On the Morphology of the Cheilostomata.

By

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With Plates 15—18.

THE observations on which the present paper is based were commenced with the examination of a Flustra-like Cheilostome, found at Port Jackson by Mr. T. Whitelegge, who sent it to me for description, believing it to belong to a new genus. Although exhibiting several remarkable features, I think it may be placed in Euthyris, Hincks, and I propose for it the name E. clathrata, in allusion to the bars which support its "frontal wall." The species possesses a large "compensation-sac," a name which is due to Jullien (1888, 1), although the structure had to some extent been described by Busk and Waters. Jullien's results have usually been discredited by later writers. The study of a number of Cheilostomatous genera has, however, not only led me to confirm the accuracy of Jullien's statements, but has resulted in various conclusions which I believe to be of importance for the proper understanding of the Cheilostomata. A summary of my principal results has been communicated to the Cambridge Philosophical Society (1901).

The present paper is divided into the following parts:

I. Methods employed.

II. List of the species specially studied.

III. Description of Euthyris clathrata, n. sp., of E. obtecta, Hincks, and of Euthyroides episcopalis, n. gen.
IV. The morphology of the compensation-sac and of the operculum.
A. Flustrina.
B. Cribrilinidæ.
C. Lepralioid genera.
D. Microporelloid genera.
E. Microporoid genera.
V. The primary zoœcium or ancestrula.
VI. Classification of the Cheilostomata.
VII. Summary.
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I. Methods employed.

The choice of species for investigation has been primarily dependent on the material available for the purpose in the collection of the University Museum of Zoology at Cambridge. Spirit material has almost exclusively been used, and I have in the main selected species in which the calcareous matter was not developed to so great an extent as to destroy the transparency of the object. The growing edges of healthy colonies have furnished the most satisfactory results. The material was in almost all cases stained, without decalcification, in diluted borax carmine for a prolonged period (five to seven days, or even more). After being placed in absolute alcohol containing picric acid, the fragments were mounted whole in Canada balsam.

All my more recent preparations have been mounted by a method to which my attention was called by Mr. H. D. Geldart, of Norwich. This consists in transferring the specimens directly from absolute alcohol to a solution of dried Canada balsam in absolute alcohol. In preparing this solution, the milky mixture which is at first produced becomes a

complete solution in the course of a few days, particularly if the bottle be left on the top of a water-bath at about 60° C. The cloudiness which appears on first mounting a preparation soon disappears from a slide left on the water-bath. This method cannot be too strongly recommended for certain Polyzoa, particularly for the more delicate Ctenostome genera, which are distorted almost beyond recognition by the use of oil of cloves.

In the case of some of the more densely calcified species I have found great advantages in the use of the method recommended in my paper on Steganoporella (1900, p. 240) of removing the basal wall, by means of a scalpel, from stained colonies (not decalcified) embedded in paraffin. I have also made use of thin slices, cut by hand, of uncalcified material embedded in paraffin. I am convinced of the great importance of studying the Cheilostomata in uncalcified Canada balsam preparations. Most of my slides have been examined with a binocular microscope and a quarter-inch objective.

II. List of the Species specially studied.

1. Euthyris clathrata, n. sp. . .	Port Jackson.
2. „ obtecta, Hincks . .	Torres Straits.
3. Euthyroides episcopalis, Busk (n. gen.)	Victoria.
4. Flustra pisciformis, Busk . .	Bass's Strait (Challenger Coll.).
5. „ papyrea, Pall. . . .	Naples.
6. „ cribriformis, Busk . .	Singapore.
7. Farciminaria hexagona, Busk .	Amboina (Challenger Coll.).
8. Dimetopia spicata, Busk . . .	Victoria.
9. Bicellaria grandis, Busk, var. producta, MacGillivray	Victoria.
10. Bugula neritina, L. . . .	Naples.
11. Membraniporella nitida, Johnst. .	S. Devon.
12. Cribrilina philomela, Busk . .	Marion Is. (Challenger Coll.).
13. „ radiata, Moll . . .	Naples.
14. Umbonula verrucosa, Esper . .	S. Devon.
15. „ pavonella, Alder . .	North Sea.
16. Lepralia pallasiana, Moll . .	Naples.

17. Lepralia dorsiporosa, Busk . .	Torres Straits.
18. „ sincera, Smitt . . .	Davis Straits.
19. „ haddoni, n. sp. . . .	Torres Straits.
20. Schizoporella linearis, Hassall .	Naples.
21. „ sanguinea, Norm. .	Naples.
22. „ australis, Haswell .	Torres Straits.
23. Urceolipora nana, MacGill. (= Calymmophora lucida, Busk) .	Victoria.
24. Smittia trispinosa, Johnst., var. arborea, Levins. . .	Greenland.
25. „ reticulata, J. MacGillivray	Naples.
26. Catenaria lafontii, Aud. . . .	Naples.
27. Vittaticella cornuta, Busk . .	Victoria.
28. Catenicella alata, Wyv. Thoms. .	Victoria.
29. „ plagiostoma, Busk, var. setigera, MacGill. .	Victoria.
30. „ hastata, Busk . .	Victoria (Challenger Coll.).
31. „ lorica, Busk . .	Victoria.
32. „ wilsoni, MacGillivray .	Victoria.
33. Calwellia gracilis, Maplestone .	Victoria.
34. „ (Onchopora) sinclairii, Busk	S. of Kerguelen Is. (Challenger Coll., Stat. 153).
35. „ (Urceolipora) dentata, MacGillivray . . .	Victoria.
36. Ichthyaria oculata, Busk . .	S.E. of Buenos Aires (Challenger Coll., Stat. 320).
37. Onchoporella bombycina, Busk (not Ell. and Sol.)	New Zealand.
38. Microporella malusii, Aud. . .	Naples.
39. „ ciliata, Pall. . .	Naples.
40. Micropora, sp.	Torres Straits.
41. Steganoporella alveolata, Harmer .	Torres Straits.

III. Euthyris, Hincks, and Euthyroides, n. gen.

Euthyris clathrata, n. sp. Pl. 16, figs. 18—31.

Zoarium Flustrine in habit, of stiff, corneous texture, composed of narrow, parallel-sided, frequently bifurcating branches, with truncated ends. Zoœcia opening on one surface only, the orifices arranged with great regularity in

oblique rows passing entirely across the branch in two intersecting directions. Orifices apparently connected by a continuous, brown, transparent epitheca, a short distance below which the frontal surface of each zoœcium is strengthened by a system of irregular calcareous bars, which tend to radiate from a point in the middle of the base-line of the operculum towards the proximal and lateral sides of the zoœcium. Basal side of the branch similarly covered by an epitheca, which each zoœcium reaches along a longitudinal line narrower and shorter than itself. Opercula large, dimorphic, the ordinary form about as long as broad (250 to 270 μ), the others with a broader base (290 to 320 μ). Both kinds of opercula are strengthened by a conspicuous Ω-shaped sclerite. The distal margin of the vestibule is provided with a chitinous lip, which is overlapped during retraction by the large lateral flanges of the operculum. Ovicells not found, and probably absent.

The material was discovered by Mr. T. Whitelegge under rock ledges, at low-tide line, Watson's Bay, Port Jackson, and in Middle Harbour, Port Jackson. Although part was in spirit, its condition was not sufficiently good to make a complete anatomical investigation possible.

The genus Euthyris was founded by Hincks[1] for a new species, E. obtecta, from North Australia. The generic name, introduced "to suggest the idea of higher structure" in the operculum, is particularly appropriate to E. clathrata, in which the operculum is specially complicated. The two

[1] 'Ann. Mag. Nat. Hist.' (5), x, 1882, p. 164. In 1871 Quenstedt ('Petrefaktenkunde Deutschlands,' Abth. I, Bd. ii, p. 442), in discussing the structure of a Brachiopod, used the following words:—"Man könnte sie daher wohl Euthyris aber nicht Athyris nennen." I have not been able to ascertain that Quenstedt made any further use of the word Euthyris, and he does not even refer the species he is discussing to that genus. It appears, therefore, that he was not in reality proposing a new genus (and he certainly did not define it), but was merely making a verbal criticism of the name Athyris. Although Euthyris (Quenstedt) is mentioned by Zittel in his well-known 'Handbuch d. Palæont.' (i, p. 684) as a synonym of Spirigera, it does not seem to me that it has any valid claim to recognition.

species agree in their habit, in their dimorphic opercula (probably associated with the absence of ovicells), and in the highly developed chitinous epitheca which overspreads the entire zoarium. E. clathrata differs from E. obtecta in having its frontal calcareous wall composed of irregular bars, instead of a simple, perforated, calcareous film, and in the fact that there is no large space between the frontal epitheca and the calcareous walls.

I feel doubtful whether Euthyris woosteri, MacGillivray,[1] is rightly referred to this genus; but, on the other hand, Carbasea moseleyi, Busk (1884, p. 56), perhaps belongs to it.

The largest colony of E. clathrata measures about 18·5 cm. or 7¼ inches in length. The branches are 2 to 4 mm. wide, averaging about 3 mm. near their free ends, but lessening towards the base of the colony, which appears to have been attached by a narrow base without rootlets. A branch 4 mm. wide has about thirteen orifices in each oblique row. The colour is brown in the older parts, yellowish near the ends of the branches. The zoarium frequently bifurcates, showing some tendency to form a unilateral cyme. The terminal divisions (Pl. 16, fig. 18) may reach a length of 3·5 cm. without bifurcating, but the ordinary length of the divisions is not more than 1·5 cm. The frontal surface is somewhat convex, the opposite surface flatter. The calcareous walls of the zoœcia are arranged as follows:—The lateral and terminal walls are everywhere complete, and are perforated by numerous pores. At the proximal end (fig. 22) the two lateral walls pass continuously into one another in a regular curve, which forms the base of the zoœcium, and is placed some distance within the basal epitheca (fig. 26, *b. ep.*). At the distal end the lateral walls approach one another basally, and are separately inserted into the basal epitheca, forming a linear mark (figs. 22, 27) constantly shorter than the zoœcium, but varying in length; this is connected with the similar part of the next zoœcium by a chitinous "mesen-

[1] 'Proc. R. Soc. Vict.' (N. S.), iii, 1891, p. 77.

tery" (fig. 22, *m.*). The effect of the arrangement indicated in fig. 27 is to keep the epitheca stretched as a flat membrane at some distance from the basal calcareous walls of the zoœcia. The cavity beneath the epitheca is divided into a series of parallel longitudinal spaces by the parts of the zoœcia above described. The linear figure formed by the insertion of the zoœcium into the basal epitheca is in some cases bifurcated proximally. On the frontal surface (figs. 20, 21) each orifice is surrounded by a somewhat irregular ring of calcareous matter, from each side of which is given off a strong condyle (fig. 21, *cond.*) or "denticle," the two condyles forming the hinge of the operculum. The frontal surface is strengthened by a highly variable arrangement of calcareous bars, the general position of which is shown in fig. 20. The bars are in the main flattened, their flat surfaces being parallel with the surface of the branch, but in curving down into the lateral walls they usually give off vertical flanges from their free surface, and these form bridges across the depressed intervals between two zoœcia, joining similar flanges in the adjacent zoœcia. At the free end of the branch the proximal parts of the bars are first formed, and they grow in a distal direction beneath the epitheca.

Along the lateral margin of the branch runs a tube (fig. 20, *m. c.*)[1] which has usually been described as a "chitinous fibre" in other forms of Flustrine habit. This is merely a part of the branch which is not divided into zoœcia, and calcareous bars (*c. b.*) extend from the marginal zoœcia nearly to the outer edge of its free surface; it contains, moreover, strands of funicular tissue which pass across its lumen. This space runs as a continuous tube along the whole margin of the branch, and it communicates with the cavity which lies between the backs of the marginal zoœcia and the basal epitheca.

E. clathrata, like E. obtecta, is characterised by the dimorphism of its opercula. This is shown in figs. 20, 21, representing the ordinary type ("A") and the second form

[1] Cf. Waters, 1896, p. 291.

("B"). The zoœcia to which the two kinds of opercula respectively belong also show some dimorphism. In the A-zoœcia the condyles for the articulation of the operculum are long recurved teeth (fig. 21), while in the B-zoœcia they are short tubercles. The distal calcareous wall of the A-zoœcium is at the same time the proximal wall of the next zoœcium in the same longitudinal line. In the B-zoœcium this is not the case. The distal zoœcium has a proximal wall (*p. w.*) of its own, from which some of its calcareous bars may spring, and this is much thinner than the distal wall (*d. w.*) of the proximal zoœcium, from which it is separated by a narrow crescentic space, passing about half round the operculum of the proximal zoœcium. This suggests that the B-zoœcia possess a vestigial ovicell. The condition of my specimens unfortunately prevents me from ascertaining whether the production of ovaries is limited to B-zoœcia. In two cases counted at random, about three A-zoœcia occurred for every B-zoœcium, no regular arrangement of the two kinds being apparent. The additional breadth of the B-operculum is correlated with a slightly increased transverse diameter of the zoœcium itself, immediately on the proximal side of the operculum. This makes an appreciable difference in the capacity of the zoœcium, a fact which is in favour of the view that the B-zoœcia are female. Similar differences in the opercula are commonly met with in other Cheilostomes, in which the operculum of an ovicell-bearing zoœcium may be wider than that of the ordinary zoœcia.

Two features in E. clathrata demand especial attention, namely, the compensation-sac and the operculum. For the discovery of the compensation-sac Jullien (1888, 1) is entitled to full credit,[1] although his results have been re-

[1] See my preliminary paper (1901) on this subject. Jullien's accounts of the compensation-sac were very short, and his figures were not adequate. He nowhere brings out the importance of the sac in the discussion of the morphology of the Cheilostomata. So far as I know, he mentions its parietal muscles in only one place. This is in the explanation of a figure of Cribrilina figularis (1888, ii, p. 272), in which he uses words which seem to

ceived with scepticism, which proves to have been unjustified.

The COMPENSATION-SAC of this species is a very large cavity which underlies practically the whole of the frontal surface of the zoœcium. In longitudinal section (fig. 26, *c. s.*) it is seen to be perfectly distinct from the body-cavity, from which it is separated by a delicate membrane, constituting the floor of the sac. This membrane passes continuously into the base-line of the operculum, immediately proximal to which the sac opens to the exterior. When the operculum is closed the aperture of the sac is a virtual transverse slit. In the case of ordinary Escharine forms this aperture is so little apparent that it has commonly been supposed that the base-line of the operculum actually articulates with the adjacent part of the calcareous wall—a state of affairs which is often by no means the case. The roof of the compensation-sac is protected by the calcareous bars (*f. b.*), and the frontal wall of the zoœcium is bevelled off on the proximal side of its aperture, in the characteristic way shown in fig. 26. The purpose of this arrangement is obvious. The sharp edge of the frontal wall of the zoœcium is in contact with the base-line of the operculum when the latter is closed. When the operculum is open (fig. 24) the plane of its free surface becomes parallel with that of the bevelled edge of the frontal wall, so that water can have unobstructed access to the sac. As supposed by Jullien, there can be little doubt that the entry of water into the sac renders the protrusion of the polypide possible, but it almost necessarily follows that the constant change of the water in the sac makes this structure an important organ of respiration.

In this species I have been able to obtain only unsatisfactory evidence, in consequence of the state of its preserva-

indicate that he had appreciated the morphological importance of his discovery. The words are as follows :—" Muscles rétracteurs de l'abdomen (fibres musculaires pariétales des auteurs). Elles rétractent en réalité la paroi abdominale, mise en évidence par la découverte de la chambre à eau de compensation ou chambre compensatrice."

tion, with regard to the existence of the "parietal muscles" which elsewhere dilate the compensation-sac; but the analogy of other Cheilostomes leaves little doubt as to their presence.

The OPERCULUM is a very remarkable piece of mechanism, which forms a most efficient means of protecting the entrance to the tentacle-sheath. Most of the existing descriptions of Cheilostomatous opercula take account of the appearance of the outer surface only of this structure—a very inadequate way of arriving at its real relations. Although E. clathrata has an operculum which, judged by the descriptions available for comparison, would appear to be unusually complex, it is in the highest degree probable that a renewed examination of other Cheilostomes will show that it is by no means unique in this particular.

The first part of the introvert which leads to the mouth of the polypide is constituted by the "diaphragm" or "vestibule" (fig. 26, *vest.*), which is a muscular invagination projecting into the tentacle-sheath, and communicating with it by a central aperture.[1] The way in which the vestibule opens and closes has been aptly compared with the action of a clasp-purse. The structures which protect the vestibule of E. clathrata have a superficial resemblance to the skull of a turtle (Chelone), the skull with the upper jaw being represented by the operculum, and the lower jaw by a chitinous lower lip (figs. 23—27, *lb.*), which I propose to term the "labium." The labium was described by Hincks[2] in a form from the Queen Charlotte Islands, named by him Lepralia bilabiata, in allusion to the existence of this structure. It is probable that it will hereafter be found in numerous Cheilostomata.

The labium can be clearly seen in those zoœcia of the dry colony in which the operculum is open (fig. 19). Between it and the edge of the downwardly projecting flange (*fl.*) of the

[1] See, for a description of this structure, Nitsche (1871, p. 432), Jullien (1888, 4, p. 38), and Calvet (1900, pp. 180, 201).

