

REPORT

ON

JOUSSEAUMIA

A NEW GENUS OF EULAMELLIBRANCHS COMMENSAL WITH THE CORALS
HETEROCYATHUS AND HETEROPSAMMIA

COLLECTED BY

PROFESSOR HERDMAN, AT CEYLON, IN 1902.

BY

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[WITH THREE PLATES.]

IN a very interesting paper describing the true nature of the commensalism between corals of the genera *Heteropsammia* and *Heterocyathus* and a Sipunculid belonging to the genus *Aspidosiphon*, E. L. BOUVIER (4) pointed out that there is a third partner in the commensalism in the form of a minute Lamellibranch which he figured and named *Kellia deshayesi*, without, however, giving any diagnosis of the species. As I shall point out in the course of this report, BOUVIER'S figure, though it gives a correct enough representation of the external form of the Mollusc, as seen lying in the left valve of its shell, is incorrect in the representation of the hinge teeth, and the Lamellibranch in question certainly does not belong to the genus *Kellia*, differing from it not only in the hinge teeth, but also in the sutural unions of the mantle edges and in other important particulars. Though BOUVIER announced that his colleague M. JOUSSEAUME intended to make a study of this commensal Lamellibranch, it does not appear to have been described or to have attracted any further notice until Dr. A. E. SHIPLEY in his report on the Gephyrea collected by Professor HERDMAN in Ceylon (13) mentioned its occurrence along with *Aspidosiphon* in the basal

chambers of *Heteropsammia* and *Heterocyathus*, and states that it was referred by Mr. E. A. SMITH to ANGAS' genus *Mysella*.

Among the solitary corals from Ceylon sent me by Professor HERDMAN were numerous spirit-preserved specimens of *Heteropsammia michelini* and *Heterocyathus æquicostatus*, and on opening the *Aspidosiphon* chamber in one of these I was at once struck by the presence of the numerous small Lamellibranchs, many of them imbedded in the skin of the posterior part of the body of the Sipunculid, as described by BOUVIER; others lying free in the innermost coils of the chamber, especially in its terminal part.

Having many specimens of the corals at my disposal, I examined a large number of them and invariably found a number of the Lamellibranchs inhabiting the *Aspidosiphon* chamber. In some of the larger specimens of *Heteropsammia* I found as many as 30 or 35 specimens of different ages, in some of the smaller specimens of *Heterocyathus* not more than a dozen or fifteen.

BOUVIER left it an open question whether the commensal Mollusc was an adult form or not. My observations quickly showed me that a proportion of the specimens inhabiting each coral were adult, and that along with them were numerous young forms in all stages of growth. With the abundant material at my disposal I proceeded to make a careful study of the anatomy, and, as far as the circumstances allowed, the development of this hitherto undescribed species, and although but few out of the many specimens were sufficiently well preserved to admit of satisfactory microscopical examination, I found a sufficient number in good enough condition to enable me to work out the structure in some detail.

DESCRIPTION OF THE GENUS AND SPECIES.

The description of the genus *Mysella* given by ANGAS (1) is based on the characters of the shell only, and his figure of the hinge apparatus is so small that it is difficult to make out the characters of the hinge teeth clearly, but it is evident that the species commensal in the two corals cannot be referred to his genus.

The specimen on which the genus *Mysella* was founded was 7.5 millims. in length, and was found in black mud near Port Jackson. The shell is inequilateral, the anterior side being the shorter and subtruncate; judging by the figure, the umbones are prosogyrous. The ligament is internal, and there is a single small diverging subcircular flattened cardinal tooth in one valve, and two short thin horizontal lateral processes in the other valve.

My specimens agree with *Mysella* in having an internal ligament, and in having a single cardinal tooth in the right valve and two teeth in the left valve; but there are in addition well-developed lateral teeth, and the shape of the shell is quite different. Moreover, the largest of my specimens does not exceed 1.5 millims. in length and the average length of the adult forms is 1.0 millim.

It is extremely difficult to get a clear view of the hinge teeth in very small bivalve shells. BERNARD (3) has remarked on the unsatisfactory results obtained from dry specimens mounted on black paper and recommends fixing them direct on a glass slide and varying the sub-stage illumination. I found that much the most satisfactory results were obtained by thoroughly cleaning the shells in potash or Eau de Javelle and then mounting them under a coverslip in glycerine jelly. By altering the sub-stage illumination and rotating the stage one can get very clear pictures of the minutest details.

After a careful examination of the shells and of the anatomy of my specimens, I satisfied myself that they belonged to two species of a new genus, which I propose to call *Jousseaumia*, in honour of the French naturalist who first discovered this Mollusc in the *Aspidosiphon* chamber of the two above-named corals. This new genus and the two species may be defined as follows:—

***Jousseaumia*, n. gen.**

Shell small, thin, triangular, equivalve, inequilateral, the anterior side the longer, with numerous fine concentric ridges or striations; umbones small, slightly opisthogyrous. Hinge heterodont, with a somewhat elongately oval internal ligament; a single styliiform more or less obtusely pointed cardinal tooth in the right valve and two curved lamellate cardinal teeth in the left valve. Lateral teeth somewhat distant, elongate, in the form of two ridges in the left valve fitting into corresponding depressions in the right valve. Adductor impressions subequal, the anterior impression somewhat elongated; pallial line entire. Mantle largely open, with a single pallial suture; no pallial tentacles and no distinct siphons. The foot elongate, linguiform, geniculate, with a byssus consisting of a few long adhesive threads; a byssal groove on the posterior edge of the foot. Gills astartiform, homorhabdic, non-plicate, with three or at most four rows of simple interfilamentar junctions. Interlamellar junctions few, irregular; the external demibranch wanting; the reflected lamella of the inner demibranch more or less developed, generally at the anterior end of the gill only and attached to the sides of the foot. Hermaphrodite and protandric.

***Jousseaumia heterocyathi*, n. sp.**

The single cardinal tooth of the right valve bluntly rounded at its extremity, with a narrower pedicle of attachment. The anterior cardinal tooth of the left valve well developed, lamella curved posteriorly; the posterior cardinal tooth a short, ill-defined diverging ridge. Found only in *Heterocythus*.

***Jousseaumia heteropsammia*, n. sp.**

The single cardinal tooth of the right valve styliiform, with a bluntly pointed extremity and a broad base of attachment. The posterior cardinal tooth of the left

valve well developed, longer than the anterior tooth, diverging posteriorly, its upper margin excavated to form the ligamentar fossa. Found only in *Heteropsammia*.

The differences in the cardinal teeth between the specimens found in *Heterocyathus* and those found in *Heteropsammia* appear to be constant, and are sufficient to justify my ranking them as distinct species. In addition, the mature individuals of *J. heterocyathi* seem to be rather smaller, the concentric ridges seem to be more prominent and the posterior and ventral margins of the valves appear to be more rounded than in *J. heteropsammia*.

As may be seen from an inspection of figs. 2 and 3, the ligament is distinctly dorsal and exterior to the posterior cardinal tooth of the left valve, and is contained in a fossa lying just behind the umbones. The hinge, therefore, is not that of a *Maetra*, to which it has a superficial resemblance from the characters of the lateral teeth, nor yet that of a *Scrobicularia* or *Syndosmya*. It may rather be compared with the hinge of a *Lucina* or *Diplodonta* in which the ligament has become very much shortened and enclosed by the overgrowth of the valve margins dorsally and posteriorly. On the other hand, the excavation of the posterior cardinal tooth suggests a first step in the evolution of the spoon-shaped ligamentar tooth of the Myidæ and many of the Anatinacea (*Thracia*, *Anatina*), and, as will be seen, the anatomy of *Jousseauxia* suggests some affinities with the Anatinacea.

