common ancestor must be sought far back among the primitive Membranimorphs; so that it did not seem too much to claim for each of these main stocks the status of a family. Within certain families were several well-defined groups, which, nevertheless, in each case had features in common, rendering it possible for all to have been derived from a common Cribrimorph ancestor; it seemed permissible, therefore, to regard these groups as subfamilies. Thus a complete evolutionary classification was drawn up for the Cretaceous Cribrimorphs, and this, in the tersest possible form, was published in the 'Annals and Magazine of Natural History' (LANG, 1916). Since the whole evolutionary scheme was implicit in the tabular analysis, it was hoped that

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* Cribrimorphs (LANG, 1916, p. 76) are Cheilostome Polyzoa having an intraterminal front-wall formed of overarching spines, as in the genus *Cribrilina*; Membranimorphs are those whose intraterminal front-wall resembles that of the Recent genus *Membranipora*.

† See, too, in this connection, BRYDONE, 1906, p. 292.

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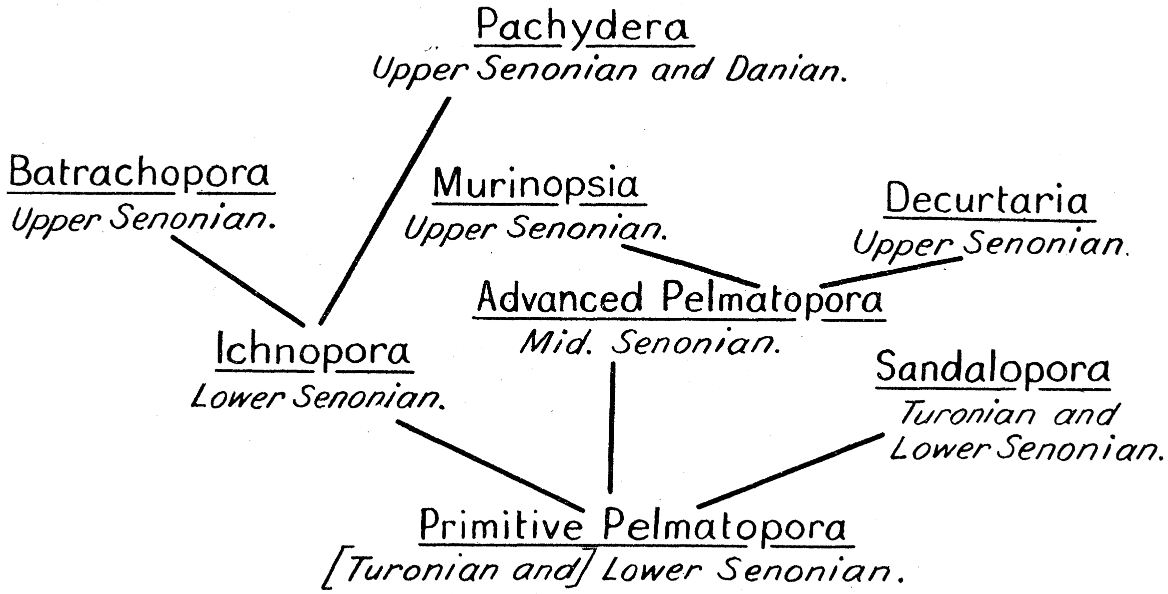
this would be lucid enough to be acceptable without further explanation. From various criticisms, it appears that this is not so, and the opportunity has been taken in this essay to select one subfamily and expand the condensed account into a fuller statement. The subfamily Pelmatoporinæ was chosen partly because of its large size, and partly because it illustrates so fully the principles of evolution exhibited by the Cretaceous Cribrimorphs generally; but other subfamilies would serve the same purpose nearly as well.

The morphology of the group is the first consideration; and since it is founded on the structure of the species *Pelmatopora calceata*, which closely approximates to the supposed ancestral form, this radical species is considered in some detail. Then, after examining the evolutionary aim of Cretaceous Cribrimorphs as a whole, we are in a position to appreciate the general evolutionary history of each character of the radical species, as it proceeds from the less to the more complex forms in the several lineages. Next, peculiar modifications of certain characters are described, giving the criteria for generic distinctions; then the evolution of forms within each genus. The results are compared with those obtained by W. K. Spencer in his work on Cretaceous Asteroidea. Next, the stratigraphical distribution of the forms is examined to see how far this corroborates the relationships established on morphic evidence; and, finally, the evidence of recapitulation, as shown in the colonial development (Astogeny), is brought to bear in connection with the other two criteria of relationships already examined.

B. The Morphic Criterion of Relationship.

1. *The Radical Pelmatopora calceata.*

Of the seven genera composing the subfamily Pelmatoporinæ (Lang, 1916), six may be derived from the remaining genus *Pelmatopora*, the most primitive species of which is thus a radical upon which all the other forms are based. In broad outlines the phylogeny may be generally expressed as follows:—



In considering, then, the evolution of the Pelmatoporinæ, it will be convenient first to describe this radical *Pelmatopora calceata* containing all the characters of the subfamily in their simplest form; next, to consider the modifications of these simple characters that have given rise to new genera, and, then, the evolution within the genus *Pelmatopora* itself and the other genera in turn.

The Pelmatoporidæ (see fig. 1) are "Cribrimorph" Cheilostome Polyzoa, that is, they have an intraterminal front-wall composed of overarching spines—*costæ*—fused to their opposite and often to their lateral neighbours to form a more or less solid roof. In this family the costæ which form the intraterminal front-wall are hollow, and, on meeting their opposite neighbours, turn upwards, and are continued as free spines; the broken ends of these spines form a double row or series of rows of hob-nail-like markings on the front-wall—*pelmata*. The first pair of opposite costæ forms the *apertural bar;* there are typically two pairs of free spines—the *apertural spines* —around the aperture; the avicularia are generally numerous and small. In the subfamily Pelmatoporinæ the costæ are stout throughout their length, and the apertural spines always four in number, though they may be altogether obscured by the up-growth around them of secondary tissue. All the above-mentioned structures are shown in the accompanying figure of *Pelmatopora calceata* (fig. 1).

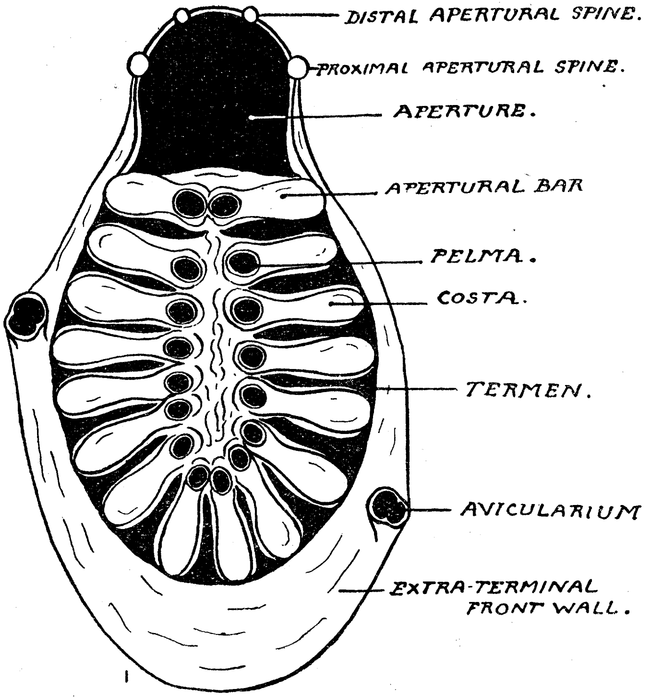


FIG. 1.—Diagram of *Pelmatopora calceata*, LANG. × about 150 diameters.

The original diagnosis of *P. calceata* (LANG, 1916, p. 102) is as follows: *Pelmatopora,* in which avicularia do not replace the distal apertural spines (*i.e.*, there is no distal shield); the median area of fusion is imperforate, and there are no secondary pelmata; the intraterminal front-wall is well-arched; there is little or no secondary interœcial tissue; avicularia are small, blunt, and sporadic. The following description supplements this terse diagnosis:—The colony (*asty*) is incrusting; the individuals (*œcia*) are 0·5 mm. to 0·65 mm. in length, and are elliptical rather than parallel-sided; the extra-terminal front-wall is visible and somewhat extensive (correlated with the absence of secondary interœcial tissue and the apparent spacing of the œcia); the intraterminal front-wall is well arched (correlated with the absence of secondary interœcial tissue and of secondary pelmata), and consists of 14 to 16 costæ; there is a double row of pelmata lying fairly close to the middle line, enclosing an imperforate area of fusion; the apertural bar bears no processes; the four apertural spines are well developed, but not secondarily enlarged; the aperture is "cribriline" and rather longer than wide, not complicated by any growth of secondary tissue; avicularia are fairly numerous (rather more so than the normal œcia), sporadic, placed on the sides of the normal œcia rather than exactly between two of them, small (diameter of apertures about a quarter that of apertures of normal œcia), and blunt; the mandibular part of the aperture is larger than the proximal part. All these points are shown in the figure of *P. calceata*.

2. *The Evolutionary Aim of Cretaceous Cribrimorph Polyzoa.*

Since the characters just described are assumed to be the raw material, so to speak, which is made up in various ways during the evolution of the group, it is well to consider each character separately, and to state, if possible, any general tendencies of development exhibited by it in every lineage; the peculiarities of each lineage will then be seen to be grafted on to this general scheme. Before doing this, it is helpful to ask what is the evolutionary aim unifying all the modifications of structure. And if it is objected that this consideration is too theoretical, it may be answered that the facts are confined to the diagnoses and descriptions of the specimens and to the records of the localities and horizons at which they occur; and, therefore, to describe each form and give it a trivial name is as far as we can go without theory; but to give a form even a specific name is to assume theoretical relationships (since this involves referring a species to a genus), and therefore to accept a doctrine of evolution by descent. We are, therefore, driven to the use of theory in order to present our facts in an intelligible order. When we talk, then, of seeking the evolutionary aim of a group, we are only attempting by further theory to make our facts more intelligible. Now, generally speaking, in the Cretaceous Cheilostomes, the facts are as follows. The skeletal (presumably originally calcareous) parts of the organisms with which we are dealing can be arranged in numerous lines (*lineages*) diverging from comparatively fewer forms. These *radical forms* are simpler, that is, there is less skeletal matter and less elaboration of structure, and they are connected, more or less gradually, by intermediate stages along the lineages with the ultimate forms that have more skeletal matter and more elaboration of structure. On the whole, this distribution of the various forms in lineages (the morphological criterion of relationship) corresponds with their distribution in time (the stratigraphical criterion), as shown by the horizons at which they are found; and, in so far as the colony shows developmental stages (the astogenetic criterion), these also correspond with the stages of the lineage. It is logical, therefore, to assume that larger deposition of Calcium Carbonate and greater elaboration of structure mark the general tendency of evolution.

It is natural, then, to ask to what purpose is this directed—what is the evolutionary aim of the group as a whole. In considering the ultimate forms of many of the lineages, it is impossible to imagine that they could have had any further evolution—they apparently are overloaded with secondary deposits of Calcium Carbonate, and, since no further developments are found, they presumably became extinct. In surveying Recent Cheilostome Polyzoa, it is seen that there are many forms whose skeletons are wholly or nearly wholly chitinous, while others are partly calcareous and partly chitinous; others, again, are almost wholly calcareous, with a slight skeleton, while others are massive with calcareous skeletal matter. In so far as there are indications of evolution among the calcareous forms (shown especially in astogenetic development, *e.g.*, in *Membraniporella*, see HINCKS, 1880, Plate 27, fig. 6), the direction is seen to be from a less to a more calcareous condition; and it is reasonable to suppose that this tendency was the same in Cretaceous times, and that there were then chitinous and slightly calcareous forms, not preserved as fossils (owing to the perishable character of chitin), as well as the more calcareous forms that we find preserved. It seems that, when once the habit of secreting Calcium Carbonate is established, it becomes increasingly constitutional, and the Polyzoa have discovered no means of checking this tendency, which finally overwhelms and obliterates the lineage. The chitinous forms, on the other hand, persist, and continually give rise to new calcareous lineages. I have elsewhere claimed (LANG, 1916) that this bionomic problem of the disposal of Calcium Carbonate after the habit of secreting it has acquired irresistible momentum, has been a pressing one among animals other than Polyzoa; that the acquisition of a tubular shell is one method of dealing with it; that, to take one other phylum, the most successful molluscs (*e.g.*, the Dibranch Cephalopods) have learnt how to resorb* their shell, while such forms as the Rudistæ ("Hippurites") have succumbed to a disease of uncontrolled super-secretion.

The evolutionary aim, then, behind the elaboration of the skeleton in the Cretaceous Cribrimorphs is the disposal of an increasing secretion of Calcium Carbonate where it will be least in the way; and it is mainly deposited, independently, in three positions, namely, on the intraterminal front-wall, so as further to solidify it; around the aperture, so as to build up a secondary aperture; and in the

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* During their phylogeny. "Gradually to avoid secreting" rather than "to resorb" would more accurately express what is meant.

interœcial depressions. To explain the increasing complexity of aperture and intraterminal front-wall thus, is not, however, to deny to the organism any power of elaborating its skeleton to a useful end.* It only claims that this secretion is unavoidably there to be disposed of, and, if the organism can employ it usefully, it is by so much the gainer; but sooner or later it will fail to cope with the abundance of its secretion, and the race will perish.

The Cribrimorph, then, only puts off the evil day. That it does put it off with some success seems likely when the more primitive Membranimorphs are considered. In a colony of these it is common to find individuals completely sealed up, with the scar of the aperture showing on the calcareous covering of the œcium. It is probable that this is the only answer that the Membranimorph individual can give to the demands of its deranged metabolism—it simply deposits Calcium Carbonate over its whole surface, building its own tomb, and thus experiencing the final doom of the race. The race, however, saved itself from such a crudely immediate ending by the capacity it acquired for limiting the areas of super-secretion to definite spots along the termen; and thus terminal spines arose, which, by further increase of size and by inter-fusion, form the Cribrimorph intraterminal front-wall. This is a possible explanation of the "closed" œcia described by LEVINSEN and others (LEVINSEN, 1902, p. 28). It is probably not on these lines that "renewed" œcia, described too by LEVINSEN (1902, p. 27, and 1907), can be explained; but even these afford an excellent opportunity for the disposal of more Calcium Carbonate to form a new termen.

3. *The Evolutionary History of Individual Characters.*

After this somewhat long digression, let us again pick up the thread of evolution in the Pelmatoporinæ; and, bearing in mind the obligation of the organism ever to secrete more Calcium Carbonate, consider the evolutionary history of the characters of *P. calceata*:—

(a) *The Colonial Habit.*—In the Pelmatoporinæ, and throughout the phylum, the direction of evolution is from an incrusting to an erect asty. It is hard to be certain, however, that an apparently erect unilaminar asty is not really incrusting, since an alga or other perishable substance may have formed its support, and a smooth basis like an alga would not give to the incrusting face of the Polyzoan the minutely-roughened surface to be seen on specimens that have grown on hard and minutely-uneven bases. It is unusual, however, to find an habitually-incrusting form in an apparently free condition, and, unless there are other reasons against it, I should advocate keeping incrusting and free, unilaminar forms specifically distinct.†

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* On various methods of building up a front-wall in Recent Cheilostomes, correlatively with differences in the soft tissues, and, therefore, probably, with bionomic differences, see HARMER, 1901, pp. 11–17.