[2] 'Ann. Mag. Nat. Hist.' (5), xiii, 1884, p. 49. The labium is the "upper lip" of Hincks's description.

operculum is seen the entrance to the vestibule, while the aperture of the compensation-sac is situated between the base of the operculum and the calcareous frontal wall of the zoœcium.

The relations of the same parts are explained by the thick longitudinal section shown in fig. 26, in which the operculum is very nearly closed. By deep focussing can be seen the calcareous condyle (*cond.*) which constitutes the hinge. The divaricator muscles (*div.*) of the operculum are paired; each originates from one of the lateral walls of the zoœcium, and passes obliquely towards its frontal surface, crossing the condyle on its proximal side, to reach its insertion into the basal sclerite of the operculum. The contraction of these muscles will obviously have the double effect of opening the vestibule and of opening the compensation-sac. The operculum is prolonged laterally into a very large triangular flange (*fl.*), whose plane is at right angles to that of its free surface (see also figs. 24, 25, 27). The occlusor muscles (*occl.*) are similarly paired, each originating from the lateral wall of the zoœcium at a deeper level than the divaricator, and passing obliquely across the base of that muscle to reach its insertion, on the distal side of the condyle, into the tip of the triangular flange. Fig. 25 shows that the insertion is by means of a broad tendon. Since the labium articulates with the operculum in this region, the effect of the contraction of the occlusor muscles will be, not only to close the operculum itself, but also to retract the labium from the position shown in fig. 24 to that shown in fig. 25. In the closed condition, the labium lies just inside the vertical flange of the operculum.

The lateral flanges are not really independent structures, but they pass into one another in a continuous curve round the distal side of the operculum, their free border, continuing the comparison with the turtle's skull, constituting the biting edge of the upper jaw. In longitudinal section (fig. 26) the upper jaw appears to be strengthened by a strong buttress (*buttr.*) which passes from the free surface of the operculum.

This is a part of the Ω-shaped figure which is seen in a surface view (fig. 21) of the operculum, an appearance which results from the fact that the thickness of the chitin is not everywhere the same. The whole of the region included within the two limbs of the Ω is much thickened (figs. 26, 27), while the rest of the free surface, as far as the edge, is composed merely of thin cuticle (fig. 29). From the median thickening a curved chitinous buttress diverges (figs. 28—31) on each side, passing down into that part of the body-cavity which immediately underlies the free surface of the operculum. In young zoœcia, the space between the buttress and the outer lamella of the operculum contains a conspicuous epithelium, which secretes the cuticular substance of which the operculum is composed. Remains of this cellular material may be seen, in the same position, in the adult operculum.

The greater part of the thickness of the operculum is constituted by a superficial layer of cuticle which readily stains yellow with picric acid. The whole of the deeper surface of this layer (and therefore both sides of the strengthening buttress which depends from the free surface), is lined by a much thinner layer of chitin (not indicated in the figures), which takes a red colour in sections stained with borax carmine and picric acid. A two-layered chitinous cuticle has been described in certain Gymnolæmata by Calvet (1900, p. 164).

The buttress of the operculum is crescentic in shape, as seen from above (fig. 21, *buttr.*). Thus, if the thin lateral parts of the outer lamella of the operculum were removed, there would be exposed a crescentic cavity, the limbs of the crescent being directed towards the proximal side of the zoœcium, the floor of the cavity being constituted by the slightly concave upper surface of the buttresses. Distally the buttress meets and fuses with the vertical flange of the operculum (fig. 26). Laterally the fusion is incomplete distally (figs. 27, 28), so that the cavity above the buttress is here continuous with the general body-cavity. In the

proximal half of the operculum the buttresses again meet the lateral flanges (figs. 29—31).

The distal half of an operculum is shown in fig. 27, which represents a transverse slice of a specimen with its calcareous parts, cut freehand[1] after embedding in paraffin. By focussing deeply are seen the labium (*lb.*) and the curved slit between it and the edge of the operculum. Into the ends of the lateral flanges of the operculum, and at the same time into the two sides of the base of the labium, are inserted the occlusor muscles (*occl.*). By focussing less deeply the free edges of the lateral buttresses are seen; while the cut surface passes through the region of the condyles (*cond.*). Fig. 26 shows that the operculum works on its condyles as a lever of the first order, the occlusors (*occl.*) and the divaricators (*div.*) passing on opposite sides of the fulcrum.

Fig. 28 shows a transverse section of the distal part of the operculum where the buttresses have a free edge. Fig. 29 is through the hinge-line. The vertical flange is still deep (cf. fig. 26), and is here strengthened by the buttresses, which have completely fused with it. On the proximal side of the condyles the depth of the flange rapidly diminishes. In the entire operculum a small circular mark (fig. 21, *x*) appears on each side near the proximal end of the Ω-shaped figure. In transverse section (fig. 30) this is seen to be due to the fact that at this point the buttresses leave the vertical flanges and are inserted into the free wall of the operculum, so that at this point the body-cavity is separated from the outside by a single layer of chitin. The small tube thus formed often stains deeply in carmine preparations. I am unable to explain the meaning of this arrangement. The tube does not communicate with the space above the buttresses. On its proximal side the operculum becomes very shallow, as indicated in fig. 31, a section just on the distal side of the basal sclerite. This forms, with the median thickening, a horizontal ⊥-shaped figure, the outline of which

[1] The hard nature of the chitin makes it difficult to prepare microtome sections of the opercula.

gives rise to the Ω-shaped mark seen in an external view of the operculum (fig. 21).

In decalcified sections the calcareous part of the condyle is seen to be surrounded by a strong layer of chitin. In longitudinal sections this has the appearance indicated in figs. 25, 26 (*cond.*), the chitin being developed especially on the proximal side of the condyle. Fig. 24, which represents an open operculum, shows that this chitinous investment is prolonged into the sharp edge (*scl.*) which surrounds the cavity in which the operculum lies (see also figs. 27, 29). This edge is continuous with a layer of chitin forming the outer wall of the cavity (figs. 28—31); and this, in its turn, becomes continuous with the deep end of the vertical flange of the operculum. The flange is strongly bent inwards so as to lie along the surface of the condyle.

I think there is great probability that these arrangements are in the nature of a spring, and that if the partially opened operculum shown in fig. 29 be imagined to be closed by the occlusor muscles, the shape of the lateral flanges and of the buttresses will be somewhat distorted by the surfaces of the condyles. The elasticity of the operculum would thus tend to commence the opening of the orifice and of the compensation-sac. This supposed elasticity probably gives a reason for the free ends of the buttresses in the distal part of the operculum, an arrangement which would facilitate the slight alterations in the vertical flanges during the movements of the operculum.

The whole apparatus, consisting of the operculum, the labium, and the chitinous cutting edge which surrounds the cavity containing the operculum, is obviously one of remarkable perfection, and is well adapted to defend the entrance to the tentacle-sheath.

The most external part of the vestibule is lined by a distinct layer of cuticle (fig. 26), which is continuous with the cuticle of the operculum and with that of the labium. The actual "biting" surface of the jaws is constituted by a thickened part of the cuticle, as shown in the same figure.

That of the operculum is so close to the insertion of the buttress into the vertical distal wall as to receive support from the buttress. That of the "lower jaw" is continuous with the main thickening of the labium, which is the deeper wall, as shown in fig. 26.

I have few observations on other points in the structure of this species. In the material at my disposal a certain amount of disintegration appears to have taken place before the specimens were preserved. The number of tentacles is, however, about twenty-two.

Euthyris obtecta, Hincks,[1] Pl. 16, figs. 32—37.

The B-zoœcia are much larger than the A-zoœcia, the ratio in volume being probably at least 2 : 1 (figs. 32, 35). The A-opercula are of much the same shape as in E. clathrata, while the B-opercula are relatively much broader. The condyles are weaker than in E. clathrata, and are situated nearer the proximal border of the operculum. But what most strikingly differentiates the two species is the character of the calcification. The calcareous wall is everywhere complete in E. obtecta, the basal wall being uniformly rounded along its whole extent. Both kinds of zoœcia are flask-shaped (figs. 34, 36), the opening of the neck of the flask being filled by the operculum. A continuous flat epitheca overspreads the entire zoarium, being stretched out in the plane of the opercula on the frontal surface of the branch, and at a considerable distance from the zoœcia on the basal surface (fig. 34, *ep.*, *b. ep.*). The space beneath the epitheca (*ep. c.*) is thus extremely large, and that of the frontal surface is continuous with that of the opposite side by means of the undivided space which runs along each edge of the frond (figs. 32, 35, *m. c.*).

On the frontal surface the epitheca is supported in the main by the edges of the orifices of the zoœcia, but in addition by a few calcareous tubercles (fig. 34, *calc. p.*), which arise irregularly from various points of the surface of

[1] 'Ann. Mag. Nat. Hist.' (5), x, p. 164; (6), xi, p. 177.

the calcareous wall (fig. 32), and pass vertically to the epitheca. Basally these tubercles are longer and are rather more regularly arranged. Their arrangement is seen in figs. 34—36, from which it is apparent that they serve to keep the epitheca stretched out at a considerable distance from the calcareous part of the zoœcium. In my preliminary note (1901, p. 16) I have pointed out that there is evidence that many Cretaceous Cheilostomes were provided with a basal epitheca, as is indicated by the presence of calcareous papillæ resembling those of E. obtecta. It may perhaps be suggested that a function of the epitheca is to protect the calcareous walls from the attacks of boring organisms (e. g. the Infusorian Folliculina) which infest many calcareous Polyzoa.

The calcified wall of E. obtecta shows no trace of the bar-like arrangement so characteristic of E. clathrata. It is, on the contrary, a continuous calcareous film, traversed by pores. As in the other species, these pores partly form communication-pores traversing the partition-walls between zoœcia, and they are partly in relation with the space beneath the epitheca. It is hardly necessary to point out that in neither case are they open pores, although the calcareous matter is deficient in these regions. The portions of the vertical walls which are actual partition-walls are of limited extent (fig. 36), so that but few of the pores are communication-pores (*c. p.*) between zoœcia. I have seen no evidence that the number of these is restricted to eight, as stated by Waters (1896, p. 282). The majority lead to the spaces beneath the epitheca, particularly to that on the basal side of the frond (figs. 35, 36). They are less numerous on the frontal side (fig. 36).

The marginal part of the frond may be strengthened by a system of bars (fig. 37) which recalls those already described in the zoœcia of E. clathrata. This system makes its appearance first in the angle between the two lobes of a bifurcation, and begins as a set of regular calcareous bars, running near the frontal surface, and originating from the

outer sides of the marginal zoœcia. Each bar is at first narrow, but soon dilates into a thickened, tuberculated, rounded head, the heads being closely apposed to form a continuous calcareous border. From the border a longitudinal vertical ridge stands up at right angles to the frontal epitheca, which it meets. A similar ridge (*l*) connects the border with the basal epitheca. In older branches each bar may be dilated at two points, and a second longitudinal ridge may be formed on each surface (fig. 37, *l*, *l*).

The marginal thickening,[1] thus constituted of a series of calcareous thickenings, gives flexibility as well as strength to the margin of the frond. There can be little doubt that the space beneath the epitheca is a kind of colonial body-cavity. The marginal bars of E. obtecta can thus be regarded as directly comparable with the zoœcial bars of E. clathrata. From the irregularity and variability of the bars in the latter I am inclined to regard this as a species in which the calcification has been reduced from a condition like that in E. obtecta.

The general arrangement of the viscera in E. obtecta is shown in fig. 34. The operculum has conspicuous lateral flanges, and there is a delicate labium (*lb.*). The occlusor muscles (*occl.*) are inserted into the apices of the lateral flanges. Some of the fibres of the divaricator muscles (*div.*) appear to reach the base-line of the operculum, but some are probably inserted into the adjacent part of the floor of the compensation-sac (*c. s.*). This structure is very large, and in an adult zoœcium it underlies the whole of the frontal surface. Fig. 33 shows its appearance in a B-zoœcium in back view. The greater part of the basal wall (*b. w.*) of the zoœcium and part of the polypide have been removed. The tentacle sheath depresses the sac medianly, but the sac bulges out on each side into a strongly convex lateral lobe. Each lobe thus formed is rounded off distally, but by deep focussing the two lobes can be seen to unite on the far side of the tentacle sheath into a single cavity, which can be traced to

[1] A similar thickening is well known in certain other flexible Cheilostomes. See, for example, Levinsen's account (1891, p. 274) of Flustra carbasea.

the proximal border of the operculum. The divaricator muscles are seen at *div.*; *occl.* indicates the position of the origin of one of the occlusor muscles, while a pair of parieto-vaginal muscles are seen at *p. v. m.* Arising from the sides of the zoœcium are a series of delicate parietal muscles (*p. m.*). There is a tendency for these to be arranged in a grouped manner. They can be traced along the basal surface of the compensation-sac, into which each is inserted.

A polypide and a compensation-sac occur in both forms of zoœcia. Reproductive organs are, unfortunately, absent, so that it is not possible to ascertain whether the dimorphism has any relation to reproduction.

The compensation-sac develops in what I shall term the Lepralioid manner; that is to say, as an invagination formed at the base of the operculum after the calcification of the front wall has been completed. Some of the details of this process are described in the account of the next species.

Euthyroides, n. gen.—I suggest this term for Carbasea episcopalis, Busk,[1] a form placed by Hincks [2] in the genus Euthyris. The diagnosis of the genus may be given as follows:

Zoarium of Flustra-like habit, bordered along each edge by a tube, interrupted at intervals, which represents a part of the body-cavity not divided into zoœcia, but without other spaces beneath the epitheca. Frontal wall more or less calcareous, covering a well-developed compensation-sac. Communication-pores large, typically four on each side. Ovicells large, external, with a wall composed of two calcareous layers.

The genus differs from Euthyris in the absence of spaces beneath the epitheca and in the presence of large external ovicells, and of a very different type of communication-pore.

The zoœcia of E. episcopalis (Pl. 15, figs. 13—17) are extremely elongated. Their vertical and basal walls are calcified, but there is so little calcareous matter in the frontal

[1] Busk (1852), p. 52; MacGillivray, 'Prod. Zool. Vict.,' I, Dec. v, 1880, p. 28.

[2] 'Ann. Mag. Nat. Hist.' (5), x, p. 164.

wall that this part may not entirely retain its shape in drying.

Large, oval communication-pores, or rosette-plates, occur in the lateral walls, at about the middle of the interval between the frontal and basal surfaces (fig. 14, *c. p.*). Each zoœcium is normally bounded by two zoœcia on each side, and it usually communicates with each of its four lateral neighbours by means of two (rarely three) rosette-plates. In the terminal partition-walls, there is a horizontal row of small pores in place of definite rosette-plates. The vertical walls have no other pores.

The transparency of this species makes it a favourable one for the study of the compensation-sac. At the growing ends of the branches the frontal surface of the zoœcium is at first an uncalcified membrane, in which calcification begins at the proximal end and gradually extends distally. The outline of the operculum becomes apparent before calcification invades its immediate neighbourhood. Shortly before the edge of the calcified frontal wall (fig. 13, *x*) reaches the region of the future operculum, the part of the uncalcified membrane immediately proximal to the opercular base-line shows a special accumulation of nuclei (*c. s.*), towards which a number of muscle-fibres radiate through the body-cavity from both lateral walls. When the calcification has advanced so far as to mark out the future orifice, two lateral calcified processes and a median tongue-like structure begin to grow up just proximal to the operculum (fig. 14, *l. p.*, *tg.*). The nuclei are arranged in a more definite mass along the proximal margin of the orifice, to which the lumen of the tentacle-sheath (*t. s.*) now extends. Still later, the two calcareous processes meet, although the suture between them is persistent. There is thus left, between them and the calcareous tongue, a crescentic pore (fig. 15), the concavity of which is directed proximally. This is an aperture of the compensation-sac, which, however, opens to the exterior at the proximal edge of the operculum as well, an arrangement which is most obvious in the fertile zoœcia. The occlusor muscles of the

operculum are large, and originate from the lateral parts of the basal wall, close to the distal end of the zoœcium. The divaricator muscles originate from the lateral walls of the zoœcium, in the same neighbourhood.

The zoarium is bounded by a tubular cavity, which is, however, not continuous, as in the preceding species. The cavity is a direct prolongation of one of the longitudinal lines of zoœcia, and may be compared with what Smitt calls a "Samknopp" (1865, p. 6). After extending a length of perhaps five ordinary zoœcia it ceases abruptly, and a new marginal tube is formed as a prolongation of the series of zoœcia next internal to it. The lateral tubes are connected with the adjoining zoœcia by communication-pores.

The ovicell (fig. 16) of this species is well known from Busk's description. It is very prominent, and is provided with a median longitudinal keel, on each side of which is a large elongated fenestra (*f.*). This is simply a membranous deficiency in the outer wall of the ovicell, which is composed of two calcareous layers. The fertile zoœcium is distinguished from the others by a peculiarity in its calcareous frontal wall. Instead of having a single pair of prominences on the proximal side of the operculum, it has several such prominences (figs. 16, 17), the arrangement of which is somewhat variable. There are either several tubular calcareous bars radiating towards a point in the middle of the zoœcium (fig. 16), or a short series of bars disposed more definitely in pairs (fig. 17). The latter arrangement seems to occur typically in those fertile zoœcia which have an ovicell on their proximal side, and the former in a fertile zoœcium which is the first of a longitudinal series.