ANATOMY AND HISTOLOGY.

As *Jousseauxia heterocyathi* and *J. heteropsammia* do not differ from one another in any important anatomical feature, the following account will apply to both species. A general view of the anatomy of *J. heterocyathi*, as seen in optical section, is given in fig. 1.

The mantle edge is thickened and muscular, but there are no pallial tentacles, no eyes or pigment spots. There is a single pallial suture (figs. 16, 17, 18, *p.s.*) separating a rather elongate anal or exhalant orifice from the large pedo-branchial orifice, the latter extending as far forward as the anterior adductor muscle. The mantle edges are somewhat prominent and the radiating muscle fibres are rather better developed in the region of the anal orifice than elsewhere, but there is no true anal siphon.

The foot is large, more or less linguiform, and geniculate like that of *Cardium*. There is a specially strong muscular band running down the posterior margin of the foot, below the byssus groove, and the sudden contraction of these fibres would have the effect of straightening the foot and enabling the animal to spring like a *Trigonia* or a cockle. It is difficult to conjecture of what use the geniculate and muscular foot can be to an animal leading a sedentary existence embedded in the skin of the *Aspidosiphon* with which it is commensalistic; but as I find it very well developed in

the youngest forms, I suspect that these may escape from the *Aspidosiphon* chamber and use the foot for progression and for springing on and attaching themselves to an *Aspidosiphon* when projected from the basal aperture of another coral. At all events, there must be some means by which *Jousseaumia* can be transferred from coral to coral, and the highly developed musculature of the geniculate foot suggests that the transference is effected in this manner. The anterior and posterior retractors of the foot are well developed and together form an elongated muscular band, by which the foot appears to be slung up in the mantle cavity. Practically the whole of the viscera are dorsal to this band. The protractor muscle of the foot is also well developed and has a separate muscular slip ventral to the anterior adductor muscle, and it is evident that, in spite of its sedentary habit, *Jousseaumia* shows no degeneration in the organs of progression.

The attachment of the young forms to an *Aspidosiphon* inhabiting another coral would be effected by means of the byssus, which has the form of a moderately stout thread, branching and ending distally in adhesive enlargements. The posterior edge of the foot is furrowed by a well-marked byssus groove leading into a byssus cavity at the hinder end of the foot. As the structure of the byssus gland and the mode of formation of the byssus has been a subject of dispute, and as some of my specimens were sufficiently well preserved to enable me to make tolerably accurate observations, I shall describe the histology of this organ in some detail. The whole of the centre of the foot is occupied by a core of more or less polygonal relatively large glandular cells which appear pale in sections stained with borax-carminé and picro-indigo-carminé, but stain deeply in hæmatoxylin or safranin. With the last-named dye the gland cells stain brilliant scarlet, and the stain is shown by high powers of the microscope to be confined to minute granules with which the cells are stuffed. The behaviour of these cells and granules will be described later. The byssus groove begins as a very shallow furrow near the pointed extremity of the foot, and gradually deepens as it passes dorsally along the posterior edge of the foot, eventually ending in a duct which enlarges to form a considerable byssus cavity contained in the upper part of that organ. Fig. 4 is a section taken through the open part of the groove near the middle of the foot. It shows the structure described by CARRIÈRE (5) and HORST (8), namely, a furrow of irregular shape opening to the exterior, and in the depth of the furrow a crescentic gutter or demi-canal ("halbmondförmige Rinne") bounded on either side by a projecting fold. Contrary to the statements of previous authors, I find in *Jousseaumia* that the furrow is lined by a low, non-ciliated epithelium continuous with that of the external surface of the foot. This epithelium has a distinct cuticle, staining blue in picro-nigrosin or picro-indigo-carminé, and though I am unwilling to make a positive assertion in consequence of the indifferent state of preservation of my specimens, I can say that I was unable to find any trace of cilia either in the furrow or on the external surface of the foot. The crescentic demi-canal, on the other hand, is lined by larger cubical or short columnar cells, with

clear cell contents and rounded nuclei, and these cells are very distinctly ciliated. Fig. 5 represents a section taken through the duct of the byssus cavity, shortly above the point where the lips of the furrow have united to enclose a canal. It can easily be seen that the duct consists of two portions, (a) a lower portion whose epithelium is continuous with that of the open furrow and, like it, is non-ciliated and provided with a cuticle; the walls of this region are thrown into a number of folds; (b) an upper portion continuous with the crescentic demi-canal, and lined by the same clear ciliated cubical or columnar cells. Fig. 6 represents a section through the middle of the byssus cavity. At the upper (really the anterior) end of the cavity is the crescentic demi-canal lined by the same clear ciliated cells as before. The remainder of the cavity is broken up by septa, of which two thick folds on either side of the demi-canal, a central partition springing from the lower (posterior) end of the cavity, and two minor lateral folds may be particularly noticed. These septa are covered by a ciliated epithelium, evidently of the same nature as that lining the demi-canal, but the cells are very much elongated and enlarged at their outer extremities. Those on the thick lateral folds are especially long, and diverge in a fan-shaped manner from the band of connective tissue and muscle fibre which forms the centre of the fold. This figure agrees in most respects with CARRIÈRES' drawing of the byssus cavity of *Cyprina islandica* (5, fig. 12, B). In a section taken through the deeper end of the byssus cavity, the characters of the epithelium are the same as those of the preceding section, but the cavity has been divided into two by the forward extension of the median septum, the crescentic demi-canal has disappeared, and the lateral septa are smaller. These two anterior prolongations of the byssus cavity end blindly close beneath the pedal ganglia. These three figures are drawn from horizontal sections of the whole animal, and are therefore nearly transverse sections of the foot. Fig. 7 is a highly magnified drawing (ZEISS' $\frac{1}{12}$ immersion) of a transverse section of the whole animal, which therefore cuts the foot and byssus cavity obliquely. It corresponds to the top part of a section rather anterior to that shown in fig. 6. The section was stained with safranin and licht-grün, and does not show the cell contours very clearly, but the granules of byssogen, stained bright scarlet, are very clearly seen. At *by.gl.* are seen the large polygonal glandular cells occupying the central part of the foot. On either side these cells may be seen to be breaking up and their granules are streaming outwards along definite lines to pass either into the central tongue-shaped projection (which is a part of the here incomplete median septum) or into the lateral swellings projecting into the byssus cavity. As they pass outwards, the granules form little pyriform or club-shaped masses, whose swollen ends are directed towards the lumen of the byssus cavity, and it is evident that they are travelling, probably by intercellular paths, to be discharged into the lumen, and there converted into the material of the byssus. The granules themselves are clearly not byssus substance, but "byssogen," as the lumen of the cavity is filled with a granular material (not shown in the figure) which is not stained either by

safranin or hæmatoxylin, and the byssus itself is similarly unaffected. The interest of this observation consists in the demonstration that the byssus gland-cells, like those of sebaceous follicles, are broken up to form the secretion, and that the secretum travels in and among the epithelial cells for relatively long distances until it reaches the lumen into which it is finally discharged. Thus the existence of a great mass of gland cells, forming a central core to the foot, and apparently distant from the byssus cavity and groove, is satisfactorily explained. The secretion is not confined to the byssus cavity, but throughout my sections I find the same indications of granules streaming between the ciliated cells of the crescentic demi-canal, but not between the non-ciliated epithelial cells of the furrow. In spite of some differences in detail, which can be accounted for by the widely different genera examined by us, my observations agree in all fundamental particulars with those of HORST (8). The byssus, as he maintained, is undoubtedly a secretion product and not a cuticular structure. Comparing HORST'S figures of *Dreissensia polymorpha* (*loc. cit.*, plate xi., figs. 2, 3, and 4) with mine, it will be seen that in the latter species the byssogenous glands are concentrated in the region of the demi-canal, and that there are numerous mucus glands, of which I could find no trace in *Jousseaumia*. And whereas he shows numerous branching and anastomosing canals passing from the cells of the byssus gland between the epithelial cells of the demi-canal, these canals becoming narrower in diameter as they approach the lumen of the byssus cavity, and gives no indication of the breaking up of the cells themselves to form the secretum, I find that the cells are broken up and the secretion travels (probably) between the epithelial cells in the form of streams or strings whose ends nearest the lumen are swollen. It appears that in both cases the secretum follows intercellular paths, and that in both cases it has the form of granules which are converted in the lumen of the byssus cavity, probably by the action of a ferment, into the material of the byssus.