† See some remarks to the point by BRYDONE, 1906, pp. 289–90. He advocates merging the incrusting and erect unilaminar species, but considering other growth-forms as specifically distinct. Since this was written, he has again referred to the matter, see BRYDONE, 1917, p. 52.

(b) *The Size of the Œcium.*—Generally speaking, the size increases with further evolution, apparently always at first, though some lineages (*e.g.*, *Pelmatopora quadrata–P. filliozati*) may become catagenetically smaller with regard to œcial size.

(c) *The Shape of the Œcium.*—This is correlated with the relative sizes of the aperture and the intraterminal front-wall. If these factors, however, are constant, the tendency is for the œcia to pass from an elliptical shape to one with parallel sides. From the astogenetic evidence referred to later, it is probable that a more tubular stage preceded the elliptical stage.

(d) *The Extraterminal Front-Wall.*—Secondary interœcial tissue obliterates the extraterminal front-wall, and, consequently, it appears only in primitive forms. Its area in the Pelmatoporinæ does not generally show any marked tendency to increase or to diminish, though in some groups it becomes larger during evolution. In forms with much secondary interœcial tissue, the extent of the extraterminal front-wall can be estimated only by the apparent distance apart of the œcia, assuming that the intraterminal front-wall is not itself partly enveloped in secondary tissue.

(e) *The Amount of Vaulting of the Intraterminal Front-Wall.*—This appears to become less during evolution; but what really happens is (1) the interœcial-secondary tissue, filling up the interœcial valleys, covers the proximal ends of the costæ, and thus makes the vaulting of the intraterminal wall appear lower; and (2) the median area of fusion tends to widen during evolution, and, since this area is flat, the top of the intraterminal front-wall tends to become less vaulted.

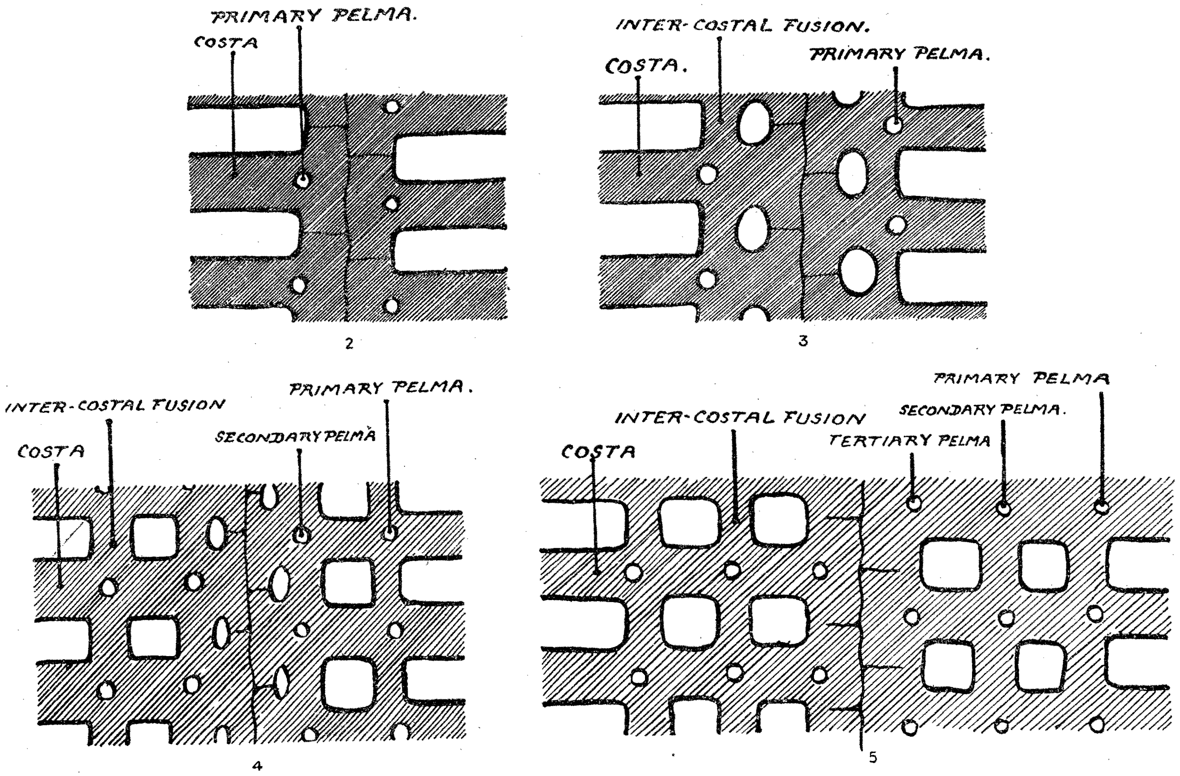
(f) *The Number of Costæ.*—This tends to increase during development, but may be very much reduced (*e.g.*, in *Batrachopora*) catagenetically.

(g) *The Number of Pelmata on each Costa and their Position with regard to the Middle Line of the Intraterminal Front-Wall.*—In the most primitive forms, the pelmata are close to the middle line (fig. 2). During phyletic (and often during astogenetic) development they retreat towards the proximal ends of each costa, carrying at the same time the lateral fusions with the neighbouring costæ with them (fig. 3). Next, secondary pelmata appear close to the middle line (fig. 4), and these in turn move away from the middle line, carrying with them their lateral fusions, and tertiary pelmata arise (fig. 5). Thus, the intraterminal front-wall finally takes the form of a lattice-work with pelmata at the nodes.

(h) *The Apertural Bar.*—The structure of the apertural bar has a different evolution in the several lineages and is necessarily correlated with that of the secondary aperture when it forms the proximal shield of that structure.

(i) *The Apertural Spines.*—These remain unaltered during evolution (except in *Sandalopora* and *Ichnopora* where the proximal pair probably fuse with the apertural bar), but in the ultimate stages tend to be swamped by secondary tissue.

(j) *The Shape of the Aperture.*—This tends to alter from being rather longer than wide to rather wider than long. A secondary aperture occurs in the most complex forms, and is generally circular or oval with the larger diameter transverse. The manner of its formation differs in the different lineages.



FIGS. 2–5.—Diagrams, very much enlarged, of part of the middle of the intraterminal front-wall of *Pelmatopora*, showing the gradual movement of the primary pelmata from the mid-line, and the acquisition of secondary and tertiary pelmata.

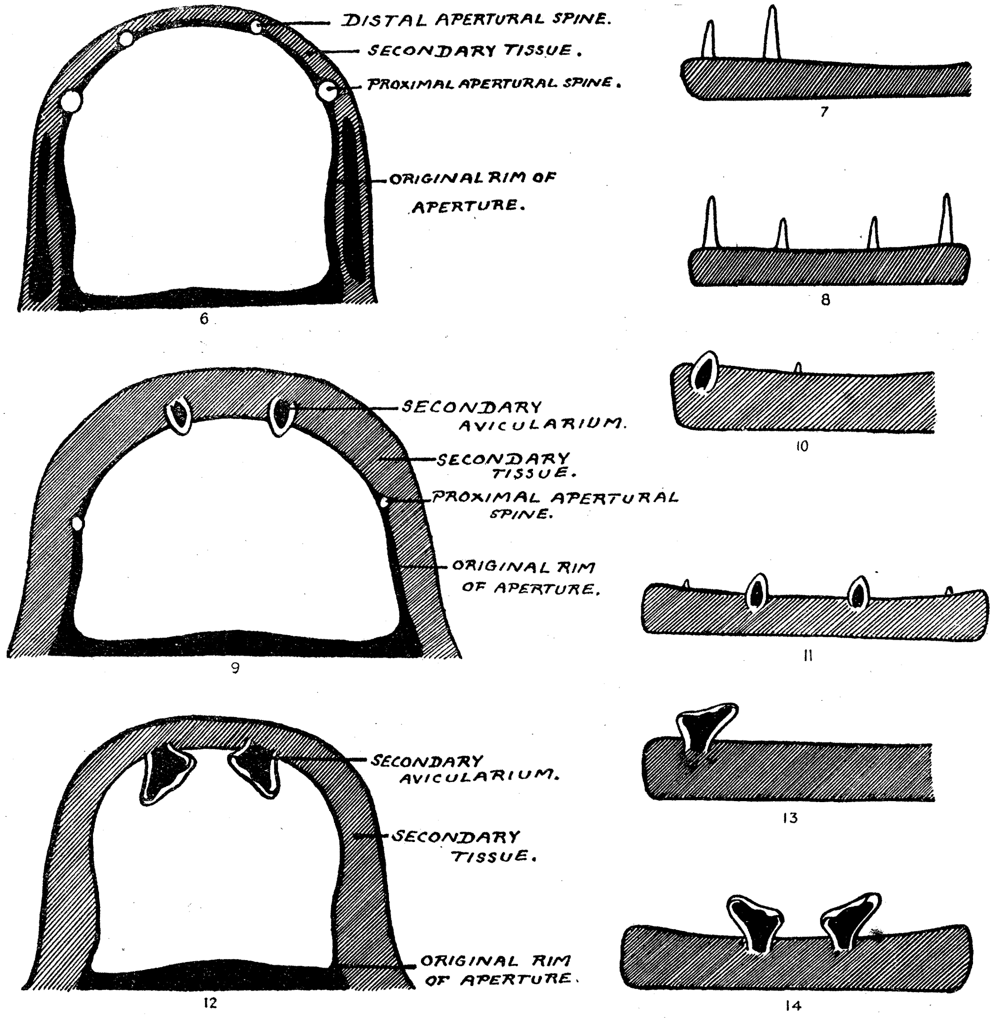
(k) *The Size of the Aperture compared with that of the Intraterminal Front-Wall.*—This tends, as a rule, to increase; but, in some cases (*e.g.*, *Pelmatopora suffulta*) becomes smaller catagenetically.

(l) *Avicularia.*—In the Pelmatoporinæ the avicularia during evolution tend to become less numerous, more definite in position, larger in size, and in their mandibular portion more pointed.

4. *The Evolution of the Genera.*

As will be seen from the evolution of the above characters, the generic history of the Pelmatoporinæ is that of the secondary aperture and the structures that may be involved in this, namely, the apertural bar, the proximal and distal pairs of apertural spines, and a pair of avicularia. As a rule, the secondary aperture is distinctly formed of proximal and distal halves—the *proximal* and *distal shields*—though in a complete secondary aperture these halves are entirely fused. A proximal shield only, or a distal shield only may be formed. As a rule, the distal shield is composed entirely of the distal pair of apertural spines and of secondary tissue growing up round them; but these may be totally swamped by secondary tissue and replaced by a pair of avicularia (in *Pelmatopora*). The proximal shield is formed by developments of the apertural bar which is often fused with the proximal pair of apertural spines and often with a pair of avicularia placed laterally and proximally with regard to the aperture. Genera with a distal shield only are *Pelmatopora*, *Decurtaria* and *Murinopsia*; with a proximal shield only, *Sandalopora*; with both proximal and distal shields (at any rate in some species), *Ichnopora*, *Batrachopora*, and *Pachydera*.

In *Pelmatopora* there is no attempt at a secondary aperture until the genus has evolved a complex intraterminal front-wall with secondary pelmata. In such forms (figs. 6, 7, 8), there is a fair amount of secondary interœcial tissue, and some of this grows round the aperture, and gradually immerses the apertural spines; next,



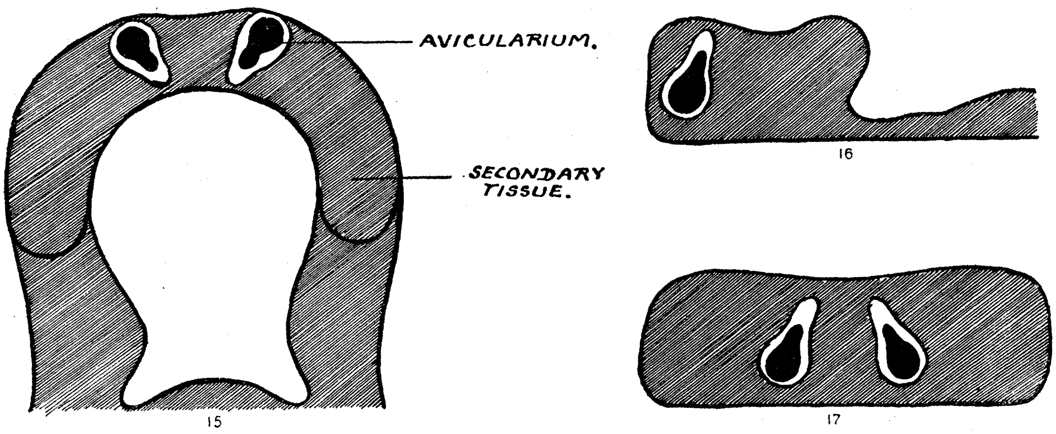
FIGS. 6–8.—Diagrams of the aperture of *Pelmatopora plantaris*, LANG, from above, from the side, and from in front, respectively.

FIGS. 9–11.—The same of *P. brydonei*, LANG. FIGS. 12–14.—The same of *P. palmata*, LANG.

All greatly enlarged.

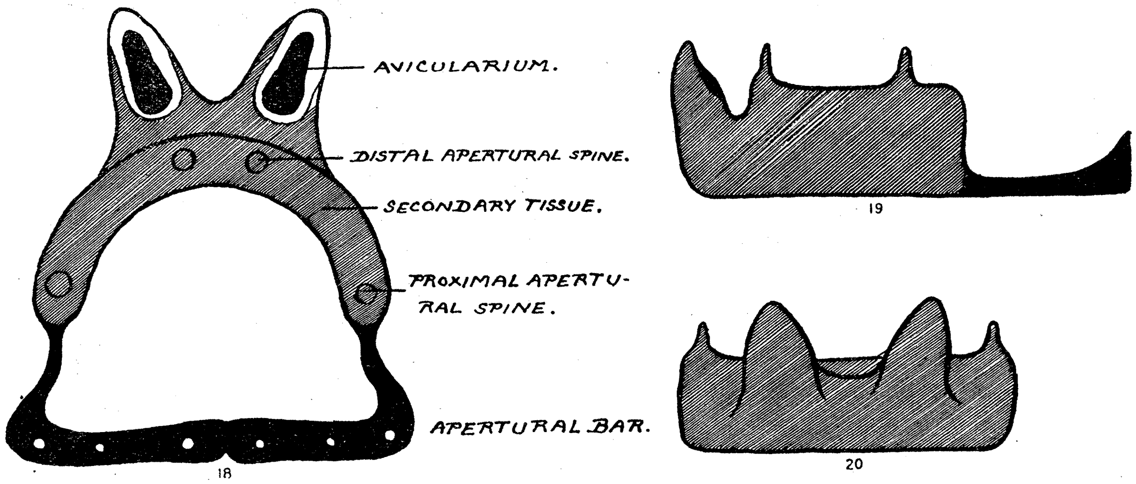
a pair of peg-like avicularia appear on the rim of the secondary aperture at the level of the distal apertural spines (figs. 9–14) (in one case—*Pelmatopora quadrivolucris*—a second pair replaces the proximal apertural spines), becoming bifid and much enlarged in the ultimate forms (figs. 12, 13, 14). No form, however, has yet been found (except in connection with ovicells) in which there is a fusion of these avicularia to form a perfect distal shield.