The resemblance of these bars to the frontal bars[1] of a

[1] I suggest the term "frontal membrane" for the membranous body-wall which is stretched over the "aperture" of a Membranipora (fig. 43). The "frontal bars," or "costules" of some authors, are the bars which grow over this membrane in a Cribrilina (figs. 8, 44); while I propose the term "frontal shield" for the calcareous part of the frontal surface of a Cheilostome. The frontal shield is probably not homologous in all Cheilostomes, but the term may be used as a purely descriptive one,

Cribrilina is very striking. They arch over a greatly reduced frontal membrane, into which parietal muscles are inserted in the immature condition of the zoœcium (fig. 17). The bars are calcareous tubes, opening by a foramen into the body-cavity just external to the frontal membrane, and each bar has a minute membranous fenestra near its tip. After the complete formation of the bars there is found (in the fertile zoœcium) a stage in the development of the compensation-sac precisely like that shown in fig. 15 in a zoœcium without an ovicell, and it can now be seen that the operculum is continuous with the floor of the compensation-sac, a wide opening into which is left between the operculum and the first pair of bars. In the mature fertile zoœcium the compensation-sac extends under the greater part of the frontal shield, as in the ordinary zoœcia.

There is little difference between the relations of the frontal bars in the fertile zoœcia of E. episcopalis and that found in certain species of Cribrilina (e. g. C. figularis), in which the frontal membrane surrounded by the bars is of reduced extent.

In the immature ovicell of E. episcopalis (fig. 17) the inner calcareous wall is a concave plate (*i. w.*) lying on the surface of the zoœcium next distal to that to which the ovicell belongs. The outer calcareous layer (*o. w.*) rises up concentrically outside it, and between the two is a mass of living tissue. It is impossible not to be struck by the resemblance between the development of the ovicell and that of the frontal bars. The ovicell may be compared with two greatly expanded bars, composed, like the others, of two layers of calcareous matter surrounding living tissue.

The median keel of the mature ovicell represents the line along which these bars meet, and corresponds, I believe, with a complete septum between their cavities. It may thus be suggested that the ovicell is formed by the fusion of a pair of greatly expanded oral spines, the bases of which should communicate with the fertile zoœcium on each side of the operculum. I cannot claim to have proved this to

be the case, though I have obtained some evidence pointing in that direction.

Dr. G. M. R. Levinsen has kindly given me permission to allude to his very interesting observation (which he proposes to publish hereafter), that in Alysidium parasiticum, Busk,[1] the ovicells develop as two arched, hollow valves, corresponding with the oral spines which occur on the ordinary zoœcia. I do not at present know what conclusions Dr. Levinsen deduces from this observation, with which I was acquainted before making my own on E. episcopalis.

In Heterocœcium amplectens, Hincks[2] has described a Membranipora-like Cheilostome, in which the ovicell is constituted by a number of spines placed distal to the operculum, which meet in a Cribrilina-like manner, and form a structure which, in other respects, resembles a normal ovicell.

Calvet (1900, pp. 57, 58, 132, pl. ii, fig. 14) states that in Bugula there is a communication-pore between the ovicell and the distal zoœcium.

It follows from the account given by Calvet and others, that the cavity of the ovicell, internal to its inner layer, is an external space which is overarched by the double wall of the ovicell. This is obviously true in a case like that of Mucronella coccinea, where the most distal oral spines of the fertile zoœcium are actually inside the cavity of the ovicell.

Further investigation is necessary to decide the morphological nature of the Cheilostome ovicell. The existence of three possibilities is generally recognised:—(1) That the ovicell belongs to the fertile (proximal) zoœcium; (2) that it belongs to the distal zoœcium; (3) that it is a modified individual, as believed by Nitsche and others. The second possibility would seem to be indicated by Calvet's observation above referred to. The relation of the operculum of the fertile zoœcium to the ovicell, the occurrence of the "internal

[1] 1852, p. 14.

[2] 'Ann. Mag. Nat. Hist.' (5), viii, 1881, p. 129, pl. iii, fig. 7; ibid. (6), ix, p. 332.

ovicells" found in certain species of Flustra and elsewhere, and in particular Dr. Levinsen's account of Alysidium parasiticum, seem to be in favour of the view that the ovicell is a part of the fertile zoœcium.

In his original account of Flustra militaris,[1] Waters suggests that this species is allied to E. episcopalis, calling attention to the resemblance between the ovicells of the two forms, but noting the existence of differences between the opercula. The two species agree in the great length of their zoœcia and in their rosette-plates; but a striking difference is seen in the frontal surface, which is membranous in F. militaris, except for a small proximal calcified region. Parietal muscles appear to be inserted into this membrane, as in an ordinary Flustra. The two strong suboral spines of F. militaris may correspond with the two projections which in E. episcopalis cut off the median pore. If the frontal surface has really the importance in classification attached to it in the present paper, I see no way of admitting the affinity of the two species (which undoubtedly resemble one another), except by assuming either that F. militaris is a species which has secondarily opened its compensation-sac, or that E. episcopalis is a modified Flustrine form. The material at my disposal is not in a condition which allows me to make a further examination of these points.

IV. The Morphology of the Compensation-sac and of the Operculum.

I have come to the conclusion that the evolution of the compensation-sac has not been identical in all Cheilostomes which possess that structure, but that in some cases it has been formed by the overarching towards the middle line of a series of marginal spines in such a way as to cover the primitive frontal membrane.[2] The evidence for the occurrence of this process is as follows:

(1) Many species of Membranipora exist in which the

[1] 'Ann. Mag. Nat. Hist.' (5), xx, p. 93.

[2] See p. 282.

arrangement of the marginal spines foreshadows the condition above indicated.

(2) The Cribrilinidæ are transitional from Membranipora to some at least of the Lepralioid genera.

(3) The arrangement of the muscles connected with the compensation-sac is derivable from the condition found in Membranipora.

(4) The study of the primary zoœcium.

(5) Palæontological evidence.

The view that the Cribrilinidæ are intermediate between the Flustrina and the Escharina is not a new one. Smitt (1868, i, p. 401) states explicitly that the frontal bars of Membraniporella nitida are homologous with the free marginal spines of Membranipora lineata; and in his next paper (1868, ii, p. 48) he shows that Cribrilina marks a further transition to the Escharines. He leaves Membraniporella in the Flustrina, while placing Cribrilina in the Escharina. Hincks, on the contrary (1880), places the two genera in the family Cribrilinidæ.

But although taking this view of the intermediate position of the Cribrilinidæ, Smitt was not in a position to show in detail how the Flustrine zoœcium could be modified into an Escharine zoœcium. The compensation-sac enters into the question as supplying the clue necessary for the solution of the problem.

The foregoing instances have given some idea of the relations of the compensation-sac in its fully developed form. I next proceed to the proposition that the compensation-sac of some Lepralioid genera has been derived from a Membranipora-like condition through a stage similar to that of existing species of Cribrilina.

(A) Flustrina.

Flustra pisciformis, Busk.[1]—Fig. 4 shows the general anatomy of a young zoœcium of this species. In the lateral

[1] 1852, p. 50.

walls the calcareous matter is in two layers separated by a chitinous lamella,[1] as described by Nitsche (1871, pp. 421, 455). Each zoœcium thus has its own calcareous lateral walls, distinct from those of its neighbours. In two regions, respectively proximal and distal to the broadest part of the zoœcium, the lateral wall is thickened at its frontal edge. At the proximal narrow end the calcareous wall becomes deficient, and the terminal partition wall, which is thicker than any of the others, belongs to the proximal zoœcium of the two which it divides. This accords with Levinsen's statement (1891, p. 251) that in many Cheilostomes the terminal wall is single, while the lateral walls are double, so that the longitudinal rows of zoœcia can be isolated from one another by boiling with caustic potash. The frontal surface is entirely membranous; the operculum is merely a part of this membrane, and has no basal sclerite. When the operculum is open (fig. 3) it is seen to have a vertical flange, produced into lateral points, as in Euthyris. A similar arrangement is described by Nitsche [2] in Membranipora membranacea. The occlusor muscles (*occl.*) are inserted into these points, and originate, as in Euthyroides episcopalis, from the basal wall. A pair of strong parieto-vaginal muscles (*p. v. m.*) pass from the tentacle sheath to the basal wall, and a smaller pair (*p. v. m.'*) connect the tentacle sheath with the frontal wall; but none pass to the vertical walls (cf. Calvet, 1900, p. 199). A pair of strong parieto-diaphragmatic muscles (*p. d.*) spring from the basal wall, just internal to the origin of the occlusor muscles, and are inserted into the diaphragm or vestibule. The retractor muscles (*r. m.*) of the polypide have their origin in one of the corners of the fish-tail-like proximal end of the zoœcium. About four

[1] In a recent paper by Schulz ('Arch. f. Naturg.,' lxvii, Bd. i, Heft 2, 1901, p. 118, pl. vi, fig. 4) this chitinous lamella is figured as a much thicker layer than anything I have ever seen. The species investigated by Schulz was M. "membranacea" (= M. monostachys, Busk; cf. Levinsen [1891], p. 277).

[2] 1871, p. 422.

groups of parietal muscles (*p. m.*) are seen, of which the distal group (*p. m.'*) originates from the basal wall, and the rest from the vertical walls, close to their junction with the basal wall.

These arrangements are moderately constant in all the zoœcia. The distal group of parietal muscles is always strong, and is commonly stronger than the others. The number of groups does not vary much, but it is important to notice that the distal group may (rarely) originate from the base of a vertical wall, and conversely that the other parietal muscles may originate from the basal wall. The distal parietal muscles thus clearly belong to the same series as the rest.

The mode of action of the parietal muscles has been well described by Nitsche (1871, p. 426), who showed that the pressure on the fluid of the body-cavity due to their contraction was the main cause of the protrusion of the polypide. A more detailed account of the same process is given by Calvet (1900, p. 63).

F. pisciformis has no distinct divaricator muscles. The opening of the operculum is probably largely due to the fluid-pressure brought about by the contraction of the parietal muscles generally; but it seems to me highly probable that the distal group of these muscles, by pulling on the membrane with which the base of the operculum is immediately continuous, may have a special effect in opening the operculum. I regard the distal parietal muscles as the starting point from which the divaricator muscles of Euthyris and its allies have been derived.

Flustra papyrea, Pall.—This species is very similar to F. pisciformis in essential respects. The more noteworthy differences are (1) the parietal muscles are more numerous, usually numbering about six to seven groups on each side;[1] (2) while each of the ordinary groups consists of not more than two or three fibres, the distal group is a much broader and more definite muscular band, composed of a considerably larger number of fibres; (3) the distal as well as the other

[1] They are shown in my paper (1892), pl. ii.

parietal muscles originate typically from the basal end of the lateral walls. The operculum resembles that of F. pisciformis.

I have observed the occurrence of typical parietal muscles in five other species of Flustra.

Membranipora.—The operculum and the parietal muscles in M. membranacea and other forms which have been examined are essentially Flustrine in their arrangement. They have been described by Nitsche (1871, p. 426) and others.

Farciminaria hexagona, Busk.[1]—The whole of the very long frontal surface is membranous. The operculum is like that of Flustra pisciformis, with no basal sclerite, and with a marginal vertical flange prolonged into two lateral points, into which the occlusor muscles are inserted. The orifice is markedly bilabiate, the operculum with the vestibule opening precisely like a clasp-purse, of which the marginal flange of the operculum forms the supporting rim of one half, while the distal edge of the zoœcium supports the other half. There are about six groups of parietal muscles on each side, the distal group probably acting as in Flustra pisciformis.

The next few species are ordinarily placed with the Cellularina, but their affinities appear to me to be with the Flustrina.

Dimetopia spicata, Busk[2] (fig. 5).—This is an instance of a dendritic form, in which the lateral zoœcial walls constitute the greater part of the exposed surface of the funnel-shaped zoœcium. The frontal membrane is small, and is situated at the broad end of the funnel, the edge of which is surrounded by seven or eight hollow calcareous spines. These originate from a massive calcareous ring which is notched externally at the base of each spine to permit the cellular tissue of the spine to communicate with that of the general body-cavity.

[1] Busk (1884), p. 51.

[2] Busk (1852), p. 35; MacGillivray, 'Prodr. Zool. Vict.,' Dec. v, 1880, p. 33.

The lumen of the spine has a characteristic globular dilatation at the point where it crosses the calcareous ring. The calcareous wall of this dilatation is completed externally by the outer wall of the zoœcium. The bases of the spines are connected with one another by a thin calcareous web, while part of the frontal membrane may project just beyond the web, internal to the bases of the spines.

The zoœcia are arranged back to back in pairs, new zoœcia (*z.'*) originating from the axial side of their distal end. The orifice is close to this region, on the axial side of the frontal wall (fig. 5). The occlusor muscles (*occl.*) originate from the lateral walls. In correlation with the reduction of the length of the frontal membrane, there is but a single pair of parietal muscles (*p. m.*).

Bicellaria grandis, Busk, var. producta, MacGillivray[1] (fig. 1).—This is another example of an infundibuliform zoœcium. The frontal membrane is obliquely placed, and is of restricted extent. The orifice is at the extreme outer end of the membrane, and the zoœcium is prolonged beyond it into a lobe which bears three or four very long spines. On the axial side of the zoœcium is a calcareous thickening[2] which surrounds the communication-pores (*c. p.*). The zoœcia have the alternate arrangement characteristic of the genus, and in most cases the calcareous thickening includes two sharply marked rings, one for the alternate zoœcium of the other side of the branch, and the other for the next zoœcium on the distal side. In fig. 1, however, there are three calcareous rings, the zoœcium being the one which precedes a bifurcation, and having consequently to give rise to two distal zoœcia. A peculiarity of this species, which I have not found in other species of Bicellaria, is that the proximal part of the "aperture" becomes filled in with a thin calcareous film (*crypt.*) which ends in a hook-like point. I am unable to state with certainty what is the function of this hook, but I think that its distal edge forms

[1] 'Prodr. Zool. Vict.,' Dec. vi, 1881, p. 38.

[2] Cf. Goldstein, 'Trans. Proc. Roy. Soc. Vict.,' xviii, p. 43.

a guide over which the tentacle sheath works in the movements of protrusion and retraction. I have not definitely settled whether the calcareous film is a superficial calcification or an internal cryptocyst, but the existence of a delicate, free, vertical edge all round the "aperture" probably indicates that there is living tissue adjacent to it (which I believe that I have been able to make out), and that the film is of the nature of a cryptocyst.

The operculum is like that of Flustra, and there is a single pair of parietal muscles, as in Dimetopia.

Bugula neritina,[1] L. The aperture is elongated, and occupies the greater part of the length of the zoœcium. The parietal muscles are arranged in a series of Flustra-like groups, which lie very close to the lateral walls of the zoœcium.

(B) Cribrilinidæ.

It has long been known that the characteristic frontal wall of certain Cribrilinidæ develops as a series of marginal spines, originating from the periphery of the aperture and converging towards one another until they meet, and so form a calcareous roof in which the intervals between the bars remain either as simple slits or as a series of pores. An excellent account of this process is given, for instance, by Hincks (1880, p. 199).

It is easy to see, by an examination of dry specimens of various Cribrilinidæ (e. g. C. annulata) that the operculum is not continuous with the calcareous frontal wall, but with the underlying frontal membrane. This may be observed either in immature zoœcia or in those from which the wall formed by the union of the bars has been broken away. Goldstein (1880, p. 48) has made the interesting observation that in C. monoceros (?) a Rotifer swam into the space between the bars and the frontal membrane. Although this is not expressly stated, it presumably entered at the distal

[1] Busk (1852), p. 44.

end of the series, between the bars and the base of the operculum.

The growth of these bars can easily be studied in the common Membraniporella nitida,[1] Johnst. The young zoœcium is completely Membranipora-like, even in the character of its operculum. The bars are hollow calcareous spines, which originate as a series of crenulations from the edge of the vertical wall of the zoœcium, each of the future bars being indicated by a round bay of the edge. By the closure of this bay the commencement of a tube is formed, which arches over the frontal membrane in such a way as to leave a considerable space between itself and the membrane. The slits between the bars are probably permanently open. Another point which is worth notice is that the calcareous bars are part of a series of which the distal ones persist as the oral spines. In Cribrilina annulata the bars originate in the same way, but the intervals between successive bars persist as a series of pores which probably remain open.

Cribrilina philomela, Busk.[2]

Dry specimens show at once that the operculum is continuous with the original frontal membrane,[3] which becomes covered over in the same way as that above indicated (fig. 44). The fully developed zoœcium (fig. 8) is covered in front by a series of alternate hollow bars, the lumen of each of which is for the most part narrow, but dilates into a rounded end near the middle line of the zoœcium. The rounded end lies more superficially than the rest of the cavity. The outer wall of each bar is considerably thicker than the inner wall.

The operculum is Flustra-like, with no basal sclerite, but

[1] Hincks (1880), p. 199.

[2] 1884, p. 132.

[3] This is shown in a diagrammatic longitudinal section of a Cribrilina figured by Canu (1900, p. 441, fig. 53, iii), where the roof formed by the united calcareous bars or "costules," is seen to be entirely independent of the operculum.

it is of firmer texture than in the preceding forms. It has the usual lateral projections of the vertical flange for the insertion of the occlusor muscles. Condyles are barely indicated, but they can just be made out as two slight knobs distal to the proximal broadest part of the operculum.