THE ALIMENTARY CANAL.—The labial palps are relatively large, and the upper and lower palps pass respectively into the upper and lower lips. Posteriorly the labial palps are continuous with the anterior ends of the gill plates. The palps are richly ciliated, the cilia being borne by large cubical epithelial cells with a very distinct limiting membrane, but the surfaces of the palps appear to be smooth, and not thrown into ridges as is usually the case in Lamellibranchia. The mouth leads into a buccal cavity lined by somewhat elongated columnar epithelial cells continuous with those covering the labial palps, and provided, like the latter, with a very distinct limiting membrane or cuticle, through which the cilia project. The pharyngeal cavity is wide and strongly compressed dorso-ventrally. As it passes back into the cesophagus, the shape of the lumen, as seen in transverse section, alters. There is a diamond-shaped central lumen (fig. 8), the lateral angles of which are produced into lateral diverticula, suggestive of a comparison with the cesophageal pouches of Gastropoda. Such pouches are only known in the Protobranchia among the Lamellibranchia, and in them, *e.g.* in *Leda pella*, as figured by PEISENER (11).

they are much more highly developed than in *Jousseauxia*, but there is a correspondence between the thinner epithelium lining the lateral pouches in his figure and in mine which leads me to believe that we have here an indication, though in a very much reduced form, of these ancestral structures.

The œsophagus is triangular in section and lined by a richly ciliated columnar epithelium. It passes insensibly into the capacious stomach, whose anterior walls are richly ciliated (fig. 13, *st.*), but posteriorly the lining epithelium changes in character. Laterally and ventrally the cells retain their columnar epithelial character, but dorsally (figs. 14 and 15, *g.l.c.*) they lose their cilia and become glandular. The cells throughout this region are rather long and columnar, and are full of green refringent granules. It is in this region that the thick cuticular lining of the stomach begins, and I have little doubt that these glandular cells of the dorsal wall secrete the cuticle, and give rise to the crystalline style with which the cuticle is continuous. The liver lobes are four in number, a right and left dorsal and a right and left ventral. They open into the stomach near its posterior end, just in front of the commencement of the intestine and cæcum, by wide ducts on either side, the ducts of the dorsal and ventral lobes of each side uniting just before they open into the stomach. The liver cells were too much macerated to enable me to say anything definite about their histological characters. The left upper end of the stomach is prolonged into a large conical cæcum (figs. 1, 16, and 17, *cæ.*), which projects backwards into the posterior part of the visceral mass and is a conspicuous object in specimens mounted whole. The cæcum is lined throughout by a very definite cubical epithelium, whose cells bear short, stiff, bristle-like cilia, as is the case in the cæca of other Lamellibranchia. In the anterior part of the cæcum the cells of its dorsal wall are transitional between the ordinary cæcal cells and those of the dorsal wall of the stomach, for they are filled with the green refringent granules, while retaining their cubical character and their stiff brush-like cilia. The cæcum is separated from the stomach by a constriction, and at the constriction the epithelial cells are elongated and their ends are produced into rather long irregular processes, apparently formed of fused cilia. These processes seem to form a straining apparatus, preventing particles of any size from entering the cæcum, for while the stomach, intestine, and rectum are full of the skeletons of diatoms, the cæcum is always devoid of such contents. The crystalline style is very large in some specimens, but small, or even wholly absent, in others. It projects some way forward into the stomach and some way back into the cæcum, but seldom extends to the posterior end of the latter.

The intestine leaves the stomach on the right lower side, close to the opening of the cæcum. It runs backwards as a widish, thin-walled ciliated tube as far as the posterior end of the cæcum, where it turns upwards and forwards to reach the dorsal surface of the visceral mass; there its diameter narrows to form the rectum, and it bends sharply backwards, running parallel with the posterior margin of the shell

over the posterior adductor muscle to end in the anus. The rectum traverses the pericardium, and is wrapped round by the ventricle.

THE CIRCULATORY SYSTEM is of the typical lamellibranchiate character, and requires no special description. The ventricle, as has been mentioned above, is traversed by the rectum. The auricles are excessively thin and can only be distinguished with difficulty in sections. Owing to the minute size of the animal the relations of the principal blood sinuses could not be determined with certainty, but I was able to distinguish a large ventral sinus above the muscular band formed by the anterior and posterior retractor muscles of the foot, and there are the usual afferent and efferent branchial sinuses at the bases of the gills.

THE GILLS, as may be seen by an inspection of fig. 1, are of a very simple type. The outer demibranch is wanting, a feature which *Jousseaumia* shares with the Lucinidæ, *Corbis*, *Scioberetia* and the Teredinidæ. The direct lamella of the inner demibranch is always well developed, and may be described as consisting of about 18 filaments, united at regular intervals by three, or in large specimens by four, rows of non-vascular interfilamentar junctions. The reflected lamella is present in many adult individuals, but is either absent or very feebly developed in others, and it is always absent in young and immature specimens. When present, it is confined to the anterior region of the demibranch, and the upper edge of the reflected lamella is fused to the body wall along the line of junction of the foot and the visceral mass. Posterior to the foot, where the reflected lamella is absent, the lower edge of the direct lamella of one side is, in all but very young individuals, fused with the lower edge of the corresponding lamella of the other side. If the reflected lamella is absent in the region of the foot, its place is taken by a continuous sheet of membranous tissue, which is attached to the sides of the upper part of the foot. Below and behind the posterior adductor muscle the upper edges of the direct lamellæ are connected with the mantle (figs. 18 and 19), and the result of this arrangement is that the gills divide the pallial cavity into an inter-lamellar or supra-branchial chamber, opening behind by the anal pallial aperture, and a large infra-branchial chamber.

Though I have spoken of filaments, the gills are not developed as separate filamentar outgrowths which subsequently form the above described unions with one another and the body wall and mantle, but by the fenestration of a pair of lateral folds of the body wall, as has been described by other authors for *Cyclas* (STEPANOFF, 14), *Teredo* (HATSCHKE, 7), and *Scioberetia* (BERNARD, 2). Although I have not been successful in finding the earliest stages of gill development, I have a complete series of post-larval stages showing that the fenestration proceeds from before backwards, and that new fenestræ are added at the posterior ends of the two gill membranes until the adult stage is reached. Fig. 27 represents a young *J. heterocyathi* in which there are five fully formed fenestrations and the commencement of a sixth posteriorly. Fig. 28 is a drawing of a somewhat older individual