In *Decurtaria* (figs. 15–17) there is no proximal shield, and the distal shield is large and thick, formed, as in *Pelmatopora*, of a pair of avicularia, but these are firmly fused and welded into a semi-circular rim of secondary tissue.



FIGS. 15–17.—Diagrams, much enlarged, of the aperture of *Decurtaria cornuta* (BEISSEL), from above, from the side, and from in front, respectively.

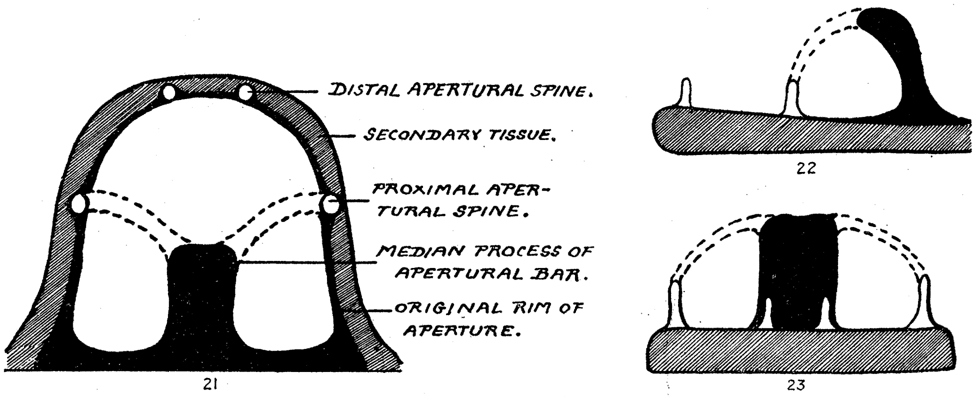
In *Murinopsia* (figs. 18–20) the apertural bar is flattened so as to form what might be regarded as a rudimentary proximal shield. The distal shield is formed by the infilling with secondary tissue of the spaces between the distal and proximal apertural spines on each side and between the distal spines themselves; both proximal and



FIGS. 18–20.—Diagrams, much enlarged, of the aperture of *Murinopsia francqana* (D'ORBIGNY), from above, from the side, and from in front, respectively.

distal pairs of apertural spines are well developed. One or more pairs of avicularia are present distal to the apertural rim.

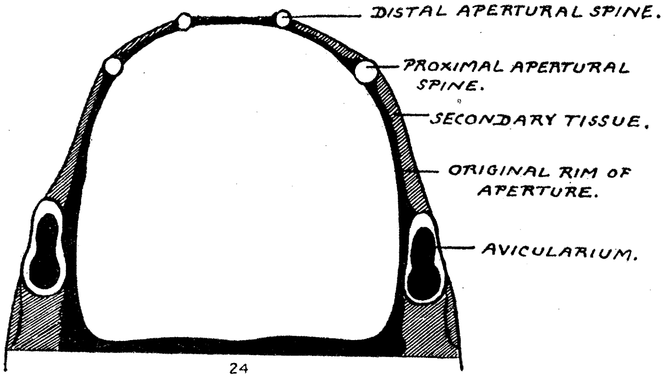
In *Sandalopora* (figs. 21–23) there is no distal shield, and the proximal shield is formed by a median process of the apertural bar which may be broad (*S. gallica*, *S. lavardinensis*) or spinous (*S. soccata*, *S. caligata*). Judging from genera of other families in which the proximal shield is formed by a median process of the apertural bar (*e.g.*, *Lagynopora*, *Diancopora*), the apertural spines of the proximal pair almost certainly fuse with this process (as shown in the diagram), but no specimen has yet been found exhibiting this fusion unbroken.



FIGS. 21–23.—Diagrams, much enlarged, of the aperture of *Sandalopora lavardinensis*, LANG, from above, from the side, and from in front, respectively.

In the remaining genera a proximal shield is produced by a development of secondary tissue at the proximal ends of the costæ that form the apertural bar. This tissue grows upwards in connection with a pair of avicularia situated proximally and laterally to the aperture. It has already been stated that the general tendency of evolution with regard to the avicularia is from a sporadic distribution to a definite position and from a smaller to a larger size ; and this tendency for a pair to take up a proximal and lateral position with regard to the aperture is a very usual one among Cretaceous Cribrimorphs. The vertical process bearing the avicularium broadens and fuses with that on the opposite side, thus forming a hoop over the proximal side of the aperture.

In its more primitive species *Ichnopora* differs from *Pelmatopora* only in having a pair of avicularia slightly larger than the rest that takes up a definite position at the proximal-lateral corners of the aperture (figs 24–26). In more advanced forms, these avicularia are carried up with the growth of that secondary tissue which appears on each side of the apertural bar, increase in size, and apparently swamp the proximal pair of apertural spines (figs. 27–29). Finally (figs. 30–32) they fuse with each other, forming the proximal shield of a secondary aperture, which takes the form of a bridge spanning the apertural bar and proximal end of the aperture. This bridge is wide enough in some cases to touch and fuse with a neighbouring



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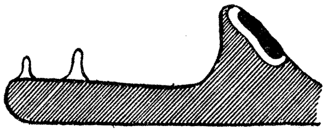

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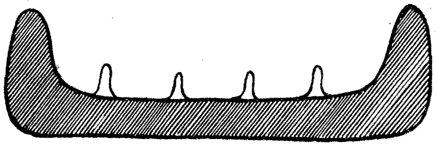

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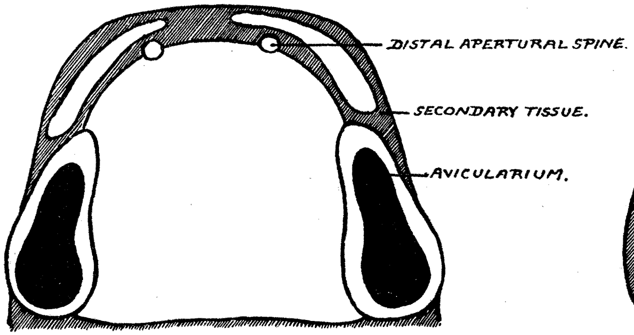

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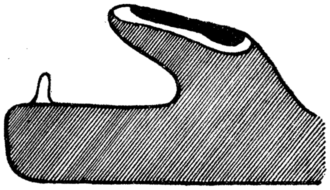

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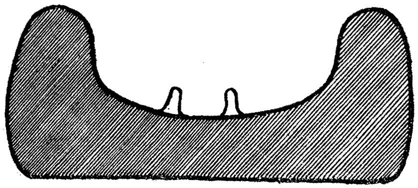

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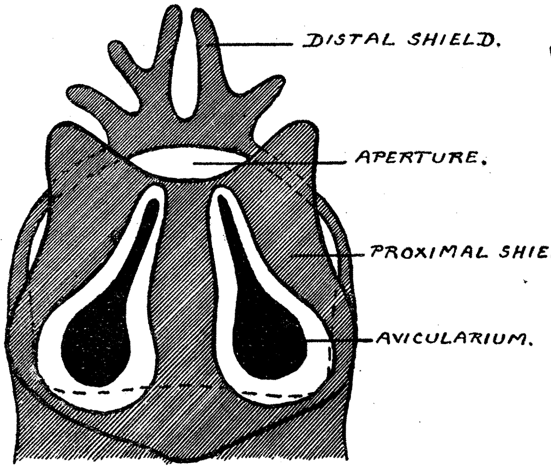

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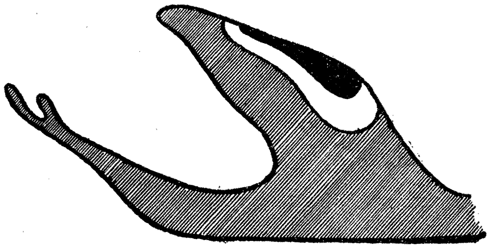

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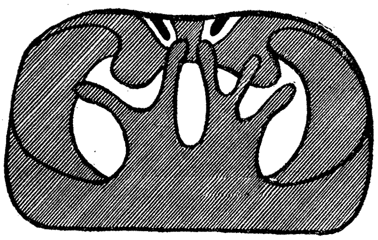

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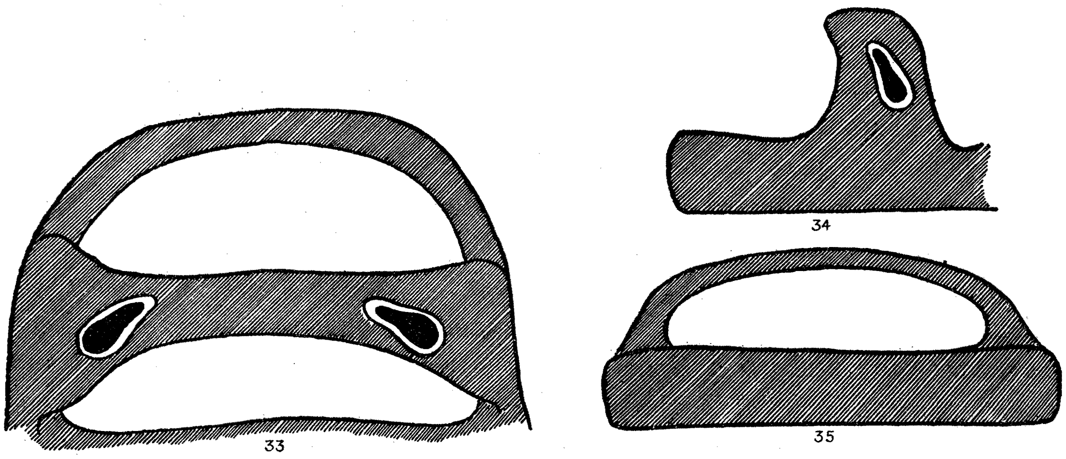
FIGS. 24–26.—Diagrams of the aperture of *Ichnopora vestigium*, LANG, from above, from the side, and from in front, respectively.

FIGS. 27–29.—The same of *I. asella*, LANG. FIGS. 30–32.—The same of *I. denticulata* (BRYDONE). All greatly enlarged.

proximal shield; and so to form an incipient "lamina peristomica,"* the characteristic feature of the "Steginomorph."† A distal shield also occurs in the most advanced forms consisting of the distal pair of spines fused at their proximal ends by secondary tissue into a solid plate, and branching at their distal ends (figs. 30–32).

In *Batrachopora* and, probably, in *Pachydera* the proximal shield is formed in the same way as in *Ichnopora*. The avicularia which take part in it, however, are not developed to such an extent as in *Ichnopora*. Moreover, these genera apparently arose from a form of *Ichnopora* whose intraterminal front-wall was more advanced than that of any known species of the genus, for in both the former genera secondary and tertiary pelmata are well developed, while in *Ichnopora* only primary pelmata (and very occasionally secondary pelmata) have as yet been observed. Also, no *Ichnopora* has yet been found above the *M. coranguinum*-zone, while *Batrachopora* and *Pachydera* occur in the zone of *B. mucronata* and higher.

Batrachopora has, as a rule, a wide aperture, and this, during evolution, tends to grow wider still; the proximal shield meanwhile spreads on all sides and forms a lamina peristomica; the distal shield is formed by secondary tissue growing up around and continuing the apertural ring; it is never so prominent as the proximal shield (figs. 33–35).



FIGS. 33–35.—Diagrams, much enlarged, of the aperture of *Batrachopora ranunculus*, LANG, from above, from the side, and from the front, respectively.

In *Pachydera* there is no lamina peristomica, but the secondary aperture becomes tubular and may be prolonged. Its structure is not easy to elucidate, but apparently the proximal and distal shields, formed as in *Batrachopora*, grow at a uniform rate, and fusing, form the tubular secondary aperture, leaving, however, fenestræ corresponding to the spaces over the apertural bar and between the proximal and distal pairs of apertural spines (figs. 36–38). The most difficult point to determine is the number and distribution of the avicularia; since there are depressions between the fenestræ,

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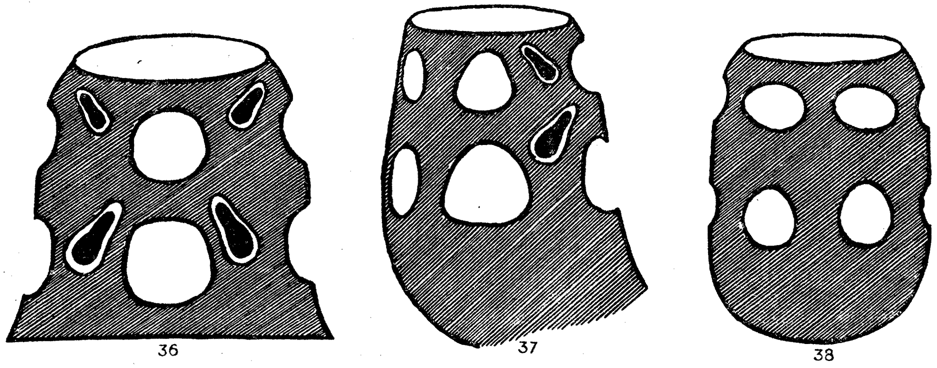
* JULLIEN, 1886, p. 609.

† LANG, 1916, p. 76.

and whether these are or are not avicularia is not by any means clear in any given instance. The distribution of avicularia, therefore, in the diagrams of the aperture of *Pachydera*, must be regarded as tentative only.



FIGS. 36–38.—Diagrams, much enlarged, of the aperture of *Pachydera grandis*, MARSSON, from above, from the side, and from in front, respectively.

The relationships, then, of these seven genera may be summed up as follows :—

Pelmatopora is the radical genus, of which the most primitive species as yet found occur in the Lower Senonian (but almost certainly arose before this, since some species of *Sandalopora*, an obvious derivative of *Pelmatopora*, come from the Turonian of France), and the most advanced species occur in the zone of *A. quadratus*. A genus, *Sandalopora* (Turonian and Lower Senonian), in which a median process of the apertural bar takes part in the proximal shield of a secondary aperture, is derived from a primitive *Pelmatopora*. There was a tendency also in primitive *Pelmatopora* for a pair of avicularia to become larger than the rest and to take up their position at the proximal-lateral corners of the aperture. Hence arose *Ichnopora* (Lower Senonian) in which these avicularia are ultimately carried upon secondary tissue and meet over the apertural bar. *Batrachopora* (Upper Senonian) arose from *Ichnopora* by acquiring secondary and tertiary pelmata, by reducing the number of costæ and by enlarging the aperture; and *Pachydera* (Upper Senonian and Danian) by acquiring the first two characters and by producing a tubular secondary aperture. *Murinopsia* and *Decurtaria* (both Upper Senonian) are derived from advanced *Pelmatopora*, both having secondary and tertiary pelmata and comparatively few costæ. *Murinopsia* has a distal shield in which the distal and proximal pairs of apertural spines retain their identity, and a distal pair of avicularia which are more or less separate from the distal shield; while in *Decurtaria* the apertural spines are immersed in the distal shield which also embraces a distal pair of avicularia.