A Flustrine series of groups of parietal muscles[1] occurs (fig. 9), among which a stronger group (*p. m.'*) on each side, immediately proximal to the operculum, probably acts as a divaricator, as in Flustra.

A few of the zoœcia are modified as vicarious avicularia. The zoœcium is normal, but the operculum is longer than usual, and the occlusor muscles originate from as much as the distal two thirds of the basal wall. These zoœcia are provided with typical parietal muscles. Polypides are absent in most parts of the preparation, but in several cases the vicarious avicularium possesses a polypide. These modified zoœcia are not provided with ovicells, which occur, here and there, on the ordinary zoœcia.

Cribrilina radiata, Moll (fig. 7).

This species, which differs in important respects from C. philomela, is considered in the following section (p. 326).

(c) Lepralioid Genera.

Under this heading I shall consider not only some of the genera which are usually referred to the Escharina, but a certain number of the branching forms at present included in the Cellularina.

Umbonula verrucosa,[2] Esper (fig. 11; see also the diagram, fig. 12).

The frontal membrane of this handsome species is permanently Flustrine; but it becomes overarched by a strong

[1] The parietal muscles of Membraniporella nitida are figured by Smitt (1865), pl. vi, fig. 1; those of Cribrilina figularis by Jullien (1888), 2, pl. x.

[2] Hincks (1880), p. 317.

calcareous roof, which extends to about the middle of the orifice, where it ends in a prominent shoulder on each side, rising in the middle line into a massive suboral umbo. This bears a strong avicularium at its base, immediately over the entrance to the compensation-sac. The rounded mandible, when closed, is directed towards the end of the umbo, and then lies in a vertical plane, transverse to the long axis of the zoœcium. The umbo, which probably belongs to the avicularium, is supported by a series of radiating buttresses of the frontal shield, and between them are deep pits, the marginal areolæ (*ar.*), closed by a layer of living tissue or epitheca.

Fig. 11 shows the commencement of the calcification of the frontal shield. The lateral partition-walls consist of a thin chitinous lamella, with a layer of calcareous matter on each side, belonging respectively to the two zoœcia separated by the wall. At a level a little lower than the free edge, the lateral and proximal partition-walls give off a calcareous film, which in the young specimen figured reaches no further than the edge of the frontal membrane. This film is pierced by a series of round holes (*p.*), one of which corresponds to each interval or areola (*ar.*) between two of the future buttresses. These holes establish a continuity between the living tissue of the body-cavity and that which occurs on the outside of the frontal shield. Beyond the origin of the frontal shield the vertical wall splits into two membranous lamellæ, one of which passes over each of the contiguous zoœcia to form its epitheca, and becomes continuous with the free edge of the frontal shield (fig. 12). The frontal membrane (*f. m.*) becomes covered by a continuation of this process—in other words, by the formation of a crescentic fold, of which the deeper lamella is calcareous, and the superficial layer is composed of a living membrane. In the incompletely calcified zoœcium the edge of the crescentic fold is always membranous. From the deep lamella rise the radiating ridges which form the buttresses.

The polypide is still young in fig. 11. With the distal end

of its tentacle sheath are connected the two "opercular glands,"[1] while somewhat more proximally are inserted the conspicuous parieto-vaginal bands (*p. v. m.*). The operculum is of delicate Flustrine structure, and has no special divaricators. Of the strong occlusor muscles (*occl.*), that of the (apparent) left side is seen to originate from the distal vertical wall, and that of the right side from the lateral wall. A series of groups of parietal muscles (*p. m.*) originate from the lateral and proximal walls, and are inserted into the frontal membrane.

There can, I think, be little doubt that the space below the calcareous roof is the homologue of the similar space in Cribrilina. The main difference between the two spaces is that that of Cribrilina is covered by a series of originally separate bars, while in Umbonula it is from the first a continuous crescentic film. The marginal pores,[2] which are the only ones that occur in the film, have, however, precisely the same relations as the communications between the cavities of the hollow Cribrilina spines and the general body-cavity. I regard the covering of the compensation-sac in Umbonula (fig. 50) as having been derived from a Cribrilina-like condition (fig. 44) by the lateral fusion of the spines with one another, the edges of the spines being indicated by the buttresses, and their cavities by the marginal areolæ and by the pores leading from those spaces to the general body-cavity. This involves the necessity of assuming that the outer calcareous layer of the Cribrilina spines is now represented by an uncalcified membrane, the epitheca. The very common occurrence of marginal areolæ in Escharine forms may be appreciated by turning over the plates of almost any paper dealing with a collection of recent or fossil forms.

[1] Cf. Waters (1892), p. 272 ("gland-like bodies"), and Calvet (1900), p. 200.

[2] The relations of these pores are well shown in a figure given by Neviani ('Boll. Soc. Geol. Ital.,' xv, 1896, p. 24).

Umbonula pavonella, Alder (= Mucronella pavonella, auctt.[1]).

The structure of the adult zoœcium (fig. 10) closely resembles that of U. verrucosa, and I venture to place the two species in the same genus. There is no umbo nor median avicularium, but the frontal shield ends in a rounded median lobe which is not raised above the level of the rest of the shield. Each of its lateral shoulders (*f. sh. d.*) bears a conspicuous avicularium (*avic.*). Its free surface rises into a series of radial buttresses, and the areolæ (*ar.*) between these communicate with the general body-cavity by pores arranged as in U. verrucosa. My preparations show with great distinctness that cords of living tissue (*w*) traverse these pores, and unite to form a continuous sheet of living substance (indicated by the brilliantly stained nuclei) which overspreads the entire frontal shield even in old zoœcia. The basal wall is not provided externally with a living membrane.

It is well known that the front surface of Cheilostome zoœcia may alter greatly with age. The original pattern may become lost, the thickness of the wall may increase very greatly, and the orifices of the zoœcia may finally be completely covered by secondary calcification. All these changes can be understood when it is realised that the frontal shield of an Escharine Cheilostome is covered by living tissue. Milne-Edwards (1836, p. 27), in discussing the alterations which take place with age in Escharine forms, came to the conclusion that the calcareous matter was a living tissue which grows like a bone. Goldstein (1880, p. 48) has stated that in Mucronella ellerii the brilliant scarlet colour "seems to be located in a fleshy epidermis, with which the stony polyzoary is coated." This is the "epitheca" of many authors, commonly seen in dry preparations as a membrane overspreading the calcareous frontal shield, and consisting, in reality, of an external cuticle and subjacent living tissue.

[1] Hincks (1880), p. 376.

The existence of the epitheca is responsible not only for the ordinary form of secondary calcification, but it explains the condition so commonly found in Cellepora, where new zoœcia originate on the free surfaces of the old ones. This appears to be the result of the separation of the epitheca from the calcareous wall, the subjacent space (which is morphologically part of the body-cavity) increasing in size and forming the body-cavity of a new zoœcium.

Lepralia pallasiana,[1] Moll (Pl. 17, fig. 41).

The frontal wall of the young zoœcium is at first Membranipora-like. Calcification begins at the proximal end by the formation of a thin calcareous film, which is perforated by large, uniformly spaced pores. This film is formed in situ beneath a delicate epithecal membrane. The process proceeds with considerable rapidity until the whole of the frontal wall is calcified, with the exception of the operculum, between which and the distal end of the zoœcium occurs a portion of the frontal wall, with a single row of large pores. In the earlier part of this process the polypide bud is small, and is at the proximal end of the zoœcium, being connected with the membranous frontal wall by a cord of cells. This becomes hollowed out to form the tentacle sheath (fig. 41), at the distal end of which appear two thickenings, the opercular glands (*op. gl.*). When the calcification is completed, the compensation-sac (fig. 41, *c. s.*) begins to be obvious as a well-marked cavity, extending from the base of the operculum beneath the calcareous frontal wall, and at first much shorter than the operculum. Into the floor of the sac are inserted the parietal muscles (*p. m.*), which, in the immature zoœcium, radiate even from distant parts of the lateral walls of the zoœcium.

The sac rapidly grows to such an extent that it underlies the whole of the frontal wall, the parietal muscles thereby acquiring an arrangement similar to those of Cribrilina.

[1] Hincks (1880), p. 297.

The process is identical with that which has been described above in Euthyroides episcopalis. The fact that the wall of the compensation-sac becomes tightly pressed against the lateral wall of the zoœcium makes it difficult to see its outline in the old zoœcia; and the same applies to many other Cheilostomata. But in a decalcified preparation the characteristic parietal muscles can be seen, even in old zoœcia, with the utmost distinctness.

The operculum articulates with two small condyles which are situated just on the distal side of its proximal broader part. The appearance of two linear longitudinal submarginal sclerites (fig. 41) is due to the special development of the vertical flange into two lateral ridges, the distal connecting part of the flange being less developed. The occlusor muscles (*occl.*) are inserted into these lateral ridges, and they originate low down from the vertical walls of the zoœcium, either from the lateral walls or from the distal wall. The divaricator muscle is the distal group of parietal muscles on each side. I am not certain whether the insertion of these is directly into the base of the operculum or into the floor of the compensation-sac close to the operculum.

The small, non-porous, suboral region of this species may be taken to indicate the former presence of a suboral avicularium[1] (as in Umbonula verrucosa). This view is confirmed by the fact that a few of the zoœcia actually possess a small avicularium with a semicircular mandible, which, when closed, lies horizontally, and points away from the operculum.

L. pallasiana is one of the forms which has been specially studied by Calvet (1900), many of whose statements I can confirm, although he has not observed the compensation-sac. In the younger zoœcium shown in his pl. xiii, fig. 20 (L. foliacea), it appears to me that he indicates the development of the compensation-sac as an ectodermic invagination at the proximal end of the operculum. In his pl. vi, fig. 1,

[1] Waters (1883, p. 430) calls attention to the common occurrence of the suboral avicularium in Cheilostomes.

which in other respects gives a good idea of the genera structure of the zoœcium, I think he has put the insertion of the occlusor muscles too near the proximal end of the operculum.

Lepralia dorsiporosa, Busk[1] (fig. 45).

In one respect this species appears to me to show more primitive characters than L. pallasiana. The distal prolongations (*f. sh. d.*) of the frontal shield do not completely surround the orifice, the point where they meet being commonly indicated by a slight emargination on the distal side of the zoœcium. Each distal prolongation typically bears an avicularium (*avic.*).

The compensation-sac is seen with great distinctness in a decalcified preparation. It underlies the whole of the frontal wall on the proximal side of the operculum, and it is provided with typical parietal muscles. The distal group on each side is specially strong, and it appears to me that the part of the compensation-sac immediately adjacent to the base of the operculum, into which these muscles are inserted, is somewhat fascia-like, an arrangement which confirms the view that the muscles function as divaricators. The condyles (*cond.*) are well-developed recurved hooks.

Lepralia sincera, Smitt.[2]

In this species, for specimens of which I am indebted to Dr. Levinsen, the compensation-sac and its muscles resemble those of the preceding species. The distal shoulders of the frontal shield extend no further than about the middle of the operculum. One of these shoulders is occasionally provided with an avicularium.

Lepralia haddoni, n. sp. (figs. 38, 39).

Zoarium encrusting or bilaminate (Escharine). Zoœcia in regular longitudinal rows, each about 700—900 μ long and about 370 μ broad. Surface covered by a distinct epitheca.

[1] 1884, p. 143.

[2] 'Öfv. k. Vet.-Ak. Förh.,' xxiv (Bihang, 1867), 1868, pp. 28, 177.

Proximal part of the frontal shield with numerous large pores, which do not extend to the distal end of the zoœcium. The oral end of the zoœcium may be somewhat raised above the general surface of the flat frontal shield. A rounded suboral lobe occurs, and may have almost the appearance of a mucro. Ordinary orifices and opercula somewhat longer than broad, with a concave proximal margin, 210—250 μ broad; fertile zoœcia with trifoliate orifice and operculum, 320—340 μ broad. External ovicells only represented by the somewhat hood-like calcareous wall at the distal end of the zoœcium. An avicularium, with long linear mandible, commonly occurs on one side of the orifice. Basal surface smooth, its intersection with the four vertical walls forming a regular oblong. Pore-chambers absent.

Torres Straits, A. C. Haddon collection, 1888–9.

This species somewhat resembles L. feegeensis, Busk, but differs from it in the absence of external ovicells. It is of interest in throwing light on the meaning of the occurrence of dimorphic opercula. The outline of the ordinary operculum (fig. 38) is not unlike that of the A-opercula in Euthyris obtecta. The B-opercula are much wider, and are trifoliate. In either kind of zoœcium there may be an avicularium on one side of the orifice, its acute mandible sloping, when closed, towards the distal end of the zoœcium. The compensation-sac is present in both kinds of zoœcia, and has typical parietal muscles. In some zoœcia it contains long wavy filaments, which may be parasitic Algæ or Fungi. In the zoœcia with trifolate operculum an ovary (fig. 39) is developed at the basal end of one of the lateral walls. A spherical ovisac, with delicate walls, makes its appearance at the distal end of the zoœcium, on the basal side of the operculum and tentacle sheath. Into this sac are inserted muscle-fibres, which radiate to it from the adjacent parts of the basal and lateral walls. In one zoœcium an egg has matured and has become filled with yolk, its diameter nearly equalling that of the zoœcium. This egg has passed into the

interior of the spherical ovisac, while the ovary still remains in its original position.

My preparations do not enable me to trace the origin of the egg-containing sac, which may, however, be a diverticulum of the vestibule, as described by Calvet (1900, fig. 42, on p. 266) in Lepralia pallasiana.

The conclusion pointed to by these facts is that the dimorphism of the opercula indicates the derivation of the species from forms provided with ovicells; in which, as is well known, the operculum of the fertile zoœcium is commonly larger than that of the other zoœcia.

Flustra cribriformis, Busk.[1]

This species is introduced at this point in further illustration of the morphology of the ovicell. Its frontal wall is, of course, typically Flustrine. The ovicell is of the type usually described as "internal,"[2] and is merely represented by a more or less hemispherical bulging of the distal zoœcial wall into the next zoœcium. Into this space projects a spherical vesicle, which lies just beneath the vestibule, as in the foregoing species. The polypides are retracted to the extreme proximal end of the zoœcium. In some cases I have been able to detect a very small ovary in one of the proximal corners of the zoœcium, near the basal wall; but in consequence of the position of the polypides I cannot say whether the ovary is parietal or attached to the polypide. The egg enters the spherical sac, in some manner which has not been observed, while it is still very small. It receives its yolk while in the sac, and when it is full grown it is so large that with its investing sac it occupies as much as half of the body-cavity.

Schizoporella linearis,[3] Hass. (figs. 48, 52).

The characteristic "sinus" or projecting proximal tongue of the operculum of this genus is very similar to the part of the operculum which in certain species of Lepralia occurs

[1] 1852, p. 51; 1884, p. 58.
[2] Cf. Levinsen (1891), p. 275.
[3] Hincks (1880), p. 247.

on the proximal side of the condyles. It appears to me that the function of the tongue is partly to close the aperture of the compensation-sac, and partly to give suitable leverage for the action of the divaricator muscles.

S. linearis is characterised by the possession of a pair of suboral avicularia, with pointed mandibles. Hincks (1880, p. 251) has described in this species a form of "oœcium," associated with a rudimentary zoœcium. My preparations show clearly that these supposed ovicells (fig. 48, *avic.*) are in reality gigantic suboral avicularia,[1] of the type well known in Retepora monilifera, var. munita, Hincks.[2] The greatly swollen region distal to the mandible is occupied by the enormous occlusor muscles, which differ only in size from those of the ordinary avicularia, their relation to which is further shown by the fact that a single gigantic avicularium may lie obliquely across the zoœcium instead of longitudinally as in fig. 48. The compensation-sac (fig. 52, *c.s.*) of the zoœcia is small, and even in zoœcia with fully mature polypides is commonly no larger than in the specimen figured.

The sinus of the operculum (fig. 52) fits into a corresponding emargination in the frontal shield. At a deeper level are seen the two condyles (*cond.*) which constitute the hinge. The frontal wall is of considerable thickness, and its distal margin, in the neighbourhood of the sinus, is bevelled off in precisely the way noticed in Euthyris clathrata (fig. 26). This results in the formation of a groove, the outer end of which is closed by the sinus of the operculum, while the inner end (fig. 52, *x*) is distinctly larger. When the operculum is open, its plane must be approximately parallel to the part of the bevelled surface which lies in the middle line. A short tube is thereby formed by which water can enter or leave the compensation-sac.

The compensation-sac develops as in Lepralia pallasiana. The calcification takes place beneath the epitheca,

[1] Waters (1885, p. 6, and 1892, p. 274) has previously stated that this is the case.

[2] 'Ann. Mag. Nat. Hist.' (5), i, 1878, p. 361.

since a layer of nuclei can be seen superficial to it. The parietal muscles are very delicate. The occlusor muscles originate from the distal wall, but I have not certainly seen divaricator muscles.

Schizoporella sanguinea, Norman (fig. 46).

This is the form described by Waters,[1] in his paper on the Polyzoa of Naples, as Lepralia pertusa, var. sinuata.