with seven fenestrations. In the youngest form of which I have cut sections the fenestrated gill lamellæ are not reflected, and at the sides of the foot the lamellæ of opposite sides are quite free from one another and from the body wall and foot. Behind the foot the lower edges of the lamellæ of opposite sides are united by a band of connective tissue, and still further back the organic connection between the lower ends is more complete; a vascular connection is established, and at the extreme hinder end of the gill, where fenestration is still in progress, the gill lamellæ of the two sides are blended in a mass of embryonic connective tissue channelled by numerous irregular blood sinuses. It follows from the above description that, if we speak of the bars between the fenestræ as gill filaments, they are at all stages of growth organically united in longitudinal series at their lower ends, and as the filaments assume their complete histological structure, the chitinous-supporting skeleton of the filaments forms a dorsal and a ventral arcade, the upper end of each hollow chitinous gill bar curving forward to unite with the bar in front of it, and a similar connection is eventually established at its lower end. In young specimens, however, the skeletal bars pass below into a mass of undifferentiated connective tissue. As growth proceeds, this undifferentiated tissue at the lower edge of the anterior part of the gill lamella grows out in the form of a membrane, and as it grows the membrane is reflected along the sides of the foot and grows upwards, becoming fenestrated as it grows, and eventually the upper edge of what we now recognise as the reflected lamella becomes attached to the body wall along the line of union of the foot and visceral mass, thus completing the separation between the supra-branchial and infra-branchial chambers. It would, perhaps, be more correct to say that, as the reflected lamella grows upwards, the fenestræ of the direct lamellæ extend into it. When the adult relations are established, the chitinous skeletal bars of the filaments form an arcade along the upper edge of the reflected lamella where it is attached to the body wall. In those adult individuals in which the reflected lamella is imperfectly developed or absent (and such individuals are not uncommon in both the species under consideration), it would appear that there is an arrest of development, and that the larval condition of the gill becomes permanent in the adult. This arrest of development suggests that the gills of *Jousseaumia* are degenerating. As may be expected from the order of formation of the gill fenestræ, the anterior gill filaments are the longest, and they decrease progressively in length from before backwards.

In the youngest specimens there are no interfilamentar junctions, but these are added in the course of growth, and, as can readily be understood from a consideration of the manner in which the gills are formed, the posterior filaments have fewer junctions than the anterior, as has been described by BERNARD for *Scioberetia*.

A few irregularly scattered interlamellar junctions are formed soon after or during the growth of the reflected lamella. These interlamellar junctions are vascular, whereas the interfilamentar junctions are non-vascular.

Owing to the very small size of *Jousseaumia* and the minuteness of the elements composing the gill filaments, I had some difficulty in making out the details of the gill structure, but as some few of my specimens were well preserved and the very minuteness of the objects was of assistance in enabling me to study optical sections under a high power, I have been able to make out some interesting points not hitherto recorded. The individual filaments are slender, and, except for the fact that their interlamellar edges are broader than their frontal edges, they have the usual lamellibranchiate structure. The central cavity is lined by the usual chitinous layer, thickened at the sides. I could not determine from my sections whether the cavity is divided by a transverse partition into an afferent and an efferent canal, but the appearances seen in optical section lead me to think that it is. The greater number of my specimens when mounted whole and viewed in optical section seemed to possess a large number of closely set ciliated discs, and the late Professor WELDON to whom I showed my preparations was of the opinion that there could be no doubt that ciliated discs were present. Further investigations led me to modify my first opinion, but disclosed an arrangement of the ciliated cells that merits a detailed description.

Figs. 20 and 21 are transverse sections through the gill filaments, the former of a somewhat young and the latter of an adult individual. The triangular shape of the section of the filament with the narrower frontal edge and broad interlamellar base is seen to be due to the great size and thickness of the cells marked *l.c.* Following the usual terminology, the short cilia on the narrow frontal edges may be called the frontal cilia; they are borne on two or three wedge-shaped cells with small nuclei, and the more laterally disposed frontal cilia are longer than the others, so much longer that I was disposed to regard them as latero-frontal cilia, but I do not think that they can be identified as such. The true latero-frontal cilia are very long and rather stiff and are borne on very definite longitudinal rows of columnar cells arranged in single series. These cells are large, with conspicuous round nuclei at their bases, and can be very clearly seen in optical section when the surface of the filament is brought into focus, fig. 22A. Their position and shape is clearly shown in the sections figs. 20 and 21, *l.f.* Following on these are one or two non-ciliated interstitial cells, and the sides of the filaments just above their basal angles are occupied by longitudinal rows of very large oblong cells with flattened elongated nuclei. These cells are best seen in optical section by focussing below the latero-frontal cells, as in fig. 22B, but they are clearly distinguishable in transverse section, though their elongate shape is, of course, not shown in this case. These cells bear a large number of very fine cilia, which interlock with those of adjacent filaments, and the interlocking is so effectual that when the tissues are contracted by the action of reagents the limiting membranes of the cells are torn off and remain adherent to the cilia in the interfilamentar spaces (figs. 20 and 21). The interlamellar bases of the filaments are covered by a few flattened non-ciliated cells with small nuclei. The false appearance of ciliated discs observable in so many of my specimens is due to the fact that in

macerated or much contracted gills the large oblong cells become loosened from their attachment to the filament and become bent up in a crescentic form with their convexities outwards. In this condition, when the cilia remain attached to them, they may very easily be mistaken for ciliated discs, and it was only after studying well-preserved preparations with the highest powers of the microscope that I discovered the real state of the case. As far as I am aware, very large elongated cells of this shape bearing the lateral cilia have not been described before, and they seem to be peculiar to *Joussecaumia*. It is, as I have said, possible to regard the longer cilia on the frontal edges as latero-frontal, and in that case the very long stiffer cilia succeeding them would be lateral cilia, and the long fine interlocking cilia borne by the brick-shaped cells might be regarded as occupying the position of and being homologous with ciliated discs. On this view the gill of *Joussecaumia* would have to be regarded as a primitive form of filibranch gill, in which the interlocking cilia are arranged in continuous lines and are not differentiated into isolated ciliated discs. But this view is hardly tenable. The gills of *Joussecaumia* are not filibranch, for they have well-developed interfilamentar junctions. Moreover, the interlocking cilia, in addition to their being arranged in longitudinal lines and not in groups, are actually finer and longer than the fronto-lateral cilia, and lack the short, stiff brush-like character of the cilia of true ciliated discs. The fact remains, however, that they interlock, and that there is therefore a ciliary union in addition to an organic union between the filaments of *Joussecaumia*. It seems to me probable, however, that the physiological rôle of the interlocking cilia is rather to form a barrier preventing solid particles from passing between the filaments than to give mutual support to the filaments, and this view is supported by their extreme fineness, while the coarser latero-frontal cilia projecting from the corners of the frontal edges are evidently effective in sweeping solid particles over the surfaces of the gills towards the labial palps and mouth.

The interfilamentar junctions are arranged in regular rows. In most specimens there are three such rows in the anterior part of the direct lamella and one or two rows in the reflected lamella. As has been stated, these junctions are non-vascular and are formed as secondary outgrowths from the filaments, bridging across the fenestræ at regular intervals. As may be seen in figs. 17 and 21, these interfilamentar junctions are curved bars, continuous with the chitinous lining of the central cavity of the filament, but the junctions themselves are solid, and as they are only clothed by a very thin protoplasmic sheath, they do not establish any vascular connection between adjacent filaments. As seen in section, the interlamellar edge of each filament appears to be prolonged to form a pair of bars which curve round to unite with corresponding outgrowths from the adjacent filaments. The lower part of fig. 22 shows the interfilamentar junctions as viewed in optical section under a very high power of the microscope. As a rule the interfilamentar bars are single, but occasionally they are double, as shown in the middle of the figure. The chief point of interest is that the bars are clearly shown to be formed by the agency

of special cells, whose nuclei are grouped about the broad bases of attachment of the bars to the filaments. These nuclei are visible in section in fig. 21*x*. There can be no doubt that the interfilamentar junctions are formed by the agency of these cells, for their position at the attached ends of the bars is invariable, and they are not to be distinguished elsewhere. Moreover, by looking through numerous preparations, I have been able to recognise these groups of cells at points where the interfilamentar junctions are in process of formation, and have seen in optical section the processes formed by the cells projecting from, but not yet bridging over the interval between adjacent filaments. These chitin-forming cells do not appear to have been recognised by previous observers, but they are probably included in the general and somewhat vague term "sub-filamentar" tissue. BERNARD (2) gives a drawing of groups of stellate cells in *Scioberetia*, which appear to coincide in position with those which I have described, but he does not attribute any special function to them, and merely refers to them as components of a "substance conjonctive transparente à nombreuses cellules" (*loc. cit.* p. 374). It is evident from a comparison of the sections drawn in figs. 20 and 21, that these junction-forming cells in *Jousseaumia* are differentiated from the flat non-ciliated cells covering the interlamellar edges of the filaments.