5. *The Evolution of the Species.*

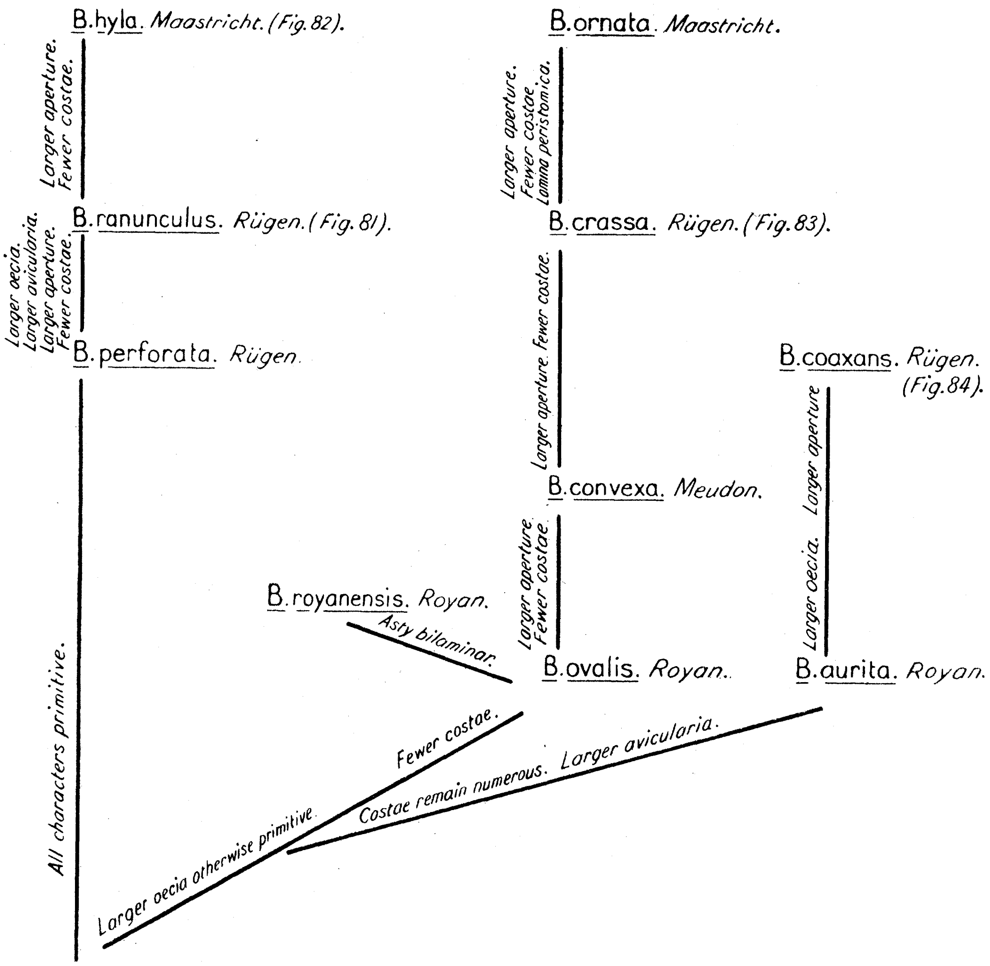
The relationships of the species within the genera remain to be considered. There are but few forms of the genera *Pachydera*, *Murinopsia* and *Decurtaria*, in fact the last genus contains but the single species *D.* [*Semiescharipora*] *cornuta* (Beissel) and therefore need not be further considered.

Pachydera contains two species: *P. grandis*, Marsson, from the zone of *B. mucronata* of Rügen, and its derivative *P. densa*, Lang, from the Danian of Faxe. *Pachydera* was seen to differ from *Pelmatopora* in having fewer costæ and a tubular aperture; so these tendencies are intensified during evolution; and *P. densa*, has, if anything, a more tubular aperture than *P. grandis*, typically five costæ compared with typically eight in *P. grandis*, and (catagenetically) fewer pelmata on each costa.

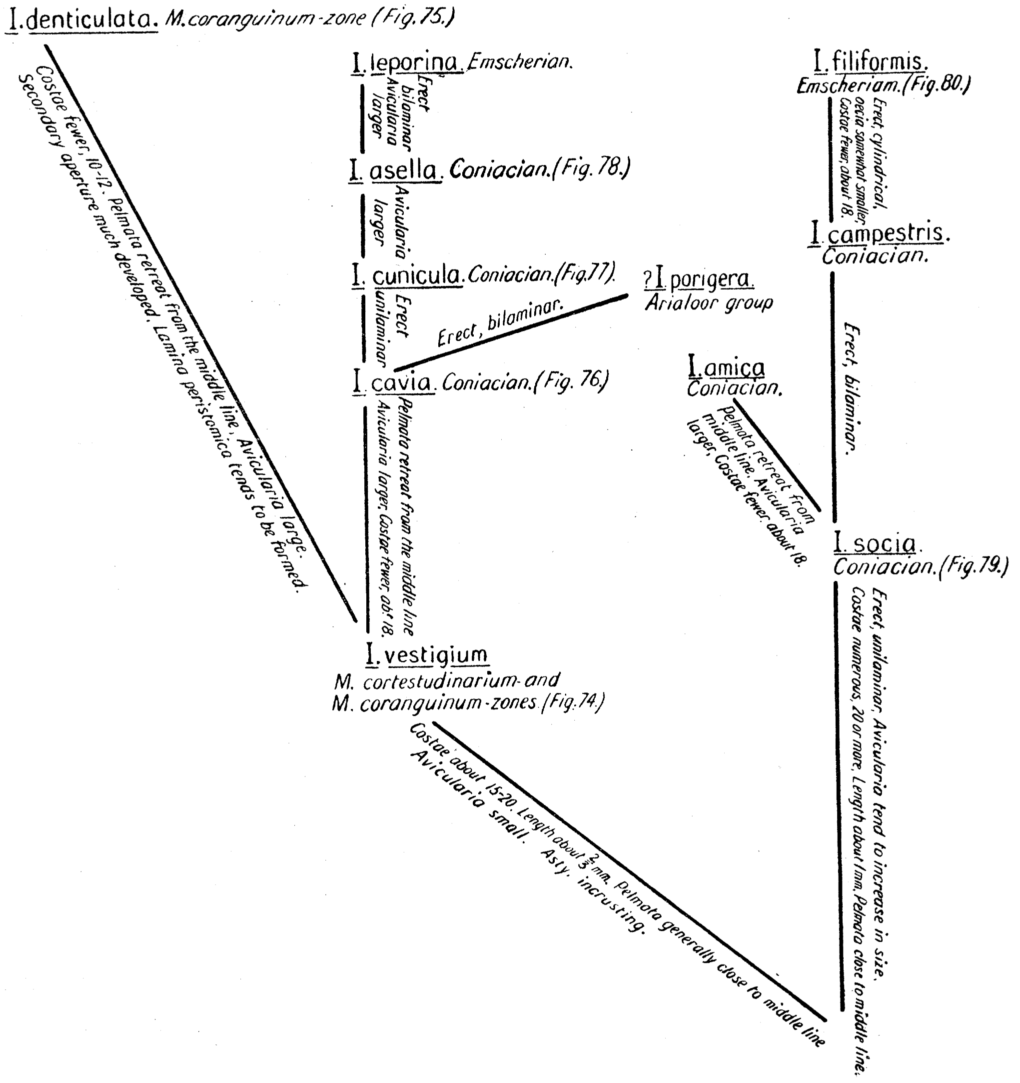
Murinopsia has but two species. *M.* [*Multescharipora*] *francqana* (d'Orbigny) from the Campanian of Meudon, near Paris, and *M.* [*Semiescharipora*] *galeata* (Beissel) from the zone of *A. quadratus* of Aachen (Aix-la-Chapelle), Germany, and possibly also from the *B. mucronatus*-zone of Rügen. I have not seen specimens of *M. galeata*, but, judging from the figures, it appears that there are more than one pair of avicularia distal to the distal shield. *M. francqana* has but one pair, but it is not possible to say which is the more primitive form.

There are ten species of *Batrachopora* if *Cellepora* (*Discopora*) *signata*, von Hagenow, from the Maastrichtian of Maastricht is excluded, probably a *Batrachopora* but really undecipherable from the figure and description. Their inter-relations are not very clear. Generally speaking, the tendency of evolution among them is to increase the size of the aperture and decrease the number of the costæ. They all come from one of four localities, Maastricht, Royan (Charente Inférieure), Rügen, and Meudon (near Paris) all very nearly at one horizon, namely, the top of the Senonian, zone of *B. mucronata*. The Maastricht Beds are sometimes considered as Danian (*e.g.*, apparently, by SPENCER, 1913, p. 150); but the Polyzoa they contain are not the same as those from Faxe (undoubted Danian). The Maastricht Polyzoa (at least the Cribrimorphs) are generally derivatives of Rügen forms, but are as likely to be modifications from Rügen in different environmental circumstances as mutations of these forms at a higher horizon. And it may be supposed that the fauna of the Maastricht Beds represents a *facies* of the fauna of the highest Senonian rather than a fauna of Danian age. The beds of Royan are generally considered as the equivalent of the Maastricht Beds (CANU, 1910, p. 65). And those of Meudon are certainly Campanian, and probably as high as the middle of the *B. mucronata*-zone (SPENCER, 1913, p. 148). Assuming for the moment that Royan and Maastricht are at the same horizon, if there is any difference of age between these beds and those of the other localities, the sequence is probably, from below, upwards, Meudon, Rügen, Maastricht and Royan, all being within the zone of *B. mucronata*. In conformity with this, we find that the two Maastricht forms, namely *Batrachopora ornata* and *B. hyla*, have the largest apertures and the fewest costæ. But the forms from Royan, namely, *B. ovalis*, *B. royanensis* and *B. aurita* are of a far more primitive type. They agree with Maastricht forms generally, however, in being of a very large size, and this suggests that the Royan and Maastricht Beds represent the same environmental conditions, but that, while the Maastricht Beds are the equivalent in time to the Rügen Beds, the Royan Beds are as low or lower than the Meudon Beds.

There would seem to be two main lineages of *Batrachopora*, the one retaining the primitive character of a comparatively small œcium (though this gradually increases in size), and the other rapidly gaining in size so that even the primitive forms are large. The first lineage, *B. perforata*, *B. ranunculus* (fig. 81), *B. hyla* (fig. 82), increases in the size of the aperture, the size of the avicularia and decreases in the number of costæ. The avicularia fuse over the apertural bar in *B. ranunculus* and presumably in *B. hyla*. The second lineage at once divides into two branches, in one of which, *B. aurita*, *B. coaxans* (fig. 84), the costæ remain numerous, though the other characters become less primitive, while in the other, *B. ovalis* (with its independent derivative *B. royanensis*), *B. convexa*, *B. crassa* (fig. 83), *B. ornata*—all the characters, including the number of costæ, advance according to the normal lines of evolution in the genus. This provisional phylogeny is expressed in the diagram below.



The twelve species of *Ichnopora* fall into two main lineages. In one, *I. socia* (fig. 79), *I. campestris*, *I. filiformis* (fig. 80), the œcia are long and narrow, and the costæ numerous, while in the second, *I. vestigium* (fig. 74), *I. cavia* (fig. 76), *I. cunicula* (fig. 77), *I. asella* (fig. 78), *I. leporina*, the œcia are comparatively short and stout and the costæ few. The tendency in both lineages is for the costæ to become fewer and the œcia to become shorter compared with their width, though not necessarily smaller; and for the other characters to follow the expected course, namely, the pelmata to retreat from the middle line, the secondary aperture to become developed, and the avicularia to become larger. *I. amica* is an independent development of *I. socia*; *I. porigera* (if an *Ichnopora*) probably arose from *I. cavia*; and *I. denticulata* (fig. 75) is a further development of *I. vestigium*. *Semiescharipora dentata*, d'Orbigny, looks like an *Ichnopora*. But Canu, who has examined the type, says of it "figure médiocre" (Canu, 1900, p. 451), and, coming from Meudon, it would appear to occur at a higher horizon than any other *Ichnopora*. It can only provisionally be placed in this genus.

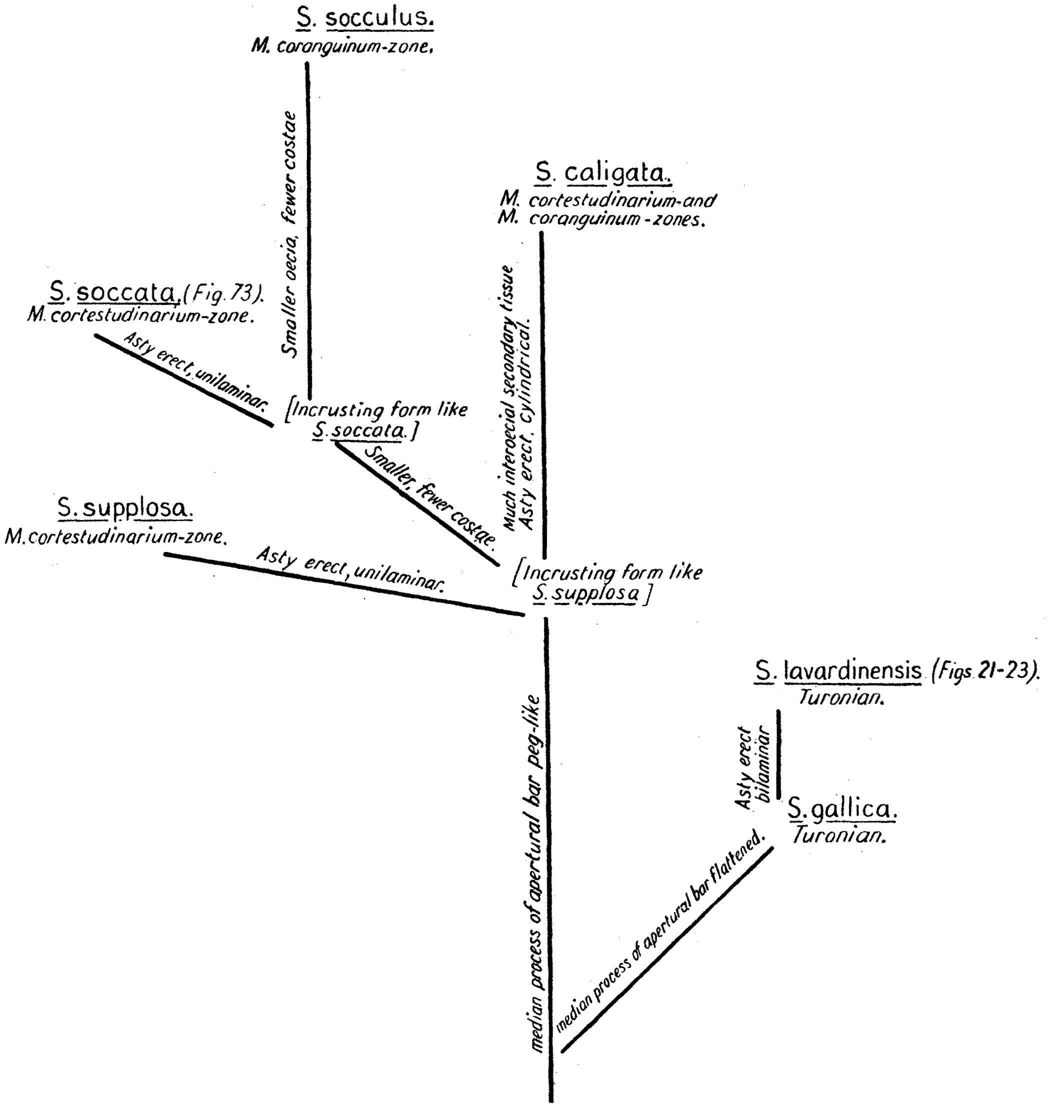


Sandalopora gallica and its derivative *S. lavardinensis* (figs. 21–23), both from the French Turonian, form an isolated lineage within the genus *Sandalopora*, characterised by the flattened condition of the median process of the apertural bar. The other species all occur at the base of the Senonian, and have a more or less

FIGS. 73–84.—Diagrams of various species of *Sandalopora*, *Ichnopora*, and *Batrachopora*, all × about 50 diameters.