The operculum is rather stronger than in S. linearis, and it has a well-marked marginal sclerite which is distinctly thickened at the points where it articulates with the condyles. The compensation-sac (fig. 46, *c. s.*) is beautifully shown in specimens from which the basal wall has been removed. The parietal muscles radiate into its lateral walls, and the external parts of its basal wall, from the lateral and proximal walls of the zoœcium. The distal parietal muscles (*p. m.'*), which stretch transversely across the zoœcium, probably act as divaricators.

Dry specimens show the epitheca, stretched over the tubercles of the reticulately thickened frontal shield.

Schizoporella australis, Haswell.[2]

This species is characterised by having an elongated avicularium on the proximal side of the orifice, with an acute mandible directed obliquely towards the proximal end of the zoœcium when closed. The condyles are strong, and have denticulated edges (fig. 47). The continuity of the floor of the compensation-sac with the sinus of the operculum is clearly seen in the preparations. The sac resembles that of S. linearis.

Urceolipora nana,[3] MacGill., 1881.

The operculum is Schizoporella-like. At its proximal border opens a large compensation-sac which extends nearly

[1] 'Ann. Mag. Nat. Hist.' (5), iii, 1879, p. 31, pl. viii, fig. 5.

[2] 'Proc. Linn. Soc. N. S. Wales,' v, 1881, p. 41.

[3] MacGillivray, 'Prodr. Zool. Vict.,' Dec. xi, 1885, p. 19; Busk (1884), p. 82 (as Calymmophora lucida).

to the proximal end of the zoœcium, a great part of the cavity of which it occupies. The two calcareous spines at the sides of the orifice have the effect of keeping the conspicuous epitheca, which invests all parts of the zoarium, stretched out at some distance from the wall of the flask-shaped zoœcium. The curved lines shown by Busk (1884, pl. xxxii, fig. 3 *b*) on the sides of the zoœcia indicate the edges of the thicker lateral calcified walls, and are probably the actual junction of the lateral and frontal walls. Their level corresponds nearly with that of the floor of the compensation-sac, which has parietal muscles. The sac originates with great distinctness as an invagination from the proximal border of the operculum.

Smittia trispinosa, Johnst., var. arborea, Lev.[1] (fig. 42).

The specimens here referred to were sent to me, determined as above, by the Upsala Museum. Fig. 42 shows that there is a large compensation-sac (*c. s.*), the opening of which is overhung by a median lobe of the frontal shield. The condyles (*cond.*) are at a much deeper level, and are long, recurved denticles, which are crossed by the submarginal lateral sclerites of the operculum. They clearly form the hinge on which that structure moves. Typical parietal muscles are present. This form can hardly be regarded as a very typical Smittia.

Smittia reticulata,[2] J. MacGillivray (fig. 40).

My evidence with regard to this species is not complete. In specimens from which the basal wall has been removed I have just been able to detect a large compensation-sac with walls of great tenuity, into which parietal muscles are inserted. The median denticle (*m. t.*) or "lyrula"[3] appears to belong to the suboral avicularium (as in Rhynchozoon).

[1] "Bryozoer fra Kara-Havet," 'Dijmphna-Togtets Zool. bot. Udbytte,' 1886, p. 16.

[2] Hincks (1880), p. 346.

[3] Cf. Waters, 'Ann. Mag. Nat. Hist.' (6), iv, p. 14.

The principal interest of this species, in the present connexion, is as an illustration of the group of Cheilostomes in which there is but a single series of conspicuous marginal pores or areolæ (*ar.*).

Catenaria lafontii,[1] Aud. (fig. 49).

I consider this species in this place on account of its possession of a typical compensation-sac; but I shall discuss its affinities later. The zoœcia are very long, curved, narrow proximally, and dilating distally. From the back of the distal end usually originate a pair of new zoœcia (*z.'*), each starting in a calcareous base containing a body-cavity, into which is fitted a chitinous joint (*j.*), which forms the connexion with the younger zoœcium. The oral extremity of the zoœcium is surrounded by a circlet of short, hollow spines (*sp.*). The ovicell (*ov.*) is placed obliquely on the distal side of the orifice, and an extremely strong suboral avicularium (*avic.*) guards the entrance to the compensation-sac. There is some evidence that the base of the avicularium has been derived from a single pair of suboral frontal spines. The porous region of the zoœcial wall in the main corresponds with the limits of the compensation-sac (*c. s.*), but a few pores occur outside that region, even on the basal surface.

The compensation-sac is extremely distinct, and is indicated in a figure by Calvet (1900, pl. viii, fig. 9), who does not, however, make any reference to the structure. It is provided with several groups of parietal muscles (*p. m.*). The operculum is placed obliquely, and its base is distinctly continuous with the floor of the compensation-sac, the orifice of which is rather large. Each occlusor muscle (*occl.*) originates from the partition wall between the body-cavity of the zoœcium and the base of the daughter-zoœcium of its own side. I have not distinguished any divaricator muscles.

[1] Busk (1852), p. 14.

Vittaticella cornuta,[1] Busk (fig. 56).

Maplestone[2] has recently suggested the generic name Vittaticella for the "vittate" species of Catenicella, the subdivision of which appears to me desirable.

Fig. 56 shows that Vittaticella is provided with a well-developed compensation-sac (*c. s.*). The younger zoœcium further illustrates the fact that the development of this structure is typically Lepralioid. The sac is figured by Jullien (1888, 3, pl. xi), in two species of Catenicella, in both the young and the adult condition. A wide crescentic opening into the sac is seen in the younger zoœcium (fig. 56) between the base-line of the operculum and the proximal border of the orifice. Amongst the parietal muscles which radiate from the wall of the sac can already be distinguished a distal group (*p. m.'*), the future divaricator muscles. In the next zoœcium the compensation-sac is so large as to underlie nearly the whole of the frontal surface.

Each vitta (*v.*) is a tubular cavity, running longitudinally along the edge of the zoœcium, and bounded externally by a delicate uncalcified membrane. The cavity communicates by a single series of funnel-shaped tubes with the body-cavity.[3] In the young zoœcia the whole of this arrangement is filled with a brilliantly staining cellular material; but the structure is identical in the older zoœcia, in which remains of cells may still be made out.

I refer to the morphology of the vittæ below when dealing with Catenicella hastata. Their function is, perhaps, to assist in the deposition of the calcareous wall. The zoœcium in this species is strengthened by a great thickening of its edge, which is more pronounced in the region of the vitta than elsewhere. The vitta extends along the whole length of the lateral thickening, and in the more elongated zoœcia it may have as many as ten pores.

[1] Busk (1852), p. 11.
[2] 'Proc. Roy. Soc. Vict.' (N. S.), xiii, 1901, p. 201.
[3] Cf. Waters (1881), p. 318.

The characteristic horns of this species are probably to be regarded as modified avicularian zoœcia. In certain zoœcia one of the horns is replaced by a large normal avicularium.

Catenicella alata, Wyv. Thomson[1] (fig. 53).

The zoœcial structure of Catenicella has been described by Busk (1852, p. 4), and by Waters (1883, p. 428). The zoœcium develops on each side three structures, which together form the great wings so characteristic of this species. Taking a case which is not complicated by the presence of the twin zoœcium (cf. fig. 56) which occurs just before a bifurcation of the branch,[2] the zoœcium is found to be somewhat spindle-shaped, each end passing into a tubular sheath which surrounds the chitinous joint by which it is connected with its neighbours. The basal surface of the zoœcium is extremely gibbous, and projects in this direction far beyond the wings. The frontal surface is nearly flat. The large orifice has, on its proximal side, a scutiform calcareous region bearing five fenestræ closed by membrane. The zoœcium is considerably wider than this scutiform plate, its convex lateral surfaces being overlapped by parts of the wings.

Each wing consists of three parts: (1) a large proximal cavity (infra-avicularian + pedal compartments of Waters), which is almost two thirds of the length of the zoœcium, and is provided on its frontal surface with two large membranous fenestræ, one at each end (fig. 53, *inf. avic.*); (2) a transverse cylindrical cavity, the free outer end of which has a membranous vacuity (*avic.*); (3) a large distal cavity with a single large fenestra, its distal point being uncalcified (*sup. avic.*). The second of these cavities is morphologically an avicularian zoœcium, as is proved by comparision with other species of Catenicella.

The five suboral fenestræ perforate the entire thickness of the calcareous frontal wall. At the level of their internal

[1] 'Nat. Hist. Review,' v, 1858, "Proc. of Societies," p. 137.

[2] Waters terms the solitary zoœcium a "globulus," and the two associated zoœcia a "biglobulus."

openings a sharply marked curved line (*x*) indicates the edge of a calcareous plate similar to that described below in C. plagiostoma. The markings between the fenestræ and the operculum are somewhat variable. In a specimen which partly dried up during its preparation, fine slits containing air were noticed, radiating from the fenestræ to the orifice.

The compensation-sac of this species is described by Jullien (1888, 3). It is well developed, but its complete outline is not easily seen in the mature zoœcium in consequence of the fact that its breadth is greater than that of the exposed scutiform frontal wall.

Catenicella plagiostoma, Busk, var. setigera, MacGillivray[1] (fig. 54).

This species is remarkable for the obliquity of its orifice, and for the enormous development of its avicularia, which may have very different forms, even on opposite sides of the same zoœcium (fig. 54). The infra-avicularian compartment (*inf. avic.*) is almost entirely closed by membrane, the single fenestra so formed extending mainly over the side and basal surface of the zoœcium. The supra-avicularian compartment (*sup. avic.*) similarly has membranous walls, a very large fenestra being common to it and the avicularian zoœcium.

The structure of the frontal wall is more easily made out than in C. alata. The outer calcareous layer is reduced to a system of conspicuous bars which unite with a calcareous framework surrounding the operculum. The internal calcareous layer is an obliquely oval plate[2] (*pl.*), which projects towards the proximal end of the zoœcium. This forms part of the roof of the compensation-sac, from which muscles (*p. m.*) can be seen radiating out to the adjacent parts of the wall of the zoœcium. The distal groups of parietal muscles (*p. m.'*) appear to act as divaricators.

In a back view of a zoœcium it is seen that the avicularian zoœcium has a very large oblique fenestra proximal to the

[1] 'Prodr. Zool. Vict.,' Dec. iii, 1879, p. 17.

[2] This structure is described by Waters (1883, p. 429).

mandible, and another distal to the same structure, and common to it and the supra-avicularian compartment. From various parts of the membrane covering the dorsal fenestræ rise the spine-like processes to which the variety owes its name.

Catenicella hastata, Busk[1] (fig. 55).

The supra-avicularian compartment (*sup. avic.*) is calcified except at its extreme tip, the walls being perforated by small pores. It forms a broad, flattened spine at the upper lateral corner of the zoœcium. The avicularian mandible is minute, but the avicularium possesses, in addition to its occlusor and divaricator muscles, a polypide rudiment (*pol.*), as in various other Cheilostomes. I have noticed a similar structure in other species of Catenicella. The infra-avicularian compartment (*inf. avic.*) is completely divided into two. The outer wall of both these cavities is usually completely calcified, but the proximal one may have a slit-like membranous fenestra, which is usually lateral. Between the proximal portion, designated by Waters (1883, p. 428) the "pedal compartment," and the zoœcium, was noticed a row of three communication pores (*c. p.*). A comparison with Vittaticella suggests that the vittæ shown in fig. 56 are the last remains of the pedal compartments with their communication pores. This view has already been maintained by Waters (p. 428), and, though not quite in the same manner, by Jullien (1888, 3). I have no suggestion to make with regard to the function of the lateral "compartments" in Catenicella.

The frontal wall has from seven to nine small fenestræ, from which tubular cavities pass transversely towards the middle line. The arrangement is strikingly Cribrilina-like, and the resemblance is intensified by the existence of irregular slit-like cavities alternating with the fenestræ, which suggest an incomplete lateral fusion of frontal bars.

The compensation-sac is usually clear. Its floor appears to be deeply pigmented, but this may be the result of the

[1] Busk (1852), p. 7; 1884, p. 10.

method employed, this preparation being the only one which I have made with Mayer's cochineal tincture. The species seems, however, to have a special development of pigment, as indicated by Maplestone.[1] The compensation-sac develops as in Vittaticella.

Catenicella lorica,[2] Busk.

The remarkable fertile zoœcia which characterise the genus Catenicella are well seen in this species to be provided with a large compensation-sac, with strong parietal muscles. The three fenestræ of the ordinary zoœcia appear to perforate only a single thin calcareous layer, the inner layer being completely absent.

Catenicella wilsoni,[3] MacGill.

The great size of the fenestra of the infra-avicularian compartment makes it an easy matter to see the outline of the large compensation-sac of this species, and the arrangement of its muscles.

(D) Microporelloid Genera.

Under this heading I consider a few of the forms with a "median pore," though I am by no means certain that all such forms are related to one another.

Calwellia gracilis, Maplestone[4] (figs. 61, 62).

The zoœcia are in pairs, back to back, the plane uniting the middle line of two zoœcia being at right angles to the

[1] 'Trans. Proc. Roy. Soc. Vict.,' xviii, 1882, p. 49.

[2] Busk (1852), p. 6.

[3] MacGillivray, 'Prodr. Zool. Vic.,' Dec. ix, 1884, p. 30.

[4] The form which I describe in this paper was figured by Maplestone, without description, in a paper entitled "Observations on Living Polyzoa," in 'Trans. Proc. Roy. Soc. Vict.,' xviii, 1882, p. 48, fig. 9 [the plate has no number]. It has not the triangular shape mentioned by Wyville Thomson (1858) in his original account of C. bicornis. It is not the species described by MacGillivray as C. gracilis in 'Trans. Proc. Roy. Soc. Vict.,' xxii, p. 128; see also the same journal (N. S.), ii, p. 106.

similar plane of the next pair. The narrow proximal part of each zoœcium extends the whole length of the subjacent pair, in such a way that each zoœcium originates from the next lower one which looks in the same direction as itself.

The two lateral horns are not calcified at their tips (fig. 62, *f*). Below the oblique orifice is a triangular region sloping to the median pore (*m. p.*), which occupies the most projecting part of the zoœcium. The middle line of this region is marked by a suture (*s.*), on each side of which is an "oculiform" pore. Besides the communication pore at each end, by which it is connected with its neighbours in the same longitudinal series, each zoœcium has a pair of distal communication pores placed on the basal side, by which its soft tissues are continuous with those of the narrow proximal half of the next distal pair of zoœcia, while its own proximal half is similarly provided with a pair of pores (*c. p.*) which lead to the two zoœcia of the subjacent pair.

The fully developed compensation-sac (fig. 62, *c. s.*) occupies a large proportion of the body-cavity. Fig. 61 represents a compensation-sac which is about half grown, with its parietal muscles. The sac does not extend to the semicircular operculum, the straight base-line of which appears to constitute the hinge. It develops in a Lepralioid manner, a small, apparently solid mass of cells appearing beneath the newly formed median pore; and to this mass the parietal muscles radiate from various parts of the zoœcium. Somewhat earlier the uncalcified, oblique, terminal wall of the zoœcium extends as a triangular point as far as the median pore, so that the sac is probably derived from the proximal part of the orifice. The suggestion has often been made (cf. Hincks, 1880, p. 237) that the Microporellid median pore has been formed by the closure of the sinus of a Schizoporella-like ancestor. The above-described immature stage of C. gracilis appears to point in this direction.

The occlusor muscles (*occl.*) are easily seen, but I have found no divaricators.

Calwellia sinclairii,[1] Busk (fig. 60).

Waters (1888, p. 17) has described the compensation-sac in this species, as well as in C. bicornis and Urceolipora dentata, and he correctly states that it opens to the exterior by means of the median pore. I agree with Waters that C. sinclairii should be placed in the genus Calwellia. It differs from C. gracilis principally in the fact that the proximal half of the zoœcium is almost as broad as the distal half, and the zoœcia do not therefore appear to be so definitely arranged in pairs.

The operculum is a segment of a circle somewhat greater than a semicircle, and having a straight base-line. From the middle line of this a longitudinal suture (*s.*) passes to the transversely elongated median pore (*m. p.*), and on each side of the suture is a round fenestra. The suture can usually be traced down the entire length of the zoœcium. The position of the lateral horns of C. gracilis is indicated by a fenestra (*f.*), in the neighbourhood of which are one or two smaller pores. The median pore is somewhat crescentic, with an anterior concavity. The lateral edge of the large compensation-sac does not pass to the base of the operculum, but turns sharply inwards at the level of the median pore, and runs into the broad tongue-like lobe of the wall of the zoœcium which gives the pore its crescentic form.

The operculum has a well-marked triangular lobe of its vertical marginal flange (*fl.*), into the apex of which the occlusor muscle is inserted, as in Flustra.

Calwellia dentata,[2] MacGillivray.

It appears to me that this species should be separated from U. nana,[3] and placed in Calwellia, the generic character of which would then have to be amended so far as relates to the arrangement of the zoœcia. In C. dentata these are placed

[1] Busk (1884), p. 103.

[2] 'Prodr. Zool. Vict.,' Dec. xi, 1885, p. 19.

[3] As suggested by Waters (1888, p. 10).

back to back, alternately, all the zoœcia looking towards one or the other edge of the branch. The zoœcial characters agree with those of C. sinclairii. There is a large compensation-sac, opening by a median pore, which is transversely elongated, but the concavity of which is on the proximal side. Between this and the operculum are two fenestræ, placed as in C. sinclairii. In addition to two lateral horns, similar to those of C. gracilis, there are three other oral spines placed more distally.