THE PERICARDIUM AND RENAL ORGANS.—Owing to the minute size and the contracted state of my specimens, the relations of these organs presented great difficulties. The pericardium is a more or less triangular sac, relatively of considerable size, lying above and in front of the posterior adductor muscle. It is traversed obliquely by the rectum, and the ventricle of the heart surrounds the latter for a considerable part of its course through the pericardium. The whole of the inner lining of the pericardial walls is glandular, constituting an extensive pericardial gland, but the glandular epithelium does not appear to extend to the investment of the ventricle and auricles. Glandular epithelia are the first to suffer from the effects of long immersion in spirit, and the preservation of my specimens was not good enough to allow me to make out the details of the pericardial glandular cells with any certainty. The most that I am able to say is that they are rather large irregularly shaped cells with oval nuclei, and coarsely granular contents which stain faintly blue in picro-indigo-carmin.

The kidneys are conspicuous from the large concentrically striated concretions which they contain. These concretions are contained in a highly vacuolated protoplasmic lining of the renal sacs. The right and left renal sacs are fused together for such a considerable extent in the middle line, below the floor of the posterior end of the pericardium, that their paired nature is obscured, and can only be recognised by an examination of the paired ducts and the paired anterior and posterior horns into which the median sac is produced. Such an extensive fusion of the two kidney sacs is characteristic of the more specialised forms of Lamellibranchia, particularly of the Myacea, Pholadidae and Anatinacea (PELSENEER, 12), and my sections through this region of the body bear a considerable resemblance to the section through the

kidneys of *Lyonsiella abyssicola* and *L. norvegica* figured by PELSENEER (11). The median sac formed by the fusion of the right and left kidney sacs in *Jousseaumia* lies just in front of and above the posterior retractor pedis muscle, near where the latter bifurcates to be attached to the right and left valves of the shell. The two posterior horns of the sac are of considerable length, and extend along the outer sides of the diverging bundles of the retractor pedis muscle, extending blindly just below the anterior end of the posterior adductor muscle. The anterior horns of the sac are smaller and pass to the outside of the retractor pedis muscle. The median sac and its anterior and posterior prolongations are lined throughout by a thick vacuolated layer of protoplasm containing relatively large oval nuclei, but I was unable to distinguish any cell outlines. The renal concretions lie in the vacuoles and are similar to those described and figured by PELSENEER (11). The relations of the renal ducts and the reno-pericardial canals are shown in fig. 23, and the renal ducts are shown in section in figs. 25 and 26, *Re.d.* They are short canals lined by a cubical ciliated epithelium and open into the supra-branchial cavity, in close contiguity to the genital apertures, on a small papilla situated to the outside of the visceral commissure. The reno-pericardial ducts are very minute, and it was difficult to discover them even with the aid of the highest powers of the microscope. They are extremely fine ciliated ducts opening into the floor of the renal sac not far in front of the uroducts. Each reno-pericardial duct runs forward close below the external part of the floor of the median renal sac, and, passing to the inside of the uroduct, turns upwards and opens by a minute ciliated aperture into the pericardial cavity.

THE NERVOUS SYSTEM.—This is of the usual lamellibranchiate type, and presents few features of interest. The nerve ganglia are relatively of great size, as may be seen in figs. 9, 12, and 19. Their proportions, relatively to the whole size of the animal, may be described as larval, and this, coupled with the fact mentioned below (p. 257), suggests that the sexual products in *Jousseaumia* are precociously developed, and that we have, in fact, an example of pædogensis. In the cerebro-pleural ganglia the separate groups of nerve ganglion cells forming the cerebral and pleural moieties of the ganglia are easily recognisable, but the cerebro-pedal and pleuro-pedal connectives leave the fused ganglia as a single nerve. The otocysts are situated above the hinder part of the large nerve mass formed by the fused pedal ganglia, and are quite separate from the ganglia and contained in special compartments of the general body-cavity or hæmocele (fig. 13, *ot.*). Each otocyst contains a single large otolith. The visceral ganglia are of great relative size, and the posterior pallial nerves are very stout. I was unable to find any trace of an osphradium in the form of a specialised patch of epithelium in the neighbourhood of the visceral ganglia, or on the course of the posterior branchial nerves.

THE GONADS AND GONADUCTS.—*Jousseaumia* is monoecious, and, as is usual among hermaphrodite lamellibranchia, is protandric. By far the greater number of the individuals examined by me contained spermatozoa only, but in some few both ripe

spermatozoa and developing ova were present in the gonads, and in about half a dozen cases the gonads contained ova only and were enormously enlarged, displacing the other viscera in the visceral mass. It would appear that *Jousseaumia* is also, to a certain extent, pædogenetic, for I discovered ripe spermatozoa in a considerable number of young forms which were clearly immature as regards the structure and development of the shell and gills.

The gonad itself shows very few traces of paired structure, and varies very much in shape and extent, according as it contains spermatocytes and spermatozoa only, or developing ova or ripe ova. It may be described as consisting of a median vestibule lying in front and ventrad of the kidney and pericardium, opening behind by paired ducts on the reno-genital papillæ, and produced anteriorly into a dorsal and a ventral tubular diverticulum. The diverticula are lined by the germinal epithelium, from which first spermatocytes, then, when the spermatozoa have ripened, oocytes, are produced. In the first stage, when the protandric phase is in evidence, the extent of the gonad is small, as is shown in fig. 1. The dorsal diverticulum extends forward and upward from the vestibule below the floor of the anterior part of the pericardium, and is continued forward below the rectum as far as the point where the latter bends sharply back on itself. The ventral diverticulum is a very short tubular outgrowth from the lower and anterior face of the vestibule, and lies ventrad of the stomachal cæcum. The dorsal or anterior end of the dorsal diverticulum is bifurcated, and the two branches often lie on either side of the rectum, this and the existence of paired gonaducts being the only evidences of paired structure in the body of the gonad. The ventral diverticulum is never bifurcated. Spermatogenesis is effected mainly, though not exclusively, in the dorsal diverticulum, which in many specimens is filled with spermatocytes and spermatids in different stages of development, but the state of my preparations did not admit of my making minute investigations on this subject. The vestibule, in this phase, is filled with ripe spermatozoa, and at a somewhat later period the whole gonad contains a mass of ripe or nearly ripe spermatozoa. This was the most common condition in the numerous specimens I examined; only in two of them could I find evidence of the simultaneous formation of ova and spermatozoa, and in those there were many ripe and a few developing spermatozoa in the dorsal diverticulum, the vestibule was filled with ripe spermatozoa, and developing ova were observed in the ventral diverticulum. The more usual course appears to be that the protandric phase is followed by a short resting stage, during which the diverticula of the gonad are empty and reduced in size, though the vestibule may remain full of spermatozoa. This is succeeded by an active development of ova in both diverticula, which become enormously distended and push their way forward among the viscera, displacing the latter to a very considerable extent. Posteriorly the vestibule bifurcates to form the right and left gonaducts. These ducts, wide at first (fig. 24, *go.d.*), rapidly diminish in diameter, and passing outwards and backwards, open just to the outside of and behind the renal apertures on the reno-genital papillæ on either