FIG. 73.—*Sandalopora soccata*, LANG.
74.—*Ichnopora vestigium*, LANG.
75.—*I. denticulata* (BRYDONE).
76.—*I. cavia*, LANG.
77.—*I. cunicula*, LANG.
78.—*I. asella*, LANG.
FIG. 79.—*Ichnopora socia*, LANG.
80.—*I. filiformis* (D'ORBIGNY).
81.—*Batrachopora ranunculus*, LANG.
82.—*B. hyla*, LANG.
83.—*B. crassa*, LANG.
84.—*B. coaxans*, LANG.

cylindrical median process of the apertural bar. During evolution the œcia tend to become smaller and have fewer costæ. Thus, disregarding for the moment the colonial habit, we see that *S. supplosa*, *S. soccata* (fig. 73), and *S. socculus* form a lineage, the œcial length of which is 0·75 mm., 0·66 mm. to 0·75 mm., 0·5 mm. to 0·66 mm. respectively, and the number of costæ 18 to 20, 15, and 12. *S. socculus*, however, is incrusting, and the others erect and unilaminar; therefore, if these characters are to be differentiated, it is necessary to assume an incrusting form of *S. soccata* to give rise to *S. socculus*, and an incrusting form of *S. supplosa* to give rise to the first. *S. caligata* remains a form primitive in size (0·75 mm. to 1·0 mm.) and in the number of its costæ (17 to 20), but showing the advanced characters of much secondary inter-œcial tissue, and of an erect, cylindrical asty.



There remain to be dealt with the numerous species of *Pelmatopora*. When it is considered that the other genera of Pelmatoporinæ are specialisations of this radical genus, it is only to be expected that *Pelmatopora* itself will for the most part exhibit no striking modifications of character, but be composed of many primitive forms, differing but slightly among themselves, in a very plastic condition, and, consequently, presenting great difficulty to one who would unravel their relationships. And this is emphatically the case. Yet it is of the utmost importance to know how the various species are inter-related, because only thus can we be sure that the genera to which *Pelmatopora* gives rise are not polyphyletic. It is always possible, for instance, that the enlargement and definite position of the two avicularia characteristic of *Ichnopora* may have come about more than once among the species of *Pelmatopora;* and similarly with the other genera. If, however, we can arrange the known species of *Pelmatopora* phylogenetically, and then find that only one stock exhibits the given tendency, we can provisionally assume that the genus arising from the realisation of this tendency is monophyletic.

We have already seen that the species of *Pelmatopora* may be divided into those primitive forms which retain the apertural spines and those advanced species in which the apertural spines are swamped by secondary tissue and the distal pair replaced by avicularia. Moreover, with the exception of *P. simplex*, all of the former kind are found below a line drawn just below the top of the zone of *M. coranguinum*, and all of the latter above this line. The critical species *P. brydonei* (figs. 9–11, 53, 54), which shows both the apertural spines and the distal avicularia, occurs very high in the *coranguinum*-zone. *P. brydonei* belongs to what is almost certainly a continuous lineage based on *P. calceata*, namely, *P. calceata* (figs. 1, 49), *P. solearis* (fig. 50), *P. plantaris* (figs. 6–8, 51), *P. pero* (fig. 52), *P. brydonei* (figs. 9–11, 53, 54), and there is no reason to suppose that all the higher forms exhibiting the distal avicularia are not developments of this stock. It is difficult to define the peculiar characters of this lineage; they are chiefly negative, and the other primitive forms of *Pelmatopora* are best described by comparing them with this normal development. The characters of *P. calceata*—the radical species—and the general developmental history of these characters have already been discussed, and in this typical lineage they follow the usual course; but it may be of service to recall the typical development as manifested in the lineage under consideration. The colonial habit passes from incrusting, through erect and unilaminar to erect and bilaminar; the size of the œcium increases; the shape of the œcium passes from elliptical to parallel-sided; the extraterminal front-wall becomes swamped by secondary tissue; the intraterminal front-wall becomes flatter, at least apparently; the number of costæ increases; the primary pelmata move away from the middle line and secondary and tertiary pelmata arise, at the same time intercostal connections at the level of the pelmata are retained; the apertural bar undergoes little or no modification towards forming a proximal shield;

the apertural spines become swamped by secondary tissue; the aperture tends to become wider compared with its length, and its general size to increase somewhat; the avicularia become somewhat larger and more pointed.

FIGS. 39–52.—Diagram of primitive species of *Pelmatopora*. All × about 50 diameters.

FIG. 39.—*Pelmatopora insignis* (CANU).
40.—*P. quadrata*, LANG.
41.—*P. pauciclavia*, LANG.
42.—*P. interrupta* (D'ORBIGNY).
43.—*P. fecampensis*, LANG.
44.—*P. gasteri*, LANG.
45.—*P. suffulta* (BRYDONE).

FIG. 46.—*Pelmatopora simplex*, LANG.
47.—*P. crepidaria*, LANG.
48.—*P. d'orbignyi*, LANG.
49.—*P. calceata*, LANG.
50.—*P. solearis*.
51.—*P. plantaris*, LANG.
52.—*P. pero*, LANG.

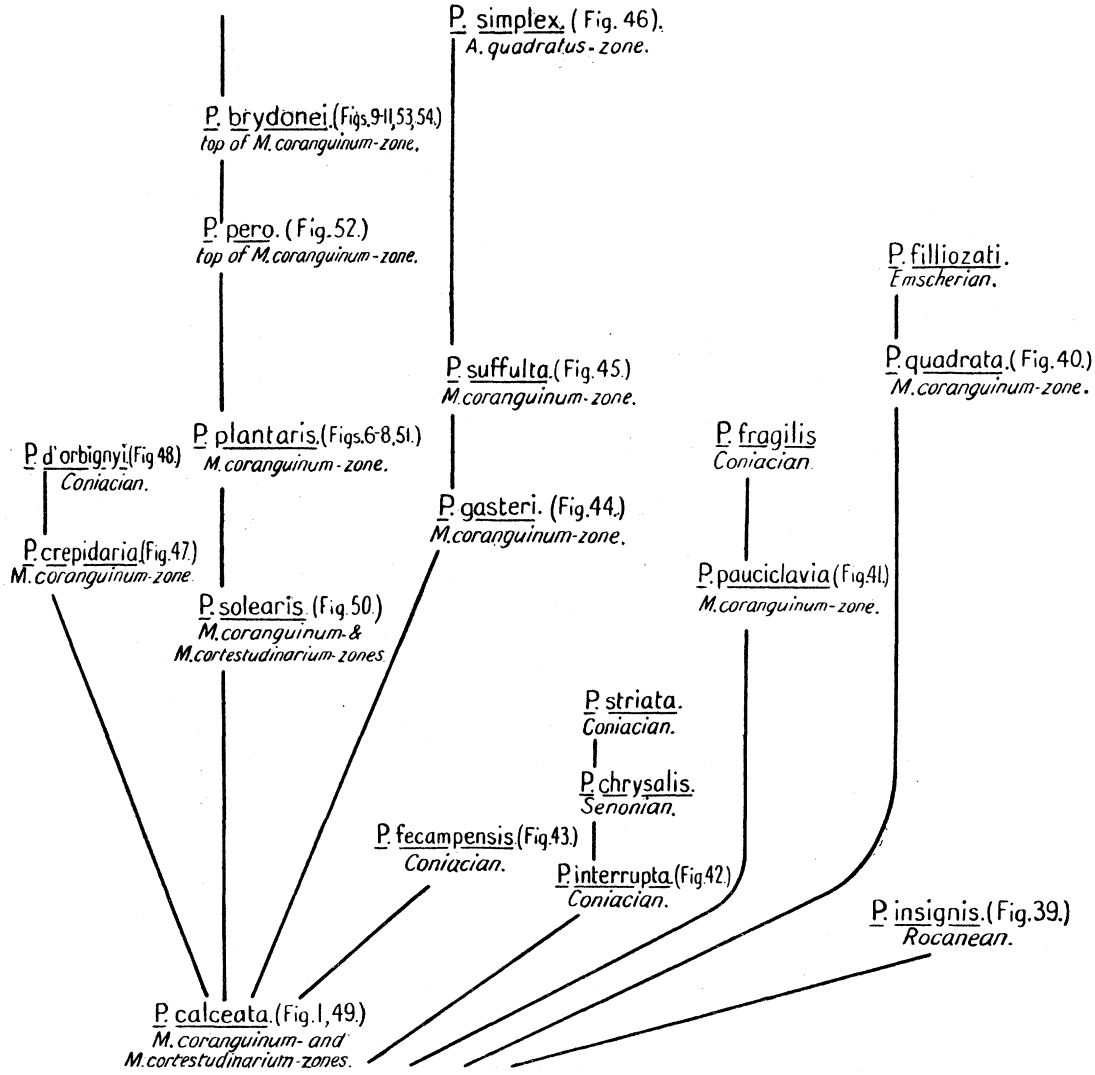
A second lineage, based on *P. calceata*, and characterised by the small size of the aperture, which increases very slightly and then catagenetically diminishes slightly, consists of *P. calceata* (figs. 1, 49), *P. gasteri* (fig. 44), *P. suffulta* (fig. 45), *P. simplex* (fig. 46). The primitive elliptical œcium is retained as far as *P. suffulta*, otherwise the characters run the same course as in the typical lineage, except that *P. simplex* is catagenetic in its length as well as in the size of its aperture.

In the lineage *P. calceata* (figs. 1, 49), *P. crepidaria* (fig. 47), *P. d'orbignyi* (fig. 48), the avicularia tend to take up a definite position proximal and lateral to the aperture, as in the genus *Ichnopora*, which probably arose from this stock. In fact, it is difficult to justify the retention of *P. crepidaria* and *P. d'orbignyi* in one genus rather than the other; and, if it is decided that *Ichnopora* arose from *P. crepidaria*, it would be a simpler course to include this species as well as *P. d'orbignyi* in *Ichnopora*. Again, if some species of *Ichnopora* arose from *P. calceata* and others from *P. d'orbignyi*, it would be necessary to remove both species to *Ichnopora* to prevent that genus being polyphyletic. Until, however, the detailed origin of *Ichnopora* is clear, it is best to keep that genus for those species which exhibit the generic tendencies in a marked degree. The lineage under consideration follows the normal course, except that the primary pelmata move but slightly from the middle line, and the aperture does not alter much in size.

The three lineages already considered are directly to be derived from *P. calceata*. The remaining primitive forms of *Pelmatopora*, though doubtless derived from the same species, or from a form very near it, have no directly connecting forms so far as is at present known, but form three or four isolated lineages. The French species *P. interrupta* (fig. 42), *P. chrysalis*, *P. striata*, form one of these, characterised by a flattish intraterminal front-wall and comparatively large apertures which tend to become more pointed; the length of the œcia remains about constant and the pelmata do not retreat from the middle line.

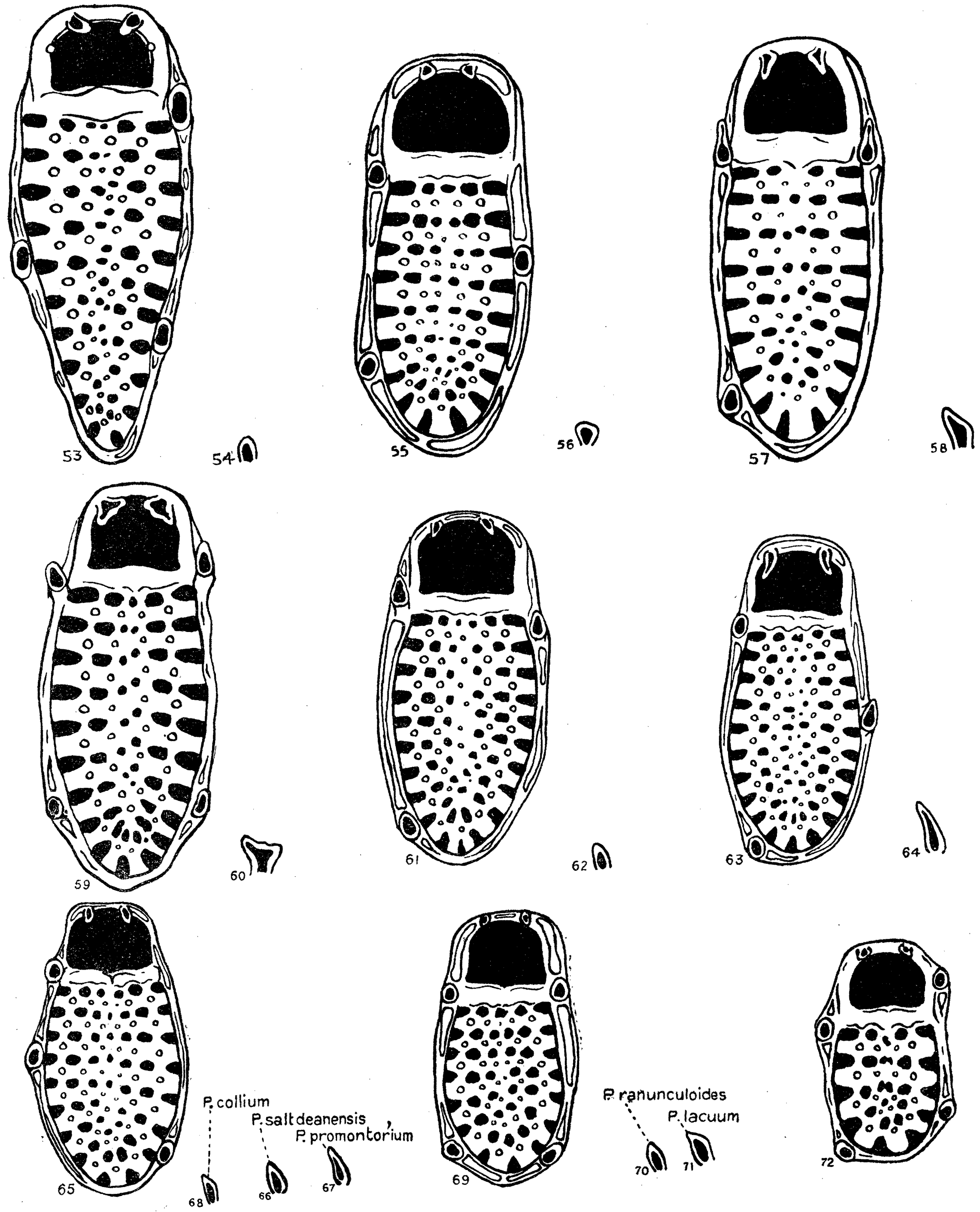
P. pauciclavia (fig. 41), *P. fragilis* are a lineage characterised by very few costæ. *P. quadrata* (fig. 40), *P. filliozâti* are another lineage with very small œcia. *P. insignis* (fig. 39) is an isolated form of large size with pelmata retreating somewhat from the median line and a total absence of secondary interœcial tissue. Finally, *P. fecampensis* (fig. 43) is another isolated form with rather large apertures, showing some affinity with *P. interrupta*.