Ichthyaria oculata, Busk[1] (fig. 59).

There can be no doubt that this species was incorrectly placed by Busk in the Bicellariidæ, a family with which it appears to have no affinity. Its more natural position would probably be in the Calwelliidæ,[2] with which it agrees in the characters of its zoœcium and of its ovicell. The zoœcia are arranged in a double alternate series, all facing in one direction. The median pore (*m. p.*) is circular, and is situated on the axial side of the middle of the zoœcium. It is connected with the operculum by a longitudinal suture (*s.*), on each side of which is a funnel-shaped fenestra, as in Calwellia. In correlation with the asymmetrical position of the median pore the abaxial fenestra is much further from the suture than is the other one. There are one or two distal fenestræ, probably indicating the former development of oral spines.

The compensation-sac (*c. s.*) is arranged as in Calwellia. It opens by the median pore, and therefore ends at some distance from the operculum. The parietal muscles (*p. m.*) occur as a series of definite groups, as in Flustra. Calcification is deficient along a line extending the whole length of the basal side of the zoœcium. The line is narrow for the greater part of its course, but dilates at each end. The older parts of the colony are supported by a calcareous

[1] Busk (1884), p. 46.

[2] Waters (1888, p. 10) places it in Calwellia, a view which seems not unreasonable.

thickening, which runs along each margin of the branch. The retractor muscles of the polypide originate from the two lateral walls. On each side there is a strong fan-shaped group passing to the base of the tentacles, and another passing to the junction of the pharynx with the œsophagus.

Onchoporella bombycina, Busk[1] (not Ell. and Sol.).

Although I have had only dry material of this species to work with, I can state that there is a well-developed compensation-sac, opening by the crescentic median pore, the tongue-like lobe to which the crescentic shape is due being distal, and seeming to be a triangular membrane which curves into the distal border of the compensation-sac (as in fig. 60). The operculum is of very delicate texture. On either side of the orifice, somewhat proximally, there is a short spine, on the proximal side of which is a pore, which is either a simple funnel-shaped deficiency of the calcareous wall, or it consists of two, or even three, funnel-shaped tubes contained in a single longitudinal groove. A similar arrangement is shown in fig. 60 (*f.*). One or two pores of the same kind may continue the line of this groove down the frontal surface of the zoœcium.

The branches have a calcareous marginal thickening, which may have a zigzag course; it is composed of numerous small pieces, an arrangement which clearly gives a certain amount of flexibility to the frond.

Microporella malusii,[2] Aud. (fig. 63).

The median pore (*m. p.*) has a distal concavity, due to the projection into it of a tongue-like process which is partly membranous. Between this and the straight base-line of the semicircular operculum is a triangular group of pores, the

[1] Busk (1852), p. 52. The species described by Ellis and Solander ('Nat. Hist. Zooph.,' 1786, p. 14), from the Bahama Islands, appears to be a Euthyris.

[2] Hincks (1880), p. 211.

apex of the group pointing to the median pore. Round the edge of the zoœcium is a single line of pores. This arrangement is constant in my Neapolitan specimens. The communication pores open into "pore-chambers" (*p. c.*), as pointed out by Levinsen (1891, pp. 250, 285).[1]

The compensation-sac (*c. s.*) is thin-walled, its outline being somewhat heart-shaped when seen from the basal surface. The median pore opens into it considerably on the proximal side of its distal margin, a triangular bay (*corn.*) of the body-cavity indenting the membrane of the compensation-sac in the immediate neighbourhood of the frontal surface. The parietal muscles (*p. m.*) are strong, and are arranged in distinct groups.

The function of the median pore in M. malusii has frequently been discussed, and my results do not agree with those of any of my predecessors. Jullien (1888, 4, pp. 36, 39) gives the name "fenestrula" to the median pore, which he describes as forming the narrow end of a funnel ("cornicula"), the other end of which opens into the tentacle sheath. Jullien figures the cornicula in pl. xv, fig. 2, from which it appears to me clear that the funnel is the part of the body-cavity which I have described above (fig. 63, *corn.*) as indenting the distal outline of the compensation-sac.

Pergens (1889, p. 507) does not believe in the existence of Jullien's compensation-sac, and describes the diaphragm or vestibule as opening into the body-cavity and not into the tentacle sheath.

The commonly received opinion that the vestibule is traversed by the tentacles during their protrusion is, however, based on too many observations to be lightly dismissed.

Pergens further states (p. 506) that the median pore of M. malusii opens into the body-cavity. The "longitudinal muscles" mentioned by him were probably parietal muscles, while I suspect that the appearance of a "sack" between

[1] For the pore-chambers of Cheilostomata see also Waters (1898), p. 658.

the operculum and the median pore can be explained in the same way as Jullien's "cornicula" mentioned above.

Levinsen (1891, p. 285) states that the median pore, like the other pores, is closed by a membrane.

Microporella ciliata,[1] Pall.

The compensation-sac is like that of M. malusii, which this species further resembles in the grouped condition of the parietal muscles. I have not made out the details of the opening of the sac. There is a membranous portion in the tongue of the crescentic pore, as in M. malusii.

(E) Microporoid Genera.

Micropora, sp.[2] (figs. 57, 58).

The large lateral foramina serve for the transmission of the tendons of the depressor muscles (fig. 58, *depr.*) of the frontal membrane, as correctly stated by Jullien (1888, 4, pp. 77—81, pl. xiv, fig. 1), who terms them "opesiules." The opesiule is a complete calcareous tube (*l. r.*), the base of which joins the basal wall or the lateral wall of the zoœcium, the two conditions often occurring on opposite sides of the same zoœcium. The tube usually gives off a curved lamella (fig. 57) on its distal side, near the basal surface. From the recess thus formed originates the occlusor muscle (*occl.*), whose long tendon passes obliquely to be inserted into one of the lateral corners of the vertical flange of the operculum. The depressor muscle (*depr.*) is much stronger. Its fibres converge to a tendon which passes through the opesiule and is inserted into the frontal membrane. I regard these muscles as a special development of the parietal muscles, which are otherwise unrepresented. The calcareous frontal wall (*crypt.*) is complete, and the relations of the depressor muscles indicate that it is a cryptocyst.

[1] Hincks (1880), p. 206.
[2] Torres Straits, A. C. Haddon Coll.

Steganoporella alveolata, Harmer.[1]

I have previously alluded[2] to the muscular system of this species. That of the B-zoœcia is more highly developed than in any other Polyzoon with which I am acquainted.

The B-operculum has the form shown in figs. 64, 66. Its mode of articulation differs in a striking way from that of the Cheilostomes previously considered. Although its base is continuous with the unmodified frontal membrane which stretches across the whole of the proximal half of the zoœcium, a strong basal sclerite (*b. s.*) is differentiated. Into the two ends of this are inserted, beneath the frontal membrane, two ligaments (*lig.*) which, continuing the direction of the sclerite, become attached to the strong condyles (*cond.*). The operculum is thus slung by two tight transverse cords between the two condyles, and this arrangement constitutes the hinge. The basal sclerite probably has the further object of playing over the projecting part of the structure which I have called the median process (fig. 66, *m. pr.*), and of preventing the operculum from being pulled too far by the contraction of the enormous occlusor muscles. Of these there are two pairs, which originate, with the divaricator and depressor muscles, deep down within the lateral recesses at the sides of the median process. The insertion of the occlusors is shown in fig. 64. One pair (*occl.*), which probably correspond with the normal Cheilostome occlusors, pass by strong tendons (*tend.*) into the occlusor tubercles (*occl. t.*) of the operculum, but the tendon is also continuous with a fascia (*f.*), which is connected with the strongly projecting proximal end of one of the main sclerites (*m. s.*) of the operculum. The second pair, which I distinguish as the distal occlusors (*occl.'*), are inserted into a strong transverse fascia (*f.'*) which lies between the two main sclerites. In fig. 64, which represents an operculum torn away from its zoœcium, this fascia has been displaced from its natural

[1] 1900, p. 287.

[2] Loc. cit., p. 230.

position, which is shown in figs. 65, 66. From these it is apparent that the median part of the fascia is exactly transverse and vertical when the operculum is closed, and that on each side it curves round in order to be attached to the proximal end of the main sclerite. It thus results that while not much more than the edge of the middle part of the fascia is seen in a view from the basal or from the opposite side, the surface of the lateral parts is seen under the same conditions. I have been unable to ascertain with certainty whether the median part of the fascia is inserted into the operculum or whether it has a free edge in this region.

The origin of the muscles can best be seen in a basal view of a zoœcium from which the basal wall has been removed in the way recommended on p. 265. The lateral recesses (*l. r.*) are here seen to be almost entirely filled by four strong muscles. Of these the distal occlusors (*occl.'*) are far the strongest, and they originate from the distal half of the floor of the lateral recesses. The proximal or normal occlusor (*occl.*) originates from the proximal half of the lateral recess, in its outer part. The course of its tendons (*tend.*) is indicated in figs. 64—66.

The distal occlusors, in helping to close the "orifice," probably tend to pull the whole operculum towards the distal end of the zoœcium, since their fascia is inserted largely into the projecting proximal ends of the main sclerite (figs. 65, 66). The proximal occlusors correct this tendency, as may be inferred from the direction taken by their principal tendons. When it is remembered that in this species each of the strong teeth of the operculum fits, when closed, into its own socket in the calcareous part of the zoœcium, it is obvious that the operculum must shut with great accuracy, and a proper correlation between the contractions of the two sets of occlusors no doubt has to be maintained. The accuracy of the closure is probably helped by the movement of the basal sclerite over the median process, and, of course, by the transverse ligaments uniting the operculum to the

condyles, as well as by the tension of the frontal membrane[1] continuous with the base of the operculum.

Although the distal occlusors are larger than the proximal pair, their tendency to shift the operculum from its proper position is probably adequately corrected by the proximal occlusors, which, although weaker than the others, have a more effective pull, in consequence of the greater obliquity of their tendon.

It appears to me that in certain positions assumed by the operculum, the distal occlusors would work to less advantage than the others. When the operculum is opened so far that its outer surface forms a right angle with the frontal membrane, the projecting ends of the main sclerites extend far to the distal side of the hinge. The operculum seen from its edge would have the appearance of a right-angled triangle, of which the hypothenuse is formed by the main sclerite, and a short side by the piece connecting the proximal end of the same sclerite with the base of the operculum. Both pairs of occlusors now probably pull, by means of their fasciæ inserted into the projecting ends of the main sclerite, on the short side of the triangle which is, in fact, an arm of a right-angled lever hinged at its angle. In so acting, the proximal occlusor probably pulls over the ligament (*lig.*) which connects the operculum with the condyle, the ligament thus forming a kind of pulley. The distal occlusors are probably specially important in the final stages of the closure.

Two muscles remain to be described. The depressor muscles (figs. 65, 66, *depr.*) originate from the innermost part of the lateral recess. Their tendon passes obliquely towards the proximal end of the zoœcium, ascending at the same time to reach the frontal membrane, into which it is inserted (fig. 66). Between the depressor and the proximal occlusor is a group of muscles which constitute the divaricator (*div.*).

[1] In my former paper I described this as the epitheca, a more general term which it would be better not to use in cases where the homology of the membrane with the frontal membrane of a Membranipora seems to be demonstrated.

At its origin this muscle is often difficult to distinguish from the depressor, but its tendon takes a different direction and is inserted into one of the ends of the basal sclerite of the operculum, or perhaps into the frontal membrane immediately adjacent to the basal sclerite.

I regard the divaricator and depressor muscles as a special differentiation of the parietal muscles of other Cheilostomes, and they are probably together the representatives of the depressor muscles of Micropora (figs. 57, 58), which occupy special cavities that may be compared with the lateral recesses of Steganoporella.[1]

In the A-zoœcia the distal occlusors seem to be completely absent. The zoœcium is more like that of an ordinary Cheilostome, with a single pair of occlusor muscles.

In view of the possibility that the B-zoœcia of Steganoporella may represent avicularia,[1] it is worth mentioning that in the gigantic avicularia of Flustra abyssicola (Davis Straits) I have noticed that the occlusors are in two groups. Of these the distal group consists of an enormous mass of muscle which fills up more than the distal half of the avicularian zoœcium, and its fibres are inserted into a broad median tendon. The proximal occlusors are paired; their tendons are at a deeper level than that of the distal occlusor, and they converge towards the base of the operculum. Jullien (1888, 4, pl. xii, fig. 3) indicates the occurrence of two sets of occlusors in the avicularium of Beania magellanica.

V. The Primary Zoœcium or Ancestrula.

The zoœcium which results from the metamorphosis of the larva is frequently found to show characters which differ

[1] This conclusion is confirmed by the figure given by Waters (1885, pl. xiv, fig. 42) of the mandible of Onychocella angulosa (? = antiqua), in which the formation of the hinge appears to be like that found in Steganoporella, while a fascia shown in the same figure closely resembles that of the distal occlusors of Steganoporella.

from those of the ordinary individuals of the colony. This, the primary zoœcium, has been termed the "ancestrula" by Jullien (1888, 4, pp. 27, 29), a name which he appears to have used merely to convey the idea that it was the actual ancestor ("zoœcie mère") of the other individuals of the colony. Smitt (1868, 1, p. 306) described the same thing as the "Tata form" of the Cheilostomes,[1] and clearly recognised their importance, stating that "Tata is for the Cheilostomes what Alecto showed itself to be for the Cyclostomes."

I am fully of Smitt's opinion with regard to this matter. The "ancestrula" is in all probability ancestral in the sense of retaining characters of phylogenetic importance. Smitt returns to the same subject in a later publication (1896), in which he again maintains the importance of the Tata form. Neviani (1898, p. 165) supports the same conclusion.

The frequency with which the Tata-like ancestrula (figs. 2, 6, 7) occurs in Cheilostomata is indeed remarkable, and there is a curiously small range of variation in the number of its marginal spines. I subjoin a few references to cases where an ancestrula of this type has been described.

Species.	Reference.	Number of marginal spines.	Remarks.
Electra pilosa, L.	Barrois, 1877, p. 241, pl. xv, figs. 5—8	5—7	
Membranipora flemingii, Busk	Hincks, 1880, p. 163	8—9	
Membranipora craticula, Alder	Hincks, 1880, p. 147	About 9	
Scrupocellaria scruposa, L.	Smitt, 1868, 1, p. 320, pl. xvii, fig. 42, etc.	8	Elongated.
Scrupocellaria scabra, Van Ben.	Smitt, 1868, 1, p. 314, pl. xvii, fig. 27	9	"
Scrupocellaria reptans, L.	Barrois, 1877, p. 183, pl. x, fig. 16	—	"

[1] The young zoœcia figured as Tata rugosa by Van Beneden ('Bull. Acad. Roy. Belgique,' xvi, pl. ii, fig. 14) are primary zoœcia of a Membranipora.

Species.	Reference.	Number of marginal spines.	Remarks.
Menipea ternata, Ell. and Sol.	Smitt, 1868, 1, p. 306, pl. xvi, fig. 15	10—11	
Bicellaria ciliata, L.	Smitt, 1868, 1, p. 335, pl. xviii, fig. 1	13	Infundibuliform.
Bugula sabatieri, Calvet	Calvet, 1900, p. 112 (fig. 13)	5	,,
Membraniporella nitida, Johnst.	Hincks, 1880, p. 201, pl. xxvii, fig. 6	14, of which 4 are oral	
Cribrilina punctata, Hass.	Hincks, 1880, p. 191	12	
Cribrilina monoceros, Busk	Jullien, 1888, 4, pl. iii, fig. 9	9	
Schizoporella spinifera, Johnst.	Hincks, 1880, p. 242, fig. 13	9—10	
Schizoporella unicornis, Johnst.	Barrois, 1877, p. 152, pl. viii, fig. 37	8	
Schizoporella crustacea, Smitt	Waters, 1900, pl. viii, fig. 13	?9	
Mucronella coccinea, Abildg.	Waters, 1900, p. 158, pl. viii, fig. 40	13	
Mucronella coccinea, Abildg.	Hincks, 1880, p. 373, fig. 17	11	
Mucronella peachii, Johnst.	Hincks, 1880, p. 361, fig. 16	11, of which 6 are oral	Modified Tata.
Mucronella variolosa, Johnst.	Hincks, 1880, p. 366	10—11	? Tata.
Porella concinna, Busk	Smitt, 1868, 2, p. 134, pl. xxvi, figs. 109—111	7—9	Variable.
Porella concinna, Busk	Barrois, 1877, p. 155, pl. vii, fig. 16	8	
Phylactella labrosa, Busk	Hincks, 1880, p. 357	"A few"	? Tata.
Microporella ciliata, Pall.	Hincks, 1880, p. 207, pl. xxviii, fig. 3	9, of which 7 are oral	
Microporella malusii, Aud.	Hincks, 1880, pp. 211, 212, figs. 10, 11	About 7, of which 2 are oral	
Microporella malusii, Aud.	Neviani, 1898, p. 6, fig. 3	10	Variable.