side. The most remarkable feature about the gonaducts is that each, just before its external opening, is joined by the short and contracted duct of an ovoid vesicle (*Vs.*, figs. 1, 24, 25) which, in nearly all cases, is filled with ripe spermatozoa, and is clearly a seminal vesicle, in which the ripe spermatozoa are stored up pending the development of the ova. These seminal vesicles, which form very conspicuous objects in sections, are lined by a well-defined, flattened, and as far as I could determine, non-ciliated epithelium, and their relations to the gonaducts are best seen in the series of sections, figs. 24, 25, and 26, drawn under a high power of the microscope. The presence of specialised accessory organs in the shape of vesiculæ seminales on the gonaducts is, as far as I know, a unique feature among the Lamellibranchia, though PELSENEER (12) makes mention of an accessory gland on the male duct of *Cuspidaria*, but this gland is not described in his detailed account of the anatomy of the genus. The numerous specimens of *Heteropsammia* and *Heterocyathus*, sent me by Professor HERDMAN, were collected in February and March, and as the more mature individuals of *Jousseaumia* inhabiting them are nearly all in the same sexual condition, viz., in the protandric phase, it seems probable that in this genus there is a seasonal alternation of male and female maturity. If this conjecture is right, it is evident that the vesiculæ seminales serve as reservoirs for the spermatozoa, which are stored up until the ova are ripe and ready to be discharged from the gonaducts.

Hermaphroditism, though it is not uncommon among the Lamellibranchia, is only characteristic of a single sub-order, the Anatinacea. In all the hermaphrodite forms protandry is the rule, as in *Jousseaumia*, and this is markedly the case in the Anatinacea, as shown by PELSENEER (11). In this sub-order, the ovaries and testes are separate, the ovaries being dorsally and the testes ventrally situated in the visceral mass. In *Pandora*, *Thracia*, and *Lyonsia*, the oviducts and spermiducts open separately by contiguous orifices on each side of the body, and the same is the case in *Lyonsiella*, but in this last genus the male and female apertures open very close together on a small genital papilla (PELSENEER, 11). In *Jousseaumia* the conditions are different; the gonad is single and alternately male and female in function, and there is only a single gonopore on each side. But its structure is interesting as indicating the manner in which the separate ovaries and testes of the Anatinacea may have been evolved. The dorsal and ventral diverticula of *Jousseaumia* correspond in position with the ovaries and testes of the Anatinacea, and, as I have shown, they are to a certain extent specialised, since the production of spermatozoa is nearly exclusively confined to the dorsal diverticulum. If the two diverticula were to become separate and acquire separate openings to the exterior and the function of producing ova were confined to the one, and the function of producing spermatozoa to the other, we should have a condition of things nearly identical with that of the Anatinacea. It must be observed, however, that in the latter group the testes are ventral, whereas in *Jousseaumia* the male diverticulum is dorsal, and at a later stage both diverticula become female.

Although I made a careful search, I was unable to find any ova or embryos in the supra-branchial chamber. It does not necessarily follow that *Jousseaumia* is not incubatory, and that the ova are not fertilised, and undergo the earlier stages of development in the branchial cavity, for as I have pointed out, there is probably a seasonal alternation of sexual maturity, and the specimens at my disposal were mostly in the male condition. Even those which had advanced beyond this stage and contained numerous ova in the gonads, did not give evidence of complete female maturity. In one specimen of *Heteropsammia* I found, in the *Aspidosiphon* chamber, a number of small ovoid ova, each surrounded by a thick radially striated egg-membrane, but I have no evidence that these are the ova of *Jousseaumia*. Nor was I successful, after a prolonged and careful search, in finding any larval or embryonic forms much younger than the specimen shown in fig. 27, though in every coral there was an abundance of young forms representing every stage of later growth. The specimen depicted in fig. 27 displays clearly the larval shell or prodissoconch, with its rectilinear hinge-line and internal ligament. A single-growth lamina has been added at the edge of the prodissoconch, so the animal cannot have passed very far beyond the larval stage. The principal organs of the body are, however, well developed. The anterior and posterior adductor muscles are fully formed, as is usual in young Lamellibranchs; the foot has the geniculate characters of the adult; the retractor and protractor muscles of the foot have the same relative size and importance as in the adult; the labial palps are well formed, and in the alimentary canal all the features of the adult—pharynx, cesophagus, stomach, cæcum, liver and intestine—are clearly distinguishable. Only the nerve centres and the gills retain embryonic characters. In the nervous system the ganglia are still larger, relatively to the whole size of the animal, than they are in adult, and the connectives are relatively very thick. In the cerebro-pleural ganglia the double nature of each member of the ganglion-pair, only recognisable in section in the adult, is evident in a surface view (fig. 27, *cg.*). The gills are in an early stage of development and show five fenestrations, with a commencement of a sixth. The organisation is much more advanced than, for instance, in the youngest *Scioberetia* figured by BERNARD (2, plate xv., fig. 4). Not only is the internal organisation well advanced, but the hinge does not show the characteristic teeth of the prodissoconch, although the valves have hardly grown beyond the prodissoconch stage. On the contrary, there is no trace of a provinculum, the anterior cardinal teeth are clearly developed, and the large lateral teeth are being formed by folds of the mantle edge just above the anterior and posterior adductor muscles. In the specimen shown in fig. 28 there are four growth laminae outside the prodissoconch. The organisation is somewhat more advanced than in fig. 27; in particular the nervous system and labial palps have assumed their adult proportions and the gills are larger and have acquired seven fenestrations, but as yet no interfilamentar junctions. The anterior cardinal teeth of the hinge are more distinct and clearly interlock with one another, and a deposition of calcareous matter round

the attachments of the ligament foreshadows the formation of the posterior cardinal tooth and the ligamentar fossa. In later stages, with seven or eight growth laminae outside the prodissoconch, the adult characters of the hinge are fully established. It would appear, then, that, as compared with the size of the shell, the visceral organs and the permanent hinge teeth are precociously developed in *Jousseauxia*, and the suppression of the provinculum and consequent abbreviation of the several stages in the evolution of the heterodont hinge may account for the ligament remaining internal and therefore in its larval condition instead of being shifted to an external position.

CONCLUSION.