The relationships of these more primitive *Pelmatopora* may be shown in tabular form as below :—



The remaining species of *Pelmatopora* are those in which secondary tissue entirely obliterates the apertural spines, and the distal pair are replaced by a peculiar pair of avicularia. In all these forms the intraterminal front-wall has reached a high degree of complexity and there are secondary and tertiary pelmata; interœcial secondary tissue is abundant. Hitherto the various forms have been included under the comprehensive name "*Cribrilina gregoryi*, Brydone." Their evolution is primarily concerned with modifications of the distal pair of avicularia which are remarkable for appearing suddenly, apparently not being modifications of pre-existing avicularia or of any other structure. Indeed their claim to be avicularia may be questioned, especially in view of their tendency to bifurcate during phylogeny. But their general appearance is so suggestive of avicularia that, until an alternative explanation is given, it is assumed that they are structures of this nature.

In *P. brydonei*, as we have already seen, they are small, and the apertural spines are often still visible. In *P. quadrivolucris* a second pair replaces the proximal pair of



FIGS. 53–72.—Diagrams of advanced species of *Pelmatopora*, × about 50 diameters, and their distal avicularia still more enlarged.

FIGS. 53, 54.—*Pelmatopora brydonei*, LANG.
55, 56.—*P. marsupitum*, LANG.
57, 58.—*P. somptingensis*, LANG.
59, 60.—*P. palmata*, LANG.
61, 62.—*P. bidens*, LANG.
63, 64.—*P. lancingensis*, LANG.

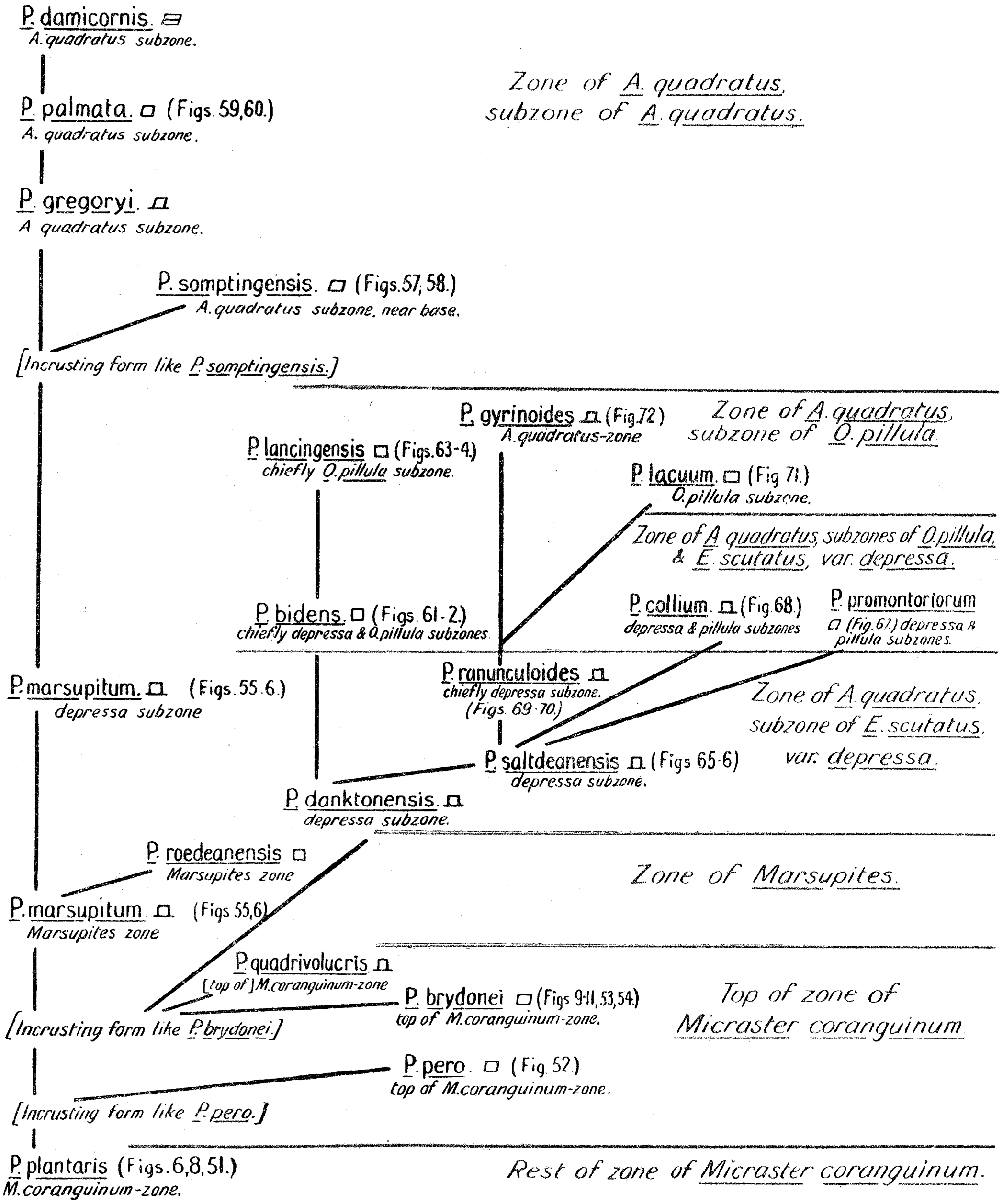
FIGS. 65, 66.—*Pelmatopora saltdeanensis*, LANG.
FIG. 67.—*P. promontoriorum*, LANG.
68.—*P. collium*, LANG.
FIGS. 69, 70.—*P. ranunculoides*, LANG.
FIG. 71.—*P. lacuum*, LANG.
72.—*P. gyrinoides*, LANG.

apertural spines. These two species are the only ones of this series hitherto observed to occur below the zone of *Marsupites.*

Besides the modifications of the distal avicularia the evolution of these advanced forms of *Pelmatopora* is marked by a catagenesis in the size of the œcia and in the number of costæ. It is necessary to assume an incrusting form, otherwise resembling *P. brydonei,* as the ancestor of the incrusting *P. marsupitum* (figs. 55, 56) and its erect unilaminar descendant *P. roedeanensis.* In these the œcia are somewhat smaller than in *P. brydonei* and the distal avicularia stouter. *P. somptingensis* (figs. 57, 58) resembles the last two species, but the avicularia widen distally and tend to bifurcate, while in *P. gregoryi* (incrusting), *P. palmata* (unilaminar) (figs. 59, 60) and *P. damicornis* (erect bilaminar) the distal avicularia are palmate with two distal processes. The six species, then, *P. marsupitum, P. roedeanensis, P. somptingensis, P. gregoryi, P. palmata, P. damicornis* compose a lineage of forms occurring from the *Marsupites*-zone to the top of the *A. quadratus*-zone. Another lineage, *P. danktonensis, P. bidens* (figs. 61, 62), *P. lancingensis* (figs. 63, 64), derived from the same stock as *P. brydonei,* is marked by its somewhat smaller size and the lengthening of the distal avicularia, which tend to bifurcate in *P. bidens*; but in this species the outer horn of each distal avicularium is much more developed than the inner (this is so in a less degree in the last lineage) and in *P. lancingensis* becomes exceedingly long.

A long avicularium is also present in the lineage *P. danktonensis, P. saltdeanensis* (figs. 65, 66), *P. ranunculoides* (figs. 69, 70), *P. gyrinoides* (fig. 72), but its chief characteristic is the decided decrease in the number of costæ correlated with a squatter œcium (that is, shorter compared with its breadth). *P. collium* (fig. 68) is a derivative of *P. saltdeanensis* with still more secondary interœcial tissue; and *P. promontoriorum* (fig. 67) is an erect, unilaminar derivative of *P. saltdeanensis,* as *P. lacuum* (fig. 71) is of *P. ranunculoides.*

The following Table represents the hypothetical relationships of the more advanced species of *Pelmatopora* together with their characteristic horizons :—



6. *The Evolution of Cretaceous Cribrimorph Polyzoa compared with that of Cretaceous Asteroidea.*

It is of interest to compare the evolutionary results obtained in the case of this sub-family of Chalk Polyzoa with those shown by other workers in somewhat similar circumstances. The latest and most comparable work, though covering a wider field,* is that of W. K. Spencer (1913) on the Cretaceous Asteroidea. And he claims similar phenomena of evolution among Palæozoic Starfishes (Spencer, 1916, p. 60)

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* It should be noted, however, that this sub-family of the Pelmatoporinæ is one only of many similar groups of Cretaceous Polyzoa whose evolution runs along essentially similar lines.

agreeing with those tabulated by VAUGHAN (1915, p. 3) with regard to the Carboniferous fauna. Let us consider these general principles first. SPENCER'S first proposition (1916, p. 60), "That the world has been peopled by successive races (or lineages), each of which has gone through a period of rise (elaboration) and fall (regression)," is exactly borne out as far as elaboration (anagenesis) is concerned, but on the whole (though a few cases of catagenesis of individual characters have been mentioned above) extinction inevitably followed excessive elaboration and we have no evidence of regression (catagenesis) in the secretion of calcium carbonate, or in the reduction of the skeleton through resorption. Nor is it easy to place a hypothetical acme at a certain point in skeletal elaboration, and say, "After this, further elaboration was detrimental to the organism." The process was one continuous piling up of skeletal matter, and all the lineages, since they could not circumvent this, were doomed.

SPENCER'S second proposition is "that the early stages of a lineage may be recognised by the fact that the forms are small, comparatively rare and unspecialised. The more mature stages are characterised by large, more specialised forms, which occur in comparative abundance. In the old age of the lineage there are marked loss of ornament and other specialised characters, and the forms are obviously tending to disappear." This, again, is seen to be true of the Cretaceous Cheilostome Polyzoa as a whole, though in some details it is necessary to modify the statement. With regard to size generally speaking, this tends to increase at first in any lineage; but it is impossible to predict whether, ultimately, a given stock may become smaller, as in the lineage *Pelmatopora brydonei* (figs. 53, 54), *P. danktonensis*, *P. saltdeanensis* (figs. 65, 66), *P. ranunculoides* (figs. 69, 70); or to continue into a race of giants like *Batrachopora convexa*, *B. crassa* (fig. 83), *B. ornata*. Again, it is difficult to admit, in the final stages, a loss of ornament. Perhaps it is permissible to differentiate "ornament" from "elaboration." When a surplus of skeletal matter is laid down piece-meal, it results in processes, spines, ridges—"ornament"; when it is poured out in floods, it results in overwhelming structures, in secondary thickenings, secondary apertures, secondary front-wall, which "elaborate" the skeleton while covering up ornamentation. Thus *Batrachopora convexa* is a highly ornamented and fairly elaborate form; *B. ornata* with a well-developed "lamina peristomica" is far more elaborate, though less ornamented.

SPENCER'S third proposition is so obviously true that it need not be laboured. "That in the various lineages there is frequently an assumption of parallel characters which may make individuals of different descents look, at first sight, very similar. Care must be taken consequently in classification to select characters peculiar to the lineage and not characters parallelled in other lineages." The whole tendency of this paper is to show that parallelism of evolution occurs in the characters of the *Pelmatoporinæ* and that the method of formation of the secondary aperture differentiates the various genera; that a similar parallelism occurs within each genus making the diagnostic features of every lineage very difficult to determine.

In his detailed work on Cretaceous Asteroidea (1913, p. 101), SPENCER similarly makes a series of evolutionary propositions. They are :—

(1) "That Cretaceous Asteroidea belong only exceptionally to modern genera. The fauna is Mesozoic and has no general relationship with the Tertiary forms." The fact that fairly complete lineages of Cretaceous Polyzoa, when followed up, lead to such massively elaborated forms that further evolution (without resorption of the skeleton) is hard to imagine, has already forced me to the same conclusion.

(2) "That the starfish may be separated into lineages ('species series') which preserve unbroken continuity during their life-history." This, in Cretaceous Polyzoa, is the theme of the present paper.

(3) "That if the variation of individual characters in a lineage be considered they are (*a*) usually of a continuous type, (*b*) frequently independent of one another." A consideration of the Cretaceous Polyzoan lineages described above, and a glance at the diagrams will verify both these points. The distal pair of avicularia in *Pelmatopora*, however, may be cited as a variation discontinuous in its origin. And the fact that the ancestrœcium (the Cheilostome protœcium, or skeleton of the first-formed individual) of *Sandalopora gallica* shows a well-developed proximal shield suggests that this may have arisen discontinuously from the plain apertural bar of a primitive *Pelmatopora*. That in their evolution the individual characters in a lineage are largely independent of one another is a most important consideration and one which a study of the Pelmatoporinæ emphasises. Thus, to take one case out of many, both the lineages of *Pelmatopora*, the one containing *P. calceata*, *P. solearis*, *P. plantaris*, *P. pero*, *P. brydonei*, etc., and the other *P. gasteri*, *P. suffulta*, *P. simplex*, are characterised by an increased elaboration of the intra-terminal front wall; that is, the pelmata move away from the middle line and secondary pelmata are formed; but, in the first, the aperture tends to increase in size and pass from longer to broader, and in the other it tends to decrease in size and hardly alters its comparative length and breadth.