Cases in which the ancestrula is not Tata-like:

Species.	Reference.	Remarks.
Membraniporella melolontha, Busk	Hincks, 1880, p. 203	Aperture membranous, but not surrounded by spines.
Cribrilina annulata, Fabr.	Hincks, 1880, p. 194	Like the ordinary zoœcia.
Lepralia pallasiana, Moll	Hincks, 1880, p. 298	Like the ordinary zoœcia.
Lepralia pallasiana, Moll	Barrois, 1877, p. 145, pl. vii, fig. 1	Like the ordinary zoœcia.
Schizoporella (Hippothoa) hyalina, L.	Barrois, 1877, p. 168, pl. ix, figs. 9—16	Like the ordinary zoœcia.
Schizoporella (Hippothoa) hyalina, L.	Jullien, 1888, 4, p. 29, pl. iv, figs. 1—4.	Tata-like; resembling the ordinary zoœcia; or intermediate.
Schizoporella cristata, Hincks	Hincks, 1880, p. 254, pl. xl, fig. 6 *a*	Intermediate.
Smittia reticulata, J. MacGill.	Hincks, 1880, p. 346	Like the ordinary zoœcia.
Temachia opulenta, Jullien	Jullien, 1883, p. 13 (sep.), pl. xiv, figs. 26, 29	Cribrilina-like.

There is no other form of ancestrula which is known to occur in a number of different types of Cheilostomes, and it is impossible not to agree with Smitt and others that the view that the primary zoœcium shows ancestral characters has much to be said for it. In the majority of described cases the ancestrula is like that shown in fig. 2, and is a typical Membranipora-like zoœcium. In certain forms with an infundibuliform zoœcium the ancestrula has already acquired this type. This is the case in Bicellaria ciliata, while in Scrupocellaria the ancestrula may show distinct tendencies in the same direction. It is hardly necessary to point out how thoroughly the common occurrence of a Tata-like ancestrula confirms the general conclusions arrived at in this paper. It may be remarked that this type of ancestrula is by no means unlike that of a Cyclostome (which has, however, no spines); and these Polyzoa may probably be regarded as forms in which the frontal surface remains

circular and uncalcified, while the greater part of the zoœcium is constituted by the cylindrical lateral walls.

I do not know of any Flustrine form in which the ancestrula is other than Flustrine in respect of its frontal wall. In Membraniporella nitida the ancestrula is Tata-like, and shows clearly that the four oral spines are of the same nature as the remaining ten marginal spines figured by Hincks. This species is particularly interesting in the fact that some of the older members of the colony produced by budding may retain the Membranipora-like condition (Hincks, 1880, pl. xxvii, fig. 7), and possess a series of irregular marginal spines which do not unite. The remaining zoœcia have their frontal spines arranged with the regularity characteristic of the Cribrilinidæ in general.

The consideration of the Cheilostomata in which the ancestrula is not Tata-like is almost as instructive as that of the first set of cases.

In Hippothoa hyalina, Jullien (1888, 4, p. 29) states that the characters of the ancestrula are variable. In European specimens the frontal wall is fully calcified. The same condition was found in specimens from Tierra del Fuego, although in most of the colonies from this locality the ancestrula was a circular Tata-like zoœcium, with a large membranous aperture bordered by six inwardly curving marginal spines (Jullien, pl. iv, figs. 1—3), while in a third case (ibid., fig. 4) the ancestrula is at first Tata-like, but the membranous aperture subsequently calcifies, so that the orifice normal for the species is contained in a calcified oral region surrounded by the circlet of marginal spines. This leads to the form described by Jullien as Diazeuxia reticulata (ibid., fig. 5), in which the orifice of the ancestrula is completely Schizoporelliform.

Neviani (1898, p. 165) describes three varieties of the ancestrula of Microporella malusii. The first of these is an ordinary Tata form with ten marginal spines. The second more nearly resembles the normal zoœcium of this species, but agrees with one of the ancestrulæ described by Jullien (see

above) in having the orifice contained in a calcareous region which is surrounded by eight short spines. The third is particularly interesting in having a Schizoporella-like orifice.

Schizoporella cristata, according to the description given by Hincks, is another form with an intermediate type of ancestrula. The Schizoporelliform orifice is contained in a calcareous oval area, on the proximal side of which are three spines, while the orifice is provided with six oral spines.

The ordinary zoœcia of the form described by Jullien as Temachia opulenta are lageniform, and without spines, somewhat resembling those of Mucronella abyssicola. The ancestrula is obviously Cribriliniform. I have myself observed an analogous case. A Cribrilina (sp.?) from Funafuti, in the collection of the British Museum, has an irregular arrangement of pores on its frontal surface, something like that found in C. monoceros. The primary zoœcium is Membraniporella-like, with a perfectly regular double series of transverse bars, separated by simple slits.

Fig. 2 shows the ancestrula of a colony of Microporella malusii, from Naples. The frontal surface and the operculum are Flustrine. The marginal spines, some of which have been lost, were ten in number (as in one of Neviani's cases). They originate, like the frontal spines of Cribrilina, from foramina in the calcareous wall, a little outside the frontal membrane. The spines resemble the three oral spines with which most of the other zoœcia of the same colony are provided.

An ancestrula of M. ciliata, also from Naples, is somewhat similar; but it differs in having a distinct "area," or calcification of the proximal part of the frontal surface. The living tissues have disappeared, and I am, unfortunately, unable to state certainly whether the calcified area is a cryptocyst or not. This is, however, indicated by the way in which it slopes down steeply from its periphery, so that its inner edge lies at a deeper level than its outer margin. There are ten long marginal spines.

One or two colonies of M. impressa (S. Devon) are particularly interesting in having a Schizoporelliform ancestrula.

In Schizoporella vulgaris (Naples) I have found an ancestrula (fig. 6), like that of Microporella ciliata, with ten marginal spines and a calcified plate (*crypt.*) which is probably a cryptocyst. This resembles the cases which I have described as "intermediate" between the typical Tata form (fig. 2) and the adult condition with a completely calcified frontal wall. It appears to me that these "intermediate" Tata forms deserve special attention. It remains to be seen whether the calcified plate internal to the circlet of spines is really a cryptocyst or not. Taking into consideration the frequency of the occurrence of a cryptocyst in the Amphiblestrum group of Membranipora (although the morphology of this part has yet to be determined in many of these cases) and in such a typical Membranipora as M. delicatula, Busk (e. g.)—and noticing, moreover, the presumed occurrence of a cryptocyst in Bicellaria grandis (fig. 1),—the presumption appears to be that the plate marked *crypt.* in fig. 6 is really a cryptocyst. The bearing of these cases on the phylogeny of the Cheilostomata is considered in a later part of this paper (p. 334).

Cribrilina radiata,[1] Moll.—The study of a young colony of this species has led me to altogether unexpected conclusions, which probably indicate that this species is not really a Cribrilina at all. The ancestrula (fig. 7) is a Tata form with eleven marginal spines, of which the proximal (*sc.*) is broad and somewhat scutum-like, lying horizontally over the frontal membrane, while the others are erect or somewhat reclined outwards. Each of the erect spines bears a minute calcareous, denticulated lobe which originates about halfway up the spine, and lies horizontally, directed inwards over the frontal membrane. The outline of the ancestrula is somewhat concealed by the basal lobes of the younger zoœcia.

Two zoœcia in contact with the ancestrula are smaller than the rest, and are doubtless those which were first formed by

[1] Hincks, 'Brit. Mar. Pol.,' 1880, p. 185.

budding. One of these (*z.'*) is on the distal side of the ancestrula, and the other (not drawn) is on its apparent left side. On each of the five oral spines of these zoœcia is a minute calcareous lobe resembling those of the marginal spines of the ancestrula. The lobes may be indicated by still smaller projections on the oral spines of the other zoœcia.

In all the ordinary individuals there occur, on the proximal side of the operculum, a pair of delicate, membranous, elongated structures (*sp.*), which are described by Hincks (1880, p. 186) as vibraculoid setæ. Smitt[1] ascribes to them a sensory function.

The structures in question have no claim to be regarded as vibracula. There is no trace of any muscles connected with them, and there can be no doubt that they continue the line of the oral spines. This line is, in reality, prolonged all round the zoœcium, the succeeding spines (*sp.'*) being delicate membranous papillæ which barely project above the calcareous surface, and are obviously in series with the oral spines and the "vibraculoid setæ." The base of each papilla is a pore in the calcareous frontal wall. Comparison with the ancestrula and with the calcareous lobes of the oral spines of the younger zoœcia seems to indicate that the membranous papillæ, together with the oral spines, correspond with the marginal spines of the ancestrula. The calcareous lobes of that individual are, in consequence, the representatives of the bars which have united to form the frontal wall of the ordinary zoœcia, while the scutum-like spine of the ancestrula is probably the equivalent of one of the denticulated lobes on the other spines.

It has usually been assumed that the radiating series of pores correspond with the slits between the bars. This is certainly the case in C. philomela (fig. 8); but in C. radiata (fig. 7) there can be no doubt that the pores are in the same radii as the membranous marginal spines. I can

[1] "Floridan Bryozoa," II, 'K. Svenska Vet.-Ak. Handl.,' xi, 1873, No. 4, p. 22.

find no indication of a double calcareous wall in this species, and it therefore appears to me that the frontal wall is in a Lepralioid condition, the inner calcareous wall alone being developed, and being perforated by a series of vacuities, while the outer wall remains membranous. The probability that a layer of living tissue (epitheca) overlies the calcareous wall is increased by the fact that the surface of the latter is ridged, a condition which is usually associated with a covering of living tissue.

The lateral junctions of the frontal bars are indicated by prominent radial ridges, each of which rises to a small tubercle just inside the line of the membranous papillæ above described. The pores consequently lie, as described by other observers, in radiating furrows. That the union between the bars has not been complete is indicated by the fact that a thin line of air in some cases underlies the ridge.

The consideration of these facts suggests that the frontal wall has here not been formed by the overarching of the main spines, but by the development of the inner lobes of branched spines. It is impossible not to be reminded of the condition described by Jullien (1886, p. 609) in the Cretaceous Steginoporidæ, where a calcareous wall[1] is formed by the growth of branched peristomial spines.

I have, unfortunately, been unable to make out the condition of the compensation-sac in C. radiata, but it is well known that this species may possess a well-marked median pore (*m. p.*). In addition to this Microporelloid feature, it may be noticed that the zoœcium is surrounded by a flat basal lobe formed of pore-chambers,[2] as in Microporella ciliata and M. malusii. These are not present in C. philomela.

There can, I think, be little doubt that C. radiata cannot be retained in the same genus with C. philomela, and it is possible that its affinities are rather with the Microporellidæ.

Cribrilina figularis, Johnst. (Plymouth), is another species in which, so far as can be judged from dry material,

[1] Which, however, would not appear to correspond with that of C. radiata.

[2] The details of the pore-chambers are not indicated in fig. 7.

there is evidence that the frontal shield is formed by a series of horizontal lobes developed from the main spines. These latter are indicated with great distinctness as a curved series of conical calcareous papillæ, the truncated end of which is a membranous fenestra, and stands up at a higher level than the frontal shield, which is encircled by the papillæ. The radiating series of pores here correspond with the intervals between the spines, as in C. philomela.

The existence of great differences between the opercula of different species at present referred to Cribrilina suggests that the genus is an unnatural one, representing a stage in the evolution of the Lepralioid zoœcium, which has been arrived at independently in several cases, and is merely the result of incomplete lateral fusion of the bars which compose the frontal shield.

VI. Classification of the Cheilostomata.

While recognising the danger of drawing taxonomic conclusions from the study of a single organ, I cannot but think (with Jullien) that the consideration of the frontal surface is capable of settling some questions of this kind in the Cheilostomata. It would, I think, be premature to propose a new classification, but the observations above described suggest certain lines along which the existing classifications may be amended. I confine myself to groups to which I have paid some attention, leaving entirely out of consideration a large proportion of recent genera.

(1) The Membraniporidæ and Flustridæ are indicated as the most primitive group of Cheilostomes by the relations of their frontal membrane and parietal muscles, and by the evidence afforded by the primary zoœcium of many other Cheilostomes. For this group I think that Smitt's name Flustrina should be retained. It remains to be seen whether many of the Amphiblestrum-like forms of Membranipora, in which a calcareous cryptocyst (?) is developed, are more nearly related to this group or to the Microporoid series.

In many of the Flustrina there is an elongated frontal membrane which is typically depressed by a series of parietal muscles. A frontal membrane of this description occurs in the Membraniporidæ (part), Flustridæ, and Farciminariidæ, and in such genera as Bugula and Beania.

In other Flustrine forms (Dimetopia, Bicellaria) the zoœcium becomes elongated and usually infundibuliform, with a concurrent reduction in the size of the frontal membrane—a tendency which may be shown even in the ancestrula. The reduction of the frontal surface may be correlated with a reduced number of parietal muscles.

(2) Another series seems to be constituted by Scrupocellaria, Menipea, and Caberea, a group of "Cellularine" forms in which certain species in each genus have the frontal membrane protected by the excessive development of a single lateral spine, the fornix or scutum, which may, however, be vestigial or absent. In some cases, as in Menipea jeffreysii,[1] Norman, the scutum is so largely developed that a complete calcareous frontal wall appears to exist. Round the edge of this is a slit which is the interval between the edge of the oval scutum and the calcareous margin of the frontal membrane. The scutum originates from a broad calcareous base just proximal to the operculum, and on its inner side. It has a nearly straight suboral edge, which meets the basal sclerite of the approximately semicircular closed operculum. On the outer side the scutum locks firmly into a strong tubercle developed from the edge of the zoœcium. If the scutum were to fuse completely with the edge of the frontal surface a compensation-sac would be produced which would have had a different phylogenetic history from that of many other Cheilostomes. I see no reason why cases of this kind should not exist,[2] and it is possible that evidence to that effect might be forthcoming in

[1] Norman, 'Ann. Mag. Nat. Hist.' (6), xii, 1893, p. 446.

[2] The figure given by Waters (1888, pl. i, fig. 1) suggests that this might be the case in Catenaria bicornis; and the structure of C. lafontii (fig. 49) is not irreconcilable with this view.

the existence of a single communication between the living tissue of the frontal wall and that of the body-cavity, corresponding with the base of the scutum.

The group is usually characterised by the high development of avicularia and vibracula.

(3) The Microporoid series includes Micropora, Thalamoporella, Diploporella,[1] and Steganoporella, all characterised by the development of a cryptocyst[2] or calcareous lamella which grows beneath the frontal membrane. In the forms which have been examined, the parietal muscles are reduced to a single pair of highly developed depressor muscles which commonly traverse opesiules[3] to reach the frontal membrane; or, in Steganoporella, to a pair of depressor muscles and a pair of divaricators. The series probably includes a large number of the Cretaceous forms allied to Onychocella, as well as the recent O. abyssicola, Smitt, etc. Some of the recent species sometimes placed in the Membraniporidæ may also belong to this group.

(4) The Cribrilinidæ, including Membraniporella and Cribrilina (part), are forms in which a calcareous frontal wall is developed, ontogenetically, by the overarching of a series of marginal calcareous spines. This process has been observed by various authors in a certain number of species. I have shown above that C. radiata differs in important respects from the typical Cribrilinidæ.

(5) In Umbonula verrucosa the frontal shield originates ontogenetically as a calcareous lamina, perforated by a conspicuous series of marginal pores, which grows over the Flustrine frontal membrane, leaving a wide space between itself and that membrane. The parietal muscles develop in the situations which they will occupy in the mature zoœcium. I consider that the marginal pores correspond with the origins of as many Cribrilina-like spines which have united to form the frontal shield. The external calcareous

[1] MacGillivray (1887), p. 207.
[2] Cf. Harmer (1900), p. 228.
[3] Ibid., p. 230.

layer of the spines is now represented only by a membranous epitheca, composed of living tissue bounded by an external cuticle, while the frontal shield itself corresponds with the deeper layer of the original series of spines (fig. 12). The frontal shield extends to the sides of the operculum as a pair of calcareous shoulders, which commonly bear avicularia, while the suboral part of the shield may support a median avicularium which guards the entrance to the incipient compensation-sac. "Mucronella" pavonella, Alder (p. 296), probably belongs to Umbonula, which may also include M. bicuspis, Hincks.[1]

So far as I can judge from dry preparations, the development of the frontal shield takes place in the Umbonuloid manner in Porella compressa, P. saccata[2] (= P. elegantula, auctt.), P. (Palmicellaria) skenei, Mucronella coccinea, and Escharoides sarsii. In specimens of U. verrucosa from Naples[3] the suboral avicularium has a mandible which closely resembles that described by Waters[4] in species of Porella, being of more or less semicircular form, with denticulated margin and conspicuous Λ-shaped main sclerite. This confirms the association of Porella with Umbonula. I am inclined to think that the presence of marginal areolæ (as shown in figs. 10, 11) is of great importance as indicating affinities in this direction.

(6) In the Lepralioid type of calcification (figs. 13—15, 41) the young zoœcium frequently has a Flustrine appearance; but the frontal shield seems to result from a direct calcification of the frontal membrane. The compensation-sac is developed, after calcification is complete, as an invagination formed at the base of the operculum. This is the case in Lepralia, Schizoporella, Urceolipora nana, Euthyris, Euthyroides, Vittaticella, and Catenicella. The

[1] 'Ann. Mag. Nat. Hist.' (5), xi, p. 201.

[2] Waters, 1900, p. 81.