I have given a full description of this interesting little Lamellibranch, because, as it seems to me, it is incumbent on students of this class to give a full anatomical account of the various forms that come under their notice. A detailed account of the anatomy of various Lamellibranchs is needed before many questions of classification can be finally settled. The researches of PELSENEER (10) have broken ground in this direction, but subsequent authors have not followed his example by dealing with the whole anatomy of the species they have investigated. The work of RIDWOOD (15), dealing with a large number of species of all orders of the Lamellibranchia, is confined to a detailed exposition of the gill-structure, and though it forms a valuable contribution to our knowledge of this single feature of Lamellibranch anatomy, its main result has been to show how little the characters of a single organ are to be relied upon in framing the smaller subdivisions of a system of classification. There are at the present time few malacologists who will question the importance of gill-structure as a basis of the general classification of the Lamellibranchia and their division into the orders Protobranchia, Filibranchia, Eulamellibranchia and Septibranchia meets with general acceptance, the more so because these orders correspond very closely with those based upon a study of the hinge characters. But when we come to subdivide the orders into sub-orders and to arrange the latter in families, and especially when we attempt to estimate the relationship and probable lines of descent of the various families grouped together in the sub-orders, the structure of the gills becomes of less value to us. Thus, to take a single instance, in the family Donacidæ we find plicate and non-plicate, homorhabdic and heterorhabdic gills with almost every variety of interfilamentar and interlamellar connection. In the large sub-order Submytilacea, we find the simple Astartiform gill at one end of the order and the extremely specialised complex gills of the Unionidæ at the other, and no very definite series connecting the two. PELSENEER (10 and 12) characterises the Submytilacea as Eulamellibranchs with smooth, *i.e.*, non-plicate gills, but RIDWOOD (15) has shown that the gills of *Diplodonta oblonga* and *Monocondylæa* are slightly and those of *Corbicula lydigina* markedly plicate. On the other hand, smooth or

non-plicate gills are common among other sub-orders of Eulamellibranchia. The detailed study of gill structure has therefore proved disappointing for classificatory purposes, and in trying to trace the connections between the sub-groups of the Eulamellibranchia we are once more thrown back on a criticism of the *ensemble* of the anatomical characters of each family. The difficulty of placing any given genus in its proper position in the system is well illustrated by *Jousseaumia*. Its heterodont hinge, sub-equal adductor muscles, entire pallial line, single pallial suture and very simple gill structure leave no doubt that it must be placed in the Submytilacea, but when one looks for its nearest allies in this very heterogeneous sub-order, the difficulties are considerable, and they are not lessened by the fact that some systematists give a certain character as diagnostic of a family, and then proceed to describe as members of that family genera in which this diagnostic character is wanting.

Thus, *Jousseaumia* shows undoubted affinities to the Erycinidæ (Leptonidæ, PELSENEER, 12). The members of this family are hermaphrodite, the ligament is internal, the foot linguiform, elongated and byssiferous, the gills simple and astartiform, with very little sub-filamentar tissue and scattered interlamellar junctions. Many members of the family are of minute size and some (*Lepton*) are commensal. BOUVIER identified *Jousseaumia* as a *Kellia*, and E. A. SMITH identified it with ANGAS' genus *Mysella*, which FISCHER (6) regards as closely allied with *Kellia*. I have shown that it cannot be placed in either of these genera, and though it might be regarded as having affinities with *Lepton* or *Lasaea*, because of the single pallial suture, it differs from the whole of the Erycinidæ in the absence of the external demibranch. This last character suggests an affinity with the Lucinidæ, and more particularly with the genus *Montacuta* placed in this family by PELSENEER; *Montacuta* has a single pallial suture, a very long, linguiform, byssiferous foot and a shell which is in many respects similar to that of *Jousseaumia*. The ligament is internal, the anterior adductor impression longer than the posterior, the cardinal teeth have analogous characters, and the anterior border is longer than the posterior, and as a small point of resemblance PELSENEER describes a protractor pedis ventral to the anterior adductor (11, p. 203) which is paralleled by the slip of the protractor in *Jousseaumia*. *Montacuta bidentata* has the habit of living in old shells, and *M. substriata* is parasitic on an Echinid, and the former habit is suggestive of the manner in which *Jousseaumia* may have come into association with the Sipunculid inhabiting the basal chambers of corals. So similar is the shell of *Montacuta* to that of the Erycinidæ that FISCHER places it in this family, but its gills not only lack the external demibranch, but the filaments have considerable interlamellar extrusions, the interfilamentar junctions are vascular and in these and other respects so closely resemble the gills of *Lucina* that there can be no doubt that it should be placed, as PELSENEER has placed it, in the Lucinidæ. And for the same reason that *Montacuta* is placed in the Lucinidæ, *Jousseaumia* must be excluded from this family. Its gill

structure is different and it is monœcious whereas the Lucinidæ are diœcious, and there are other anatomical characters in which it differs from *Montacuta* (see PELOSENEER, 11, pp. 203, 204).

The only other members of the Submytilacea in which the external demibranch is wanting are the Corbidæ and *Scioberetia*. *Joussecaumia* has clearly no affinities with the Corbidæ, but, as has been pointed out, it has certain features in common with *Scioberetia*. Both are hermaphrodite, commensal or semiparasitic, have a similar gill structure and a single pallial suture, but in *Joussecaumia* the mantle is not reflected over the shell and it therefore must be excluded from the Galeommidæ, to which *Scioberetia* belongs.

The balance of evidence is in favour of placing *Joussecaumia* among the Erycinidæ in spite of the absence of the external demibranch. This last character, taken by itself, is of no systematic importance, since it occurs in forms as far apart as *Lucina*, *Scioberetia*, and *Teredo*. RIDEWOOD has shown that the external demibranch is liable to modification and partial suppression in a large number of widely separated genera, and its total suppression may well be accounted for by changed conditions of life affecting the respiratory and alimentary functions. I have shown that there is evidence that the gill is degenerating in *Joussecaumia*, and that the reflected lamella of the existing demibranch, never very well developed, is rudimentary in a certain number of adult individuals. The conditions which are causing the degeneration of the reflected lamella of the inner demibranch may well have caused the total suppression of the outer demibranch. On the other hand, the details of the gill structure agree very closely with those of the Erycinidæ, particularly with that of *Lasaea*, and the internal ligament, the shell characters, the hermaphroditism and other anatomical features point to a close relationship, particularly to the last-named genus, in which the external demibranch is very short and has no reflected lamella. It may be further observed that *Joussecaumia* presents an interesting example of the admixture of primitive and specialised characters which is so puzzling to the systematist. RIDEWOOD rightly regards the gills of *Astarte* as being among the most primitive of all Eulamellibranch gills. In their essential structure the gills of *Joussecaumia* are still more primitive, but at the same time they are specialised, and specialised in the direction of reduction and degeneration, as is shown by the absence of the outer demibranch, the slight development, and even the suppression of the reflected lamella of the inner demibranch, which in some individuals is only represented by a continuous sheet of tissue reflected and attached to the body wall in the region of the foot. It is obvious that this kind of reduction, if carried still further, would lead to the condition found in the Septibranchia, though I do not mean to suggest that *Joussecaumia* is closely related to this order.

As other evidences of primitive characters we may note, in *Joussecaumia*, the relics of paired œsophageal pouches (if I am right in regarding the lateral grooves in the œsophagus as such), the obvious cerebral and pleural moieties of the cerebro-pleural

ganglia in the young forms, the simplicity of the alimentary tract (but this may be due to degeneration), and such minor characters as the persistence of the internal embryonic hinge ligament, the single pallial suture, &c. On the other hand, the extensive fusion of the kidney-sacs in the middle line is characteristic of more highly specialised Eulamellibranchs, such as the Anatinacea, and the presence of vesiculæ seminales is a unique feature of specialisation in connection with the reproductive apparatus.

Taking all these facts into consideration, we must regard *Jousseaumia* as an offshoot of a primitive Eulamellibranch stock, which in consequence of its commensal habits has been largely modified in the directions indicated, and that its nearest allies are the Erycinidæ and Galeommidæ, which are similarly primitive Eulamellibranchs modified in various directions in relation to their different habits of life.

It is interesting to note that the commensalism between a coral, a sipunculid, and a lamellibranch must be still further extended. In almost every specimen examined, whether of *Heterocyathus* or *Heteropsammia*, I found in the *Aspidosiphon* chamber one or two specimens of a small copepod belonging to the family Harpacticidæ, but as I am obliged to bring this paper to a close to be in time for the issue of the last volume of the "Reports on the Ceylon Pearl Oyster Fisheries," I have not had time to identify the genus and species. Furthermore, *Jousseaumia*, minute as it is, and protected within the *Aspidosiphon* chamber of the coral, is liable to the attacks of parasites. In one series of sections I found a minute trematode, distinguishable as such by its well-developed suckers, encysted in one of the dorsal lobes of the liver, and in another series a larger specimen of what is apparently a trematode, but I could not easily determine its nature from the sections, lying free in the supra-branchial cavity.