(4) "That the types of variation which arise in each lineage are predetermined and limited by innate causes." This seems obvious among the Cretaceous Polyzoa. It is quite possible, as has been done, to predict the general course of evolution of a given primitive form. The list of characters with their usual evolution on pp. 196–198 gives data for such predictions in the Pelmatoporinæ.

Of the remaining two propositions, one concerns the effect of environment on the course of variation in such a case as that discussed on p. 205 of the Maastricht, Royan, Rügen, and Meudon species of *Batrachopora*, while the other is more conveniently dealt with in the stratigraphical considerations further on.

A further evolutionary point touched on by SPENCER is that "Elaboration is often Periodic" (1913, p. 156). Unfortunately the skeletons of Polyzoa do not lend themselves to record ontogenetic changes as readily as the serially constructed shells of Ammonites (*e.g.*, *Sonninia*, see BUCKMAN, 1892, pp. 314, 315) and Corals (see LANG, 1909, p. 289), when the ontogeny of the ornament often indicates at least a phyletic periodicity. The ornament of Polyzoa, as has been suggested above, presents a somewhat different phenomenon from that of the costæ and tubercles of Molluscs and costal ornament of Corals. Yet periodicity in evolution is, at least, hinted at in one or or two instances. It is assumed that the Cheilostomes arose from the Cyclostome Polyzoa. Now, the typical shape of the Cyclostome œcium is tubular—that of the Cheilostome box-like; the "intra-terminal front-wall" of the Cheilostome (the lid of the box), with its trapdoor-like opening, or orifice, represents a covering of the mouth of the tube of the Cyclostome. This covering, chitinous in the most primitive Membranimorphs, becomes gradually calcified during evolution, and the tendency of the Cheilostomes is to revert to a tubular-shaped œcium. Without considering the relation of the Cribrimorph front-wall to the chitinous front-wall of Membranimorphs (see HARMER, 1901, p. 13), it is clear that in the Cribrimorphs, as shown by comparing the primitive forms of a lineage with the later forms, *e.g.*, *Pelmatopora calceata* with *P. brydonei*, as well as the ancestrœcium (of, say, *P. simplex*) with the ephebastic stages, the œcial shape tends to pass from a more tubular to a more box-like form. Finally, the advent of a tubular secondary aperture and its great development, causing the original front-wall to fade away into comparative insignificance, gives to the œcium a generally tubular aspect. Thus, evolutionary periodicity is shown in the œcial shape—tubular in the Cyclostome, box-like in the primitive Membranimorph, tubular in the primitive Cribrimorph, box-like in the more advanced Cribrimorph, and tubular again in the final "Tubulimorph," or Cribrimorph, like *Pachydera*, with a tubular secondary aperture.

Another case of periodicity is seen in the history of the intra-terminal front-wall. This (if we are right in supposing that the space it covers in Membranimorphs is the homologue of the tubular mouth of Cyclostomes) consists of the periodical roofing-over of a previous space by an ultimately calcareous covering. It happens in Cyclostomes as an individual lapse, when œcia occasionally cover their apertures with a calcareous closure. It is normal in Membranimorphs whose intra-terminal front-wall is a plain chitinous covering, which ultimately becomes more or less calcified. In primitive Cribrimorphs another intra-terminal front-wall, consisting of calcareous spines, is built over-arching the first. The more advanced Cribrimorphs give rise to Steginomorphs which produce a third front-wall over-arching the subjacent ones. Thus, to take examples from the sub-family under consideration, *Ichnopora vestigium* (figs. 24–26, 74) arose, presumably, from a Membranimorph, and its Cribrimorph front-wall over-arched the original chitinous front-wall of its ancestor; *I. vestigium* gave rise to *I. denticulata* (figs. 30–32, 75) which has a lamina peristomica forming a partial secondary (rather tertiary) front-wall overlying the Cribrimorph front-wall. The lineages *Batrachopora ovalis*, *B. convexa*, *B. crassa*, *B. ornata*, and *B. perforata*, *B. ranunculus*, *B. hyla*, furnish forms with only the Cribrimorph front-wall in the primitive members, and a lamina peristomica, forming a tertiary front-wall, in *B. ornata* and, probably, in *B. hyla*.

A third way in which the evolution of Cretaceous Cribrimorphs may be regarded as periodic is seen in periods of plasticity and abundance of species and individuals within a lineage. This, again, is parallelled by SPENCER among Cretaceous Starfishes (SPENCER, 1913, p. 155). The evolution of *Pelmatopora* has two periods; in the first, the evolutionary effort is, so to speak, applied to the elaboration of the intraterminal front-wall, and many series run through their evolution ending with such forms as *P. pero* (fig. 52) and *P. simplex* (fig. 46), with primary pelmata retreating far from the middle line and with secondary and even tertiary pelmata present. When this elaboration is beginning, *i.e.*, in the hemera of *M. cortestudinarium* and early in that of *M. coranguinum*, both species and individuals are abundant. One of these lineages, that of which *P. pero* was the last term considered, persisted into *quadratus*-times, and meanwhile elaborated the distal pair of avicularia which had appeared as a new feature in *P. brydonei*, a species co-existent with *P. pero*. In the middle of this second period of elaboration, *i.e.*, in the hemeræ of *Echinocorys scutatus* var. *depressa* and of *Offaster pillula*, forms of *Pelmatopora* are again very abundant both in species and in individuals. The genus *Pelmatopora*, then, may be said to exhibit periodic outbursts of activity during its evolution.

C. THE STRATIGRAPHIC CRITERION OF RELATIONSHIP.

The criteria of relationship discussed in the preceding section have been mainly morphological; the different species and genera of Pelmatoporinæ have been compared with regard to their form, and other evidence has been brought in but incidentally. It is well, before dismissing the group, to consider more particularly the stratigraphical distribution of the forms, and afterwards the evidence that astogeny brings to bear on their relationships.

The earliest known Pelmatoporinæ are *Sandalopora lavardinensis* and *S. gallica* from the Turonian of Lavardin, S.E. of Montoire, Loir-et-Cher, France; but *Pelmatopora calceata*, the most primitive form, comes from the Lower Senonian of Chatham. It is probable, then, that *Pelmatopora calceata* extends below the Senonian. *Pelmatopora* ranges as high as the top of the *quadratus*-zone and its two evolutionary outbursts took place at the junction of the *M. cortestudinarium*- and *M. coranguinum*-zones, and in the lower part of the *A. quadratus*-zone, *i.e.*, in the *depressa*- and *pillula*-sub-zones. *Sandalopora* (except for the Turonian species mentioned) and *Ichnopora* are confined to the *M. cor-testudinarium*- and *M. coranguinum*-zones. *Decurtaria* and *Murinopsia* occur in the *quadratus*- and *mucronatus*-zones and *Batrachopora* in the *mucronatus*-zone only; while *Pachydera* is found in the *mucronatus*-zone and in the Danian.

The following list mentions all the known undoubted Pelmatoporinæ, with their typical horizons. In some cases a given form may range above or below the horizon given, but in these (which are few) the erring specimens are comparatively rare :—

Danian :

Pachydera densa, Lang, 1916, p. 112 ; Faxe.

Senonian, *mucronatus*-zone :

P. grandis, Marsson, 1887, p. 100, Plate 10, fig. 14 ; Rügen.
Decurtaria cornuta (Beissel), 1865, p. 58, Plate 7, figs. 77–81 ; Maastricht (see also below).
Batrachopora ornata (Goldfuss), 1826, p. 26, Plate 9, fig. 1 ; Maastricht.
B. hyla, Lang, 1916, pp. 111, 112 ; Maastricht.
B. coaxans, Lang, 1916, p. 111 ; Rügen.
B. ranunculus, Lang, 1916, p. 111 ; Rügen.
B. crassa, Lang, 1916, pp. 110, 111 ; Rügen.
B. perforata (Marsson), 1887, p. 98, Plate 10, fig. 11 ; Rügen.
B. royanensis, Lang, 1916, pp. 110, 111 ; Royan.
B. ovalis (d'Orbigny), 1852, Plate 719, figs. 13–16, 1853, p. 488 ; Royan.
B. convexa (d'Orbigny), 1852, Plate 720, figs. 1–3, 1853, p. 492 ; Meudon.
Murinopsia francqana (d'Orbigny), 1852, Plate 734, figs. 6–8, 1853, p. 497 ; Meudon.

Senonian, *quadratus*-zone, sub-zone not specified :

Decurtaria cornuta (Beissel), 1865, p. 58, Plate 7, figs. 77–81 ; Aix-la-Chapelle district (see also above).
Murinopsia galeata (Beissel), 1865, p. 55, Plate 6, figs. 70–75, Plate 7, fig. 76 ; Aix-la-Chapelle district.
Pelmatopora damicornis, Lang, 1916, pp. 103, 107 ; Seaford, Sussex.
P. simplex, Lang, 1916, pp. 102, 105 ; Newhaven, Sussex.

Senonian *quadratus*-zone, *quadratus*-sub-zone :

P. palmata, Lang, 1916, pp. 103, 107 ; Winchester, Hants.
P. gregoryi (Brydone), 1906, p. 300, text-fig. 13 on p. 300 ; Upham, Hants.
P. somptingensis, Lang, 1916, pp. 103, 106 ; Sompting, Sussex.

Senonian, *quadratus*-zone, *pillula*-sub-zone :

P. lacuum, Lang, 1916, pp. 103, 106 ; North Lancing, Sussex.
P. lancingensis, Lang, 1916, pp. 103, 106 ; North Lancing, Sussex.

Senonian, *quadratus*-zone, *pillula*- and *depressa*-sub-zones :

P. promontoriorum, Lang, 1916, pp. 103, 106 ; North Lancing, Sussex.
P. collium, Lang, 1916, pp. 103, 106 ; North Lancing, Sussex.
P. bidens, Lang, 1916, pp. 103, 105 ; North Lancing, Sussex.

Senonian, *quadratus*-zone, *depressa*-sub-zone :

P. ranunculoides, Lang, 1916, pp. 103, 106 ; E. of Brighton, Sussex.
P. saltdeanensis, Lang, 1916, pp. 103, 106 ; E. of Brighton, Sussex.
P. danktonensis, Lang, 1916, pp. 103, 106 ; Sompting, Sussex.

Senonian, *Marsupites*-zone:

P. marsupitum, Lang, 1916, pp. 103, 105; Brighton, Sussex.
P. roedeanensis, Lang, 1916, pp. 103, 105; Brighton, Sussex.

Senonian, extreme top of *coranguinum*-zone:

P. quadrivolucris, Lang, 1916, pp. 102, 105; West Horseley, Surrey (exact horizon assumed).
P. brydonei, Lang, 1916, pp. 103, 105; Epsom, Surrey.
P. pero, Lang, 1916, pp. 102, 105; Epsom, Surrey.

Senonian, middle and lower parts of *coranguinum*-zone:

Ichnopora denticulata (Brydone), 1910, p. 481, Plate 36, figs. 1–3; Kent.
I. leporina (d'Orbigny), 1851, Plate 686, figs. 13–16, 1852, p. 230; Villavard, France (Emscherian).
I. filiformis (d'Orbigny), 1852, p. 232, Plate 700, figs. 13–15; Fécamp, France (Emscherian).
Sandalopora socculus, Lang, 1916, p. 108; Gillingham, Kent.
Pelmatopora plantaris, Lang, 1916, pp. 102, 105; Alton, Hants.
P. gasteri, Lang, 1916, pp. 102, 105; Cuckmere Haven, Sussex.
P. suffulta (Brydone), 1913, p. 436, Plate 14, fig. 4; Gravesend, Kent.
P. quadrata, Lang, 1916, pp. 102, 104; E. of Cuckmere Haven, Sussex.
P. fragilis (d'Orbigny), 1852, Plate 717, figs. 8–11, 1853, p. 480; Fécamp, France (Emscherian).
P. filliozati, Lang, 1916, pp. 102, 105; Fécamp, France (Emscherian).
P. crepidaria, Lang, 1916, pp. 102, 103; Wooburn Green, Bucks.

Senonian, lower part of *coranguinum*-zone, and *cortestudinarium*-zone:

Ichnopora asella, Lang, 1916, pp. 109, 110; St. Avertin, France (Coniacian).
I. cunicula, Lang, 1916, pp. 109, 110; La Ribochère, France (Coniacian).
I. cavia, Lang, 1916, pp. 109, 110; St. Avertin, France (Coniacian).
I. amica, Lang, 1916, pp. 109, 110; Fécamp, France (Coniacian).
I. vestigium, Lang, 1916, p. 109; Kent.
I. campestris, Lang, 1916, p. 109; Fécamp, France (Coniacian).
I. socia, Lang, 1916, p. 109; Fécamp, France (Coniacian).
Sandalopora caligata, Lang, 1916, p. 108; Kent.
Pelmatopora fecampensis, Lang, 1916, pp. 102, 105; Fécamp, France (Coniacian).
P. insignis (Canu), 1911, p. 252, Plate 6, figs. 7–10; Roca, Argentine (Rocanean, exact horizon assumed).
P. d'orbignyi, Lang, 1916, pp. 102, 104; St. Avertin, France (Coniacian).
P. striata (d'Orbigny), 1851, Plate 686, figs. 9–12, 1852, p. 229; France (Coniacian).

P. chrysalis (d'Orbigny), 1851, Plate 686, figs. 6–8, 1852, p. 228; France (exact horizon assumed).
P. interrupta (d'Orbigny), 1852, Plate 719, figs. 5–8, 1853, p. 478; France. (Coniacian).
P. solearis, Lang, 1916, pp. 102, 103; S. England.

Senonian, *cortestudinarium*-zone:

Sandalopora soccata, Lang, 1916, p. 108; Cuckmere Haven, Sussex.
S. supplosa, Lang, 1916, p. 108; Cuckmere Haven, Sussex.
Pelmatopora calceata, Lang, 1916, pp. 102, 103; Chatham, Kent (exact horizon assumed).

Turonian:

Sandalopora lavardinensis, Lang, 1916, p. 108; Lavardin, France.
S. gallica, Lang, 1916, p. 108; Lavardin, France.

Now, it is evident that the stratigraphical distribution of the forms can be used only negatively as a criterion of their relationships. For instance, if form A occurs only at a higher horizon than form B, it cannot be the ancestor of that form. If, on the other hand, the stratigraphical distribution coincides with the supposed evolution of the forms, that is to say, if the supposed later-developed species occur at higher horizons than the supposed more primitive species, the evidence of their distribution in time admits supposed relationships as possible, but does not, of course, certify them. And the latter case is seen on the whole to be true of the Pelmatoporinæ. The advanced genera *Pachydera*, *Decurtaria*, *Batrachopora*, *Murinopsia*, and the advanced species of *Pelmatopora* are found in the Danian and Upper Senonian, while *Ichnopora*, *Sandalopora* and more primitive *Pelmatopora* are confined to the Lower Senonian. And the stratigraphical distribution of the species within each genus shows, on the whole, a similar correspondence with their supposed evolution. The exceptional case of the two Turonian species of *Sandalopora* has already been discussed.