[3] It is, however, possible that this form is not identical with the littoral form common on the south coast of England, which I have alluded to as U. verrucosa.

[4] 1900, pl. xi.

parietal muscles at first radiate to the base of the operculum (figs. 13, 14), but their insertions become shifted by the growth of the compensation-sac, until in the fully formed zoœcium (figs. 33, 46) they have much the same relations as those of Umbonula (fig. 11) or of Cribrilina philomela (fig. 9). It seems difficult to avoid the conclusion that the floor of the compensation-sac represents in all cases the original frontal membrane, as indicated in the diagrammatic figs. 43, 44, 50. From this it would appear to follow that in the Lepralioid mode of development the phylogenetic history of the compensation-sac implied by those figures has been modified ontogenetically, in such a way that the apparent frontal membrane of the young zoœcium is in reality an epitheca (cf. fig. 12, *ep.*), that the calcareous frontal shield is next formed beneath the epitheca, and that the frontal membrane only makes its appearance when the compensation-sac is invaginated. The fully developed frontal wall of a Lepralia would, on this view, be represented by a completely fused series of Cribrilinid spines, of which the outer layer is membranous (= epitheca) and the inner layer is calcareous (fig. 50) ; the marginal pores on this view corresponding with the original communications between the Cribrilinid frontal bars and the general body-cavity.

Another view is, however, possible. The membranous covering of the young zoœcium may be, as it appears to be, the frontal membrane, and the frontal shield may be a cryptocyst which grows beneath the membrane towards the distal end of the zoœcium.

Thus in fig. 34 the calcareous frontal wall from which the papilla (*calc. p.*) is seen to arise would be the cryptocyst, which has grown distally beneath the frontal membrane (*ep.*). The invagination of the compensation-sac would then represent an ingrowth of a fold of the frontal membrane round the free distal border of the cryptocyst. The actual ontogeny of the organ would then agree completely with its supposed phylogeny in such cases as Lepralia, Schizoporella, and Euthyris. The Microporoid series of genera would thus

acquire great importance in throwing light on the structure of some of the Escharine forms. If a given species has a Cribrilinid ancestry, it might be expected that the roof of the compensation-sac would be formed by the deeper surface of the frontal shield (figs. 12, 50). If, on the contrary, the frontal shield is a cryptocyst, it might be anticipated that the compensation-sac would have a membranous roof distinct from the frontal shield. Although this arrangement is indicated in fig. 34 (Euthyris obtecta) I cannot assert positively that it is the case in that species. There is, however, no doubt of the existence of a complete membranous roof to the compensation-sac in Euthyris clathrata (figs. 26, 27).

There are other considerations which indicate that the frontal shield may, in certain Escharina, be a cryptocyst. Numerous Membraniporidæ, both recent and fossil, show a tendency to develop a cryptocyst, although in many cases complete proof that the calcified "area" is of this nature is not yet forthcoming. The case of Bicellaria grandis (fig. 1) is again uncertain. But the fact which is, perhaps, most significant is that in certain species of Schizoporella (fig. 6), Microporella, etc., the region encircled by the marginal spines of the primary zoœcium is partially calcified proximally. It appears to me to be of great importance to ascertain whether this calcified portion is of the nature of a cryptocyst or not;—in other words, whether the frontal membrane extends as far as the sharp ridge on the inner side of the base of the spines. I can hardly doubt that this is the case; and if so, the Microporoid origin of Escharine forms in which the compensation-sac develops as an invagination at the base of the operculum would appear to be indicated. The Cribrilina-like character[1] of certain species of Catenicella, in which the sac develops in this way, is, however, a difficulty which requires further explanation.

[1] This character is indicated in fig. 55 of the present paper, and in many figures on pls. i and ii of MacGillivray's "Monograph of the Tertiary Polyzoa of Victoria" ('Trans. Roy. Soc. Vict.,' iv, 1895). The Escharine nature of the Catenicellidæ is noticed by Smitt (1868, 2, p. 46).

It may perhaps indicate that the cryptocyst may have co-existed with a Cribrilina-like frontal shield, and it is not indeed impossible that the plate *pl.* in fig. 54 may represent the cryptocyst.

Calvet (1900, pp. 163, 436), who gives an excellent account of the structure of many marine Ectoprocta, has already expressed the opinion that in Lepralioid forms the calcified frontal wall is a cryptocyst. He states that while in most species the cryptocyst and the more external "ectocyst" (= epitheca) occur only on the frontal wall, in Retepora the whole external surface is two-layered. This and the analogous case of Urceolipora nana require further study.

Calvet does not recognise the compensation-sac, although it is indicated clearly in his pl. viii, fig. 9 (Catenaria lafontii), and its development is partly described on p. 399 and figured in pl. xiii, fig. 20 (Lepralia foliacea). The account which he gives (p. 168) of the median pore of Microporella does not agree with my results. I think that the discrepancies are easily to be explained by the fact that in highly calcified species the compensation-sac is so delicate that it may easily be overlooked in sections which have been distorted by decalcification and embedding in paraffin.

Calvet, after quoting in extenso (p. 276) Jullien's very accurate account of the mode of articulation of the operculum and its relations to the compensation-sac, proceeds to give it a complete denial (p. 278). He explains the existence of the parietal muscles in species with a calcified frontal wall by supposing that wall to have an amount of flexibility sufficient to allow itself to be depressed by the parietal muscles. The fact that these muscles are not inserted into the calcified wall is a sufficient answer to this suggestion.

Euthyris may be regarded as a highly modified Escharine form, which has acquired a Flustra-like habit. The irregularity of the bars of E. clathrata, and the fact that they are entirely beneath the epitheca, suggest that they do not represent the tubular frontal bars of Cribrilina, but are due to deficiencies in the calcification of

what was once a completely calcified wall. The epithecal investment is particularly obvious in Euthyris. It is possible that the basal epitheca is a reminiscence of a time when the frond was composed of two layers of zoœcia, placed back to back. I have previously (1901, p. 17) pointed out that there is evidence that many Cretaceous Cheilostomes were provided with a similar basal epitheca.

(7) In the Microporelloid series the compensation-sac opens by a "median pore," which has probably resulted from the closure of a Schizoporelliform sinus. This view, which has been adopted by Gregory[1] as the basis of his division Schizothyriata, receives support from the occasional occurrence in the group of an ancestrula with a Schizoporella-like operculum (cf. p. 324). Gregory's classification places Schizoporella with Microporella, and separates both from Lepralia. It appears to me, on the contrary, that Lepralia and Schizoporella cannot be separated from one another, whereas Microporella is a distinct step in advance of the other two.

This section includes Microporella, and perhaps "Cribrilina" radiata among encrusting forms; while Calwellia (in which I place Urceolipora dentata), Ichthyaria, and Onchoporella also belong to it. I think Miss Jelly[2] goes too far in placing Siphonicytara in Calwellia. Onchoporella may include O. bombycina, auctt., O. ligulata, Busk,[3] and O. selenoides, Ortmann,[4] but there seems to be little except its habit to distinguish it from Calwellia. The suture which in the latter genus connects the middle line of the operculum with the median pore probably indicates the

[1] 1893, p. 224.

[2] 1889, p. 33.

[3] 'Quart. Journ. Micr. Sci.,' viii, 1860, p. 282. This species has a close resemblance to O. bombycina, auctt. It was clearly by an oversight that Busk (1884, p. 104, n.) referred Scruparia diaphana instead of Carbasea ligulata to his genus Onchoporella; the original figures of the two species having appeared on the same plate of this Journal.

[4] 'Arch. f. Naturg.,' lvi (i), 1890, p. 28.

incomplete fusion of two suboral calcareous spines by which the median pore has been cut off from the orifice. The characteristic infundibuliform pores on either side of the suture are perhaps parts of these spines.

It may be pointed out in conclusion that the principal results of this paper appear to be completely in accordance with palæontological evidence. In Canu's important memoir on Cretaceous Cheilostomata (1900), the rarity of the Cretaceous Monodermata, a group instituted by Jullien, which corresponds in the main with the Escharina of other authors, is pointed out (p. 458), and only three pages are devoted to their consideration. Nearly all the remaining species belong to the groups designated as Flustridæ, Onychocellidæ, Opesiulidæ, and Costulidæ. The Flustridæ correspond with the Flustrina of other authors. The Onychocellidæ are an important series, still represented by the recent genus Onychocella, characterised by the great development of the cryptocyst, and usually by the presence of a peculiar form of vicarious avicularium known as an onychocellium. The Opesiulidæ include the recent Microporidæ and Steganoporellidæ. The Costulidæ are equivalent to the Cribrilinidæ. These four groups are all represented by a large number of genera and species.

Gregory (1896, preface) states that "it is among the Jurassic deposits that we have to seek the ancestors of existing types of Bryozoa." His Catalogue of Jurassic forms includes only two Cheilostomes, one of which is a Membranipora and the other an Onychocella.

It thus follows that the Jurassic and Cretaceous Cheilostomes belonged, for the most part, to the Diplodermata of Jullien (= Athyriata, Gregory, 1893, p. 223). Both Jullien, in a memoir (1888, 4, p. 8) published subsequently to the original introduction of his term Diplodermata, and Gregory include the Cribrilinidæ in the sub-orders respectively adopted by them. It appears to me that the Cribrilinidæ would be better left out of the sub-order. They do not agree with Jullien's definition of the Diplodermata as forms with a

double "ectocyst;" that is, as forms in which there is a calcareous cryptocyst internal to the frontal membrane. Although Gregory was justified in regarding the Cribrilinidæ as forms in which the frontal membrane persists, the view which I take of the compensation-sac involves the conclusion that the membrane persists even in the Escharine genera. The Cribrilinidæ may be regarded as a transition-group between the Flustrine and the Escharine forms; but, as I have pointed out above, it appears to me that the family, as at present constituted, is not a natural one.

Although it is very difficult to draw a line between the more simple species of Membranipora and those in which a definite cryptocyst occurs, it is hardly possible to speak of some of the former as diplodermatous. Although the term Athyriata is antedated by Diplodermata, it is more in accordance with the structure of recent genera than Jullien's term, and in the present state of our knowledge it would perhaps be well to accept it as the name of a group including those forms in which the frontal membrane persists in more or less its primitive form, whether a cryptocyst is present or not below it.

The Athyriata are thus, on palæontological evidence, the oldest group of Cheilostomes. In the Cretaceous period they had already differentiated themselves into the types of structure represented by Membranipora, Onychocella, and Micropora, in the latter two of which the cryptocyst is well developed. The Cretaceous period is also characterised by the occurrence of a number of species belonging to the transitional Cribrilinid type. So far as the evidence goes at present, the true Escharine forms were then much inferior in number to the dominant Athyriate group.

With regard to the other parts of Gregory's classification (1893, p. 223), it appears to me that the sub-order Stolonata includes several families of very different affinities, the Eucrateidæ at any rate probably belonging to the Athyriata. Some of the Cellularina are also Athyriate, while I agree

with Gregory (p. 222) that Catenicella, which he places nevertheless in the Cellularina, has but little to do with the other Cellularines. I cannot accept the divisions Schizothyriata (forms with a sinus or a median pore) and Holothyriata (other Escharine genera), because it seems to me that there is no essential difference between the Schizothyriate Schizoporella and the Holothyriate Lepralia. Both these genera probably require a good deal of rearrangement and subdivision; but among recent species there are certainly cases in which it is an open question to which genus they should be referred. It would perhaps have been better to institute a new sub-order for the Microporelloid genera. The question is complicated by the fact that all "median" pores are not homologous structures. It is a well-known fact, for instance, that in some cases (e. g. Adeonella) the median pore is simply a peristomial opening.

VII. Summary of the more Important Results.

(1) A large number of Cheilostomata are provided with a "compensation-sac," a structure described by Jullien, which opens at the proximal border of the operculum or by a "median pore." Muscles which usually originate from the lateral walls of the zoœcium are inserted into the floor of the compensation-sac, which they dilate by their contraction, thereby helping to force out the polypide. The constant change of water in the compensation-sac probably has a respiratory importance. The sac is frequently found in zoœcia whose polypides have undergone histolysis.

(2) The floor of the compensation-sac corresponds in whole or in part with the membranous frontal surface (for which the name "frontal membrane" is suggested) of a Membranipora; and its muscles are homologous with the parietal muscles of the same genus. The compensation-sac appears to have been evolved in more than one way.

(3) In Cribrilinidæ it is well known that a calcareous wall (for which and for other calcareous frontal walls the name

"frontal shield" is suggested) is developed as a series of marginal spines, which overarch the frontal membrane. This leads to the condition found in some Escharine forms, in which, as in Umbonula, the calcareous frontal shield similarly overarches the frontal membrane.

(4) The frontal shield of the Microporidæ and Steganoporellidæ is of the nature of a cryptocyst,[1]—that is to say, of a calcareous lamella, which grows horizontally across the body-cavity beneath the frontal membrane. This has, perhaps, led to the condition found in Lepralia, Schizoporella, and other genera, in which the compensation-sac is developed as an invagination at the base of the operculum and passes to the deeper side of the frontal shield, which is on this view a cryptocyst.

(5) The epitheca, or layer of living tissue, bounded by a cuticle, which covers the frontal shield, may represent the entire frontal membrane (Microporidæ, etc.), or only a part of that membrane (Lepralia, etc.), or it may have been derived from the outer calcareous layer of the frontal bars of a Cribrilina-like form (Umbonula). The epitheca is frequently responsible for the addition of secondary calcareous matter to the frontal shield, and in some cases (Cellepora, etc.) for the formation of new generations of zoœcia which are superposed on the older ones.

(6) The operculum, in its more primitive condition, is merely part of the frontal membrane strengthened by a semicircular marginal flange. It acquires a firmer texture and a more elaborate arrangement of its thickened parts as the result of its articulation with calcareous portions of the zoœcium. While occlusor muscles may be regarded as an essential adjunct of the operculum, definite divaricators seem to have been evolved as a modification of the distal pair of parietal muscles.

(7) The consideration of the relations of the frontal surface involves considerable rearrangements in the Cheilostomata (see section on classification, p. 329).

[1] Cf. Harmer (1900), p. 228.

(8) The results of the study of the compensation-sac and frontal surface generally are confirmed by an examination of the primary zoœcium or "ancestrula" (Jullien).

(9) Two new species (Euthyris clathrata and Lepralia haddoni) are described, and a new genus (Euthyroides) is suggested for Euthyris episcopalis, Busk.

(10) The operculum of E. clathrata is of a specially complicated type. The vestibule, or first part of the introvert, is provided with a chitinous distal lip, for which the name "labium" is suggested.

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[1] Many of the references are given as foot-notes.

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EXPLANATION OF PLATES 15—18,

Illustrating Mr. Sidney F. Harmer's paper "On the Morphology of the Cheilostomata."

REFERENCE LETTERS.

ar. Marginal areolæ. *avic.* Avicularium. *b.* Polypide-bud. *b. b.* Brown body. *b. ep.* Basal epitheca. *buttr.* Buttress of operculum. *cæ.* Cæcum of stomach. *calc. p.* Calcareous papillæ. *cond.* Condyle, or chitin surrounding the decalcified condyle. *c. p.* Communication pore. *c. s.* Compensation-sac. *crypt.* Cryptocyst. *depr.* Depressor muscle of frontal membrane. *div.* Divaricator muscle of operculum. *d. w.* Distal wall of zoœcium. *ep.* Epitheca. *ep. c.* Cavity beneath epitheca. *f.* Membranous fenestra. *f. b.* Frontal bars or costules. *fl.* Vertical flange of operculum. *f. m.* Frontal membrane. *f. sh.* Frontal shield. *f. sh. d.* Distal lobes of frontal shield. *inf. avic.* Infra-avicularian compartment. *j.* Chitinous joint. *lb.* Labium. *l. r.* Lateral recess. *m. c.* Marginal cavity of frond. *m. p.* Median pore. *m. t.* Median tooth (lyrula) of Smittia. *occl.* Occlusor muscles of operculum. *op.* Operculum. *op. gl.* Opercular glands. *ov.* Ovicell. *p.* Pores. *p. c.* Pore-chambers. *p. d.* Parieto-diaphragmatic muscles. *p. m.* Parietal muscles. *p. m.'* Distal group of parietal muscles. *p. v. m., p. v. m.'* Parieto-vaginal muscles and bands. *p. w.* Proximal wall of zoœcium. *p. z.* Primary zoœcium. *r. m.* Retractor muscles of polypide. *s., s.'* Suture in calcareous wall. *scl.* Chitinous sclerite. *sp.* Spine. *sup. avic.* Supra-avicularian compartment. *t.* Tentacles. *t. s.* Tentacle sheath. *v.* Vitta. *vest.* Vestibule (= diaphragm). *z.'* Daughter-zoœcium.

Fig. 12 (Pl. 15) and Figs. 43, 44, 50, and 51 (Pl. 17) are diagrammatic representations of the points respectively illustrated by them. Fig. 18 (Pl. 16) is × 1. Figs. 19, 20, 22, 32, 35, and 36 (Pl. 16) were drawn to the same scale (camera lucida, Zeiss, A obj.). Fig. 19 was not reduced, but the others were reduced ½. All the remaining figures are more highly magnified (Zeiss, C obj.; afterwards × ½).

The specimens figured belong to the Museum of Zoology at Cambridge.