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EXPLANATION OF PLATES.

LETTERING IN ALL THE FIGURES.

<i>A.ad.</i> , anterior adductor muscle.	<i>Li.</i> , liver.
<i>A.ap.</i> , anal or exhalant aperture.	<i>Lig.</i> , hinge ligament.
<i>An.</i> , anus.	<i>Ln.int.</i> , internal lamella of demibranch.
<i>A.r.p.</i> , anterior retractor pedis muscle.	<i>Ln.ext.</i> , external lamella of demibranch.
<i>Br.m.</i> , branchial muscles.	<i>L.p.</i> , labial palps.
<i>Bucc.</i> , buccal cavity.	<i>M.</i> , mantle.
<i>By.</i> , byssus.	<i>Oe.</i> , oesophagus.
<i>By.c.</i> , byssus cavity.	<i>or.exh.</i> , exhalant or anal pallial orifice.
<i>By.g.</i> , byssus groove.	<i>ot.</i> , otocyst.
<i>By.gl.</i> , byssus gland cells.	<i>P.ad.</i> , posterior adductor muscle.
<i>Cæc.</i> , cæcum.	<i>Pc.</i> , pericardium.
<i>C.g.</i> , cerebro-pleural ganglion.	<i>P.g.</i> , pedal ganglion.
<i>Cr.s.</i> , crystalline style.	<i>P.r.p.</i> , posterior retractor pedis muscle.
<i>Cu.</i> , cuticular lining of stomach.	<i>P.s.</i> , pallial suture.
<i>Dbr.</i> , internal demibranch.	<i>Ptr.</i> , protractor pedis muscle.
<i>F.</i> , foot.	<i>Ptr.¹</i> , ventral slip of the protractor pedis muscle.
<i>fr.</i> , frontal cilia.	<i>R.</i> , rectum.
<i>gl.c.</i> , glandular cells of stomach.	<i>Re.</i> , kidney.
<i>Go.</i> , gonad.	<i>Re.a.</i> , renal aperture.
<i>Go.a.</i> , genital aperture.	<i>Re.d.</i> , renal duct.
<i>Go.c.</i> , gonaduct.	<i>R.pd.</i> , reno-pericardial canal.
<i>Go.d.¹</i> , dorsal diverticulum of gonad.	<i>St.</i> , stomach.
<i>Go.d.²</i> , ventral diverticulum of gonad.	<i>Spz.</i> , spermatozoa.
<i>Ht.</i> , ventricle of heart.	<i>Vb.</i> , vestibule of gonad.
<i>ifj.</i> , interfilamentar junctions.	<i>Vc.</i> , visceral commissure.
<i>ilj.</i> , interlamellar junctions.	<i>Vg.</i> , visceral ganglion.
<i>l.</i> , lateral cilia.	<i>Vs.</i> , vesicula seminalis.
<i>l.c.</i> , oblong cells bearing lateral cilia.	<i>x.</i> , cells of the interfilamentar junctions.
<i>lf.</i> , latero-frontal cilia.	

PLATE I.

- Fig. 1. An adult specimen of *Jousseaumia heteropsammia* lying in the right valve of the shell. × 85.
- „ 2. Valves with hinge teeth of *J. heterocyathi*. × 85. *c.*, the single cardinal tooth of the right valve; *c.a.*, the anterior, and *c.p.*, the posterior cardinal teeth of the left valve; *foss.*, ligamentar fossa; *lig.*, ligament; *lant.*, anterior lateral, and *l.post.*, posterior lateral teeth; *L.V.*, left valve; *R.V.*, right valve.
- „ 3. Valves with hinge teeth of *J. heteropsammia*. × 85. Lettering as in the preceding figure.
- „ 4. Section through the byssus groove of *J. heterocyathi* highly magnified, showing the ciliated demicanal, *d.c.*, in the depth of the groove; *mus.*, muscle fibres of the foot.
- „ 5. A section through the duct of the byssus cavity, higher up than fig. 4. The ciliated demicanal, *d.c.*, retains the same shape as in fig. 4; the remainder of the duct is not ciliated, but lined by a thick cuticle formed by the underlying epithelial cells.

- Fig. 6. A section through the byssus cavity. The demicanal, *d.c.*, is still apparent, but the whole cavity is lined by a similar ciliated epithelium. *m.sp.*, median septum; *l.sp.*¹, the thick lateral septa on either side of the demicanal; *l.sp.*², smaller lateral septa.
- „ 7. A portion of a section through the byssus cavity, somewhat anterior and oblique to the section drawn in fig. 6. The byssus gland cells, *By.gl.*, are seen to be breaking up, and the granular secretum stained red with safranin is passing between the epithelial cells. The granular secretion in the cavity itself is omitted. ZEISS' $\frac{1}{2}$ hom. imm. Comp. Oc. 4.
- „ 8. A transverse section through the oesophagus of *Jousseaunia heterocyathi*. *lat.div.*, lateral diverticula of the oesophagus, resembling the oesophageal pouches of Protobranchia. ZEISS' $\frac{1}{2}$ hom. imm. Comp. Oc. 4.

PLATE II.

Figs. 9 to 19. A series of transverse sections through *Jousseaunia heteropsammiae*. Fig. 9 passes through the cerebral ganglia and fig. 19 through the visceral ganglion pair. All the figures are fully lettered.

PLATE III.

- Fig. 20. A section through the ventral end of the demibranch of an immature individual of *J. heteropsammiae*. ZEISS' $\frac{1}{2}$ hom. imm. Comp. Oc. 4.
- „ 21. A section through two adjacent gill filaments of a mature individual of *J. heteropsammiae*, showing the interfilamentar junctions.
- „ 22. Optical sections of two gill filaments of *J. heterocyathi*. A represents the filaments as seen with a high focus, and shows the latero-frontal cilia, *lf.*, borne on columnar cells. B represents a section as seen with a somewhat deeper focus, and shows the lateral cilia, *l.*, borne on the large oblong cells, *l.c.* C, taken at a still deeper focus, shows the interfilamentar junctions, which are occasionally double, as in the centre of the figure, and the cells *x*, which give rise to the outgrowths forming the junctions.
- „ 23. A diagram showing the relations of the kidney, pericardium, and gonads in *Jousseaunia*, from a reconstruction of a series of sagittal sections.
- „ 24. A horizontal section through the gonaducts, vesiculae seminales, and posterior part of the kidney of *J. heteropsammiae*. ZEISS' $\frac{1}{2}$ hom. imm. Comp. Oc. 4. *Con.*, renal concretions.
- „ 25. A section somewhat lower down from the same series as fig. 24, showing the renal duct, *Re.d.*, and the opening of the vesicula seminalis into the gonaduct; *br.*, attachment of branchial filament to the body-wall.
- „ 26. A section next but one in the series to that shown in fig. 25, showing the renal (*Re.a.*) and genital (*Go.a.*) apertures.
- „ 27. A young individual of *J. heterocyathi* with one growth lamella outside the prodissoconch, and with five gill fenestrations and the commencement of a sixth; *pr.diss.*, outline of the prodissoconch; *Card.a.*, anterior cardinal hinge tooth. $\times 150$.
- „ 28. A somewhat older individual of the same species with seven gill fenestrations and four growth lamellae outside the prodissoconch. $\times 150$.