It is seen that there are faunal breaks, one high in the zone of *Micraster coranguinum* and the other between the *quadratus*- and *mucronatus*-zones. Below the middle of the *coranguinum*-zone we have the genera *Sandalopora* and *Ichnopora* and forms of *Pelmatopora* without the distal avicularia. Above the middle of the *coranguinum*-zone and below the *mucronatus*-zone *Sandalopora* and *Ichnopora* are absent, and the forms of *Pelmatopora* without the distal avicularia are rare; on the other hand *Pelmatopora* with the distal avicularia is abundant and *Murinopsia* and *Decurtaria* occur (probably in the highest part only). Above the *quadratus*-zone *Pelmatopora* is absent, and the Pelmatoporinæ are represented by *Batrachopora* and *Pachydera* as well as *Murinopsia* and *Decurtaria*.

SPENCER also found a low-, mid-, and high-zonal fauna among the Cretaceous Asteroids; but it is interesting to observe that the line dividing his low- and midzonal forms was drawn at three-quarters way down the zone of *M. coranguinum*, and his higher line between the sub-zones of *Offaster pillula* and of *Actinocamax quadratus* in the *quadratus*-zone; in each case a little lower than the Polyzoan faunal lines. The zone *Micraster coranguinum* is very barren with regard to Polyzoa between a point a little below half-way and the extreme top. So the faunal break occurs at this barren band and cannot be more accurately placed.

D. The Astogenetic Criterion of Relationship.

Besides the evidence afforded by morphology and stratigraphic position of the various forms, a certain amount can be gathered from a study of growth-stages. The law of recapitulation postulates that ontogeny repeats phylogeny, and Cumings (1904, p. 50) has shown that astogeny, or the development of the colony, may be regarded in Polyzoa as equivalent to ontogeny. Ontogeny in Polyzoa can only be studied by seeing the growth of individual œcia, and is not, consequently, a suitable method, though not without some value for elucidating their phylogeny.

Unfortunately, specimens exhibiting astogeny at all completely are comparatively rare. Even when the ancestrœcium is present, it is not always well enough preserved to show its detailed characters. Some of its characters have been made out, however, in *Pelmatopora simplex*, *P. saltdeanensis*, and *P. somptingensis*; and neanastic stages are exhibited in specimens of *P. calceata*, *P. crepidaria*, *P. solearis*, *P. insignis*, *P. plantaris*, and *Sandalopora gallica*.

It has been shown that *Pelmatopora calceata*, *P. solearis*, and *P. plantaris* are the first three terms of a long lineage of which *P. somptingensis* is a later term; and the trend of development of each character in this lineage was that set forth in detail on pp. 6–9. The growth-stages of any member of this series should conform with the series as a whole. Let us see how far this is the case. The lettering of each character corresponds with that in the general scheme; and a character that does not show astogenetic change is ignored.

P. calceata.—In passing from neanastic to ephebastic stages, (*b*) the size of œcium increases, and (*f*) the number of costæ increases.

P. solearis.—In passing from neanastic to ephebastic stages, (*b*) the size of œcium increases, (*c*) the shape of œcium becomes less elliptical and more parallel-sided, (*d*) the extraterminal front-wall becomes more obliterated with secondary tissue, (*e*) the intraterminal front-wall becomes flatter at the median area of fusion (correlated with *g*), (*g*) the pelmata tend to move away from the middle line, and (*f*) the number of costæ increases.

P. plantaris.—In passing from neanastic to ephebastic stages, (*b*) the size of the œcium increases, (*c*) the shape of œcium becomes less elliptical and more parallel-sided, (*d*) the extraterminal front-wall becomes obliterated by secondary tissue, (*e*) the intraterminal front-wall loses its vaulting, both because of the upgrowth of interœcial secondary tissue and of the retreat of the primary pelmata from the mid-line, (*f*) the number of costæ increases, (*g*) the primary pelmata move away from the mid-line and secondary and even tertiary pelmata are developed, (*i*) apertural spines are enlarged, (*j*) the shape of the aperture changes from slightly longer than broad to about as long as broad, and (*l*) the avicularia become larger. In its early neanastic stages, *P. plantaris* has, generally, the characters of an ephebastic *P. calceata* (which is, therefore, the *morphic prefiguration* of these stages; see BUCKMAN, 1892, p. 315), and in its later neanastic stages the characters of *P. solearis* with a more advanced intraterminal front-wall.

P. somptingensis.—A specimen (British Museum, D. 28747) shows the ancestrœcium though poorly preserved. In passing from the ancestrœcium to the neanastic œcia, (*b*) the size of the œcium increases, (*c*) the shape of the œcium passes from more parallel-sided to more elliptical (compare the change later), (*e*) the intraterminal front-wall from vaulted becomes flat-topped (correlated with *g*), (*f*) the number of costæ increases, (*g*) the pelmata retreat further from the middle line, and secondary and possibly tertiary pelmata (at any rate tertiary perforations in the middle line of fusion) occur ; in the ancestrœcium the primary pelmata are not far removed from the median area of fusion, and a line of perforations is already present. *i.e.*, the ancestrœcium, as far as this character is concerned (and, in fact, generally, though not in one or two characters, such as the shape of the œcium, which is more primitive, and the absence of apertural spines, which is more advanced), is the *morphic representation* (BUCKMAN, 1892, p. 315) of an ephebastic *P. solearis* further back in its lineage. It is interesting to note that, apparently, the distal avicularia are already present in the ancestrœcium of *P. somptingensis*, and the apertural spines already swamped by secondary tissue.

In passing from the neanastic to the ephebastic stages, there is (*b*) increase in the size of the œcium ; (*c*) a change of shape from more elliptical to more parallel-sided, from comparatively shorter to comparatively longer ; (*d*) the extraterminal front-wall is blotted out by secondary tissue ; (*f*) the number of costæ increases ; (*g*) tertiary pelmata are distinctly developed ; (*k*) the size of the aperture is comparatively smaller ; (*l*) the sporadic avicularia increase in size, and the distal avicularia are comparatively larger and more bifurcate. Except with regard to the distal avicularia and the absence of apertural spines, the neanastic stages of *P. somptingensis* are, on the whole, the morphic representation of an ephebastic *P. plantaris.*

The lineage of *P. somptingensis* is somewhat catagenetic with regard to size after the term *P. brydonei ;* but this is not, apparently, reflected in the astogeny.

Pelmatopora crepidaria lies on a lineage between *P. calceata* and *P. d'orbignyi.* Some individuals that are hardly ephebastic are (*b*) smaller and (*f*) have fewer costæ than decidedly ephebastic individuals.

Pelmatopora insignis is an isolated form with no very near affinities. Passing from less ephebastic to more ephebastic individuals, it shows (*b*) increase in size of œcium, (*f*) increase in number of costæ, (*g*) an advance in complexity of intraterminal front-wall, and (*l*) an increase in the size of the avicularia.

Pelmatopora simplex is the end of a lineage with *P. suffulta* as its preceding term, but is catagenetic from this form in (*b*), the size of the œcium, and from *P. gasteri* in (*k*), the size of the aperture compared with that of the intraterminal front-wall. In passing from the ancestrœcium to the neanastic stages, (*b*) the œcium increases in size (the œcium directly following the ancestrœcium, however, is slightly smaller than the ancestrœcium), (*c*) the œcium becomes more elliptical in shape, (*e*) the intraterminal front-wall becomes a little flatter, (*g*) the primary pelmata retreat from rather near to the middle line (there is a row of secondary perforations in the median area of fusion of the ancestrœcium) to far from it with secondary and tertiary pelmata, (*k*) the aperture decreases in comparative size.

In passing from the neanastic to the ephebastic stages, there is seen to be (*b*) an increase in size, (*d*) rather more secondary tissue, (*e*) a somewhat greater flattening of the intraterminal front-wall, (*f*) an increase in the number of costæ, and (*l*) an increase in the size of the avicularia. The phylogenetic catagenesis in size does not appear to be reflected in the astogeny, and if that of the size of the aperture is expressed, it occurs between the ancestrœcium and the neanastic stages.

P. saltdeanensis belongs to a lineage characterised by catagenesis in the number of costæ and in the length compared with the breadth of the œcium, as well as in its actual size. In passing from the ancestrœcium to the neanastic stages, the following points are seen :—(*b*) the size of the œcium increases slightly; (*c*) its relative breadth increases; (*d*) there is slightly more secondary interœcial tissue; (*e*) the intraterminal front-wall is somewhat flatter; (*f*) the number of costæ increases; (*g*) there are secondary pelmata and tertiary perforations of the median line of fusion in the ancestrœcium, and hardly more than this in the early neanastic stages; (*i*) both ancestrœcium and neanœcia have apertural spines and no distal avicularia (cf. *P. somptingensis*).

The passage from the neanœcia to the ephebœcia is marked (*b*) by considerable increase in size, by (*d*) more secondary tissue, (*e*) greater flatness of the intraterminal front-wall, (*f*) increase in number of costæ, (*g*) slight further retreat of pelmata, (*i*) apertural spines are swamped in secondary tissue and distal pair replaced by avicularia, and (*j*) aperture becomes comparatively broader. The catagenesis of the size of the œcium and the number of costæ is not reflected in the astogeny, but the relative shortening of the œcia is shown between the ancestrœcium and the neanœcia.

Sandalopora gallica.—The most interesting feature in the ancestrœcium of *S. gallica* is the process of the apertural bar, which is as complete and comparatively large as in the ephebastic œcia. Otherwise the chief changes from the ancestrœcium to the neanœcia, and from these again to the ephebœcia, are (*b*) increase of size of the œcium, (*d*) increase in the amount of secondary tissue, and (*f*) increase in number of costæ.

On the whole, then, the evidence of astogeny concerning the relationships of the various forms, as far as it goes, bears out the results of morphological comparison and of stratigraphical distribution.

E. Conclusion.

The conclusions based on the stratigraphical distribution and astogenetic development of the different forms are consistent with those deduced from their detailed morphological examination; they confirm the proposition that the Pelmatoporinæ embrace a number of allied species that can be arranged in lineages of similar, but gradually changing forms, and that these lineages can be grouped into genera according to developmental differences. That is, the Pelmatoporinæ form a natural group, which contains earlier and simpler forms that may be seen to pass, as a rule through continuous gradations, to species that appear later in time and are more specialised in structure. Fundamentally, the specialisation consists in laying down more Calcium Carbonate along definite tracts. This results in a parallelism in the evolution of each lineage, tending to produce homœomorphic forms, and suggesting a predisposition in the parental stock to evolve along determined lines; but the distinguishing marks of each lineage are to be seen in the concentration of effort on certain points in the building of a secondary skeleton as well as in the method and details of architecture. Excessive elaboration with consequent loss of ornament was a common, if not invariable, prelude to extinction. It follows that Tertiary and Recent Cribrimorph genera must be independent developments from less specialised forms. Finally, both in structure of individuals and in such points as plasticity and multiplication of species, the evolution shows a periodic tendency.

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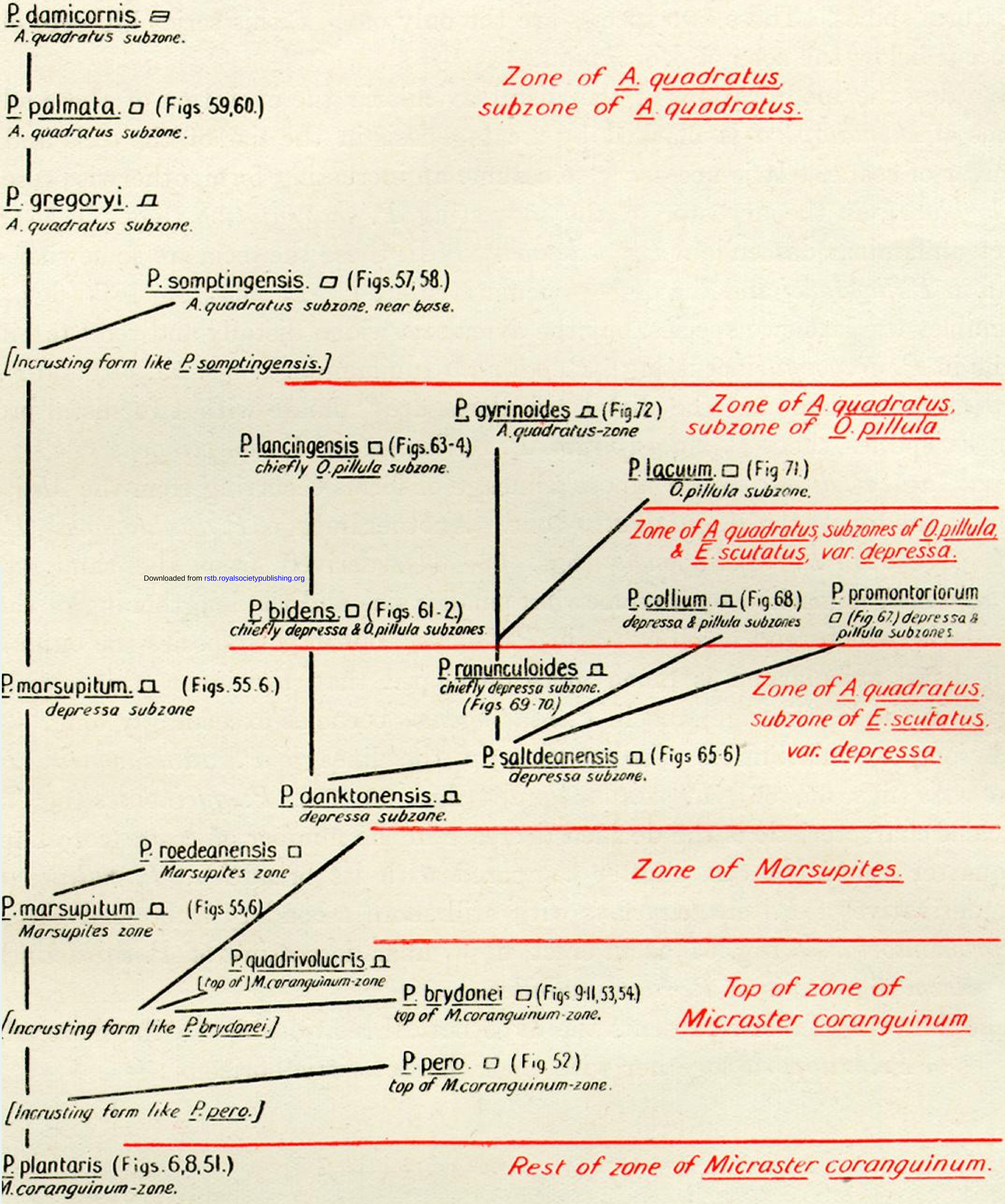

. The Evolution of Cretaceous Cribrimorph Polyzoa compared with that of Cretaceous Asteroidea.