PART II.—THE EDGE OF THE MANTLE AND THE EXTERNAL ORNAMENTATION OF THE SHELL.

By N. ANNANDALE.

In the first part of this paper Major Sewell has described the structure of the free part of the mantle of *Vivipara bengalensis* in general terms and has pointed out, as Leydig [1] observed in the embryo of *V vivipara*, that the margin bears three short processes corresponding in position with the three rows of minute chaetae on the surface of the embryonic shell. He has further noted that in the adult additional processes are both intercalated between the three primary processes and produced to the left of the outermost row of chaetae in correlation with the development of dark spiral bands on the shell.

Similar facts struck me forcibly when examining two very large and peculiar species of Viviparidae in Manipur, namely *V oxytropis* (Benson), the shell of which is ornamented with dark and prominent spiral ridges, and *Lecythoconcha lecythis* (Benson),[2] the shell of which is almost smooth and unicolorous.

The observations made on these species, supported as they were by Major Sewell's independent observations on *V bengalensis*, led me to examine the edge of the mantle and the embryonic shell in all species of Viviparidae in which living or properly preserved material was available. The species I have examined living are *V bengalensis* (Lamarck), *V dissimilis* (Muller) [= *V remossii* (Benson)], *V oxytropis* (Benson) and *L. lecythis* (Benson). I have also examined preserved material of the remarkable genera *Margarya*, Nevill, and *Taia*, Annandale, in both of which the shell is more highly and fantastically sculptured than in any species of *Vivipara*. My specimens of *Margarya melanoides* were collected in Yunnan by Mr. J Coggin Brown, and those of *Taia intha*, *T elitoralis*, *T shanensis* and *T naticoides* were preserved with great care by Dr. F. H. Gravely in the Southern Shan States. Some of them are in excellent condition for histological study.

In addition to this Asiatic material I have been enabled by the very kind assistance of Prof. J H. Ashworth of Edinburgh University, to examine several series of fine sections of both the embryo and the adult of *V contecta* (Millet), a European species with a smooth, broadly banded shell.

The material examined thus includes specimens and preparations of species both with smooth and with highly sculptured shells, both with almost unicolorous and with conspicuously banded shells.

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[1] Leydig, *Zeits. f. wiss. Zool.* II, pl. xi, fig. 16 (1850).

[2] For the latter species I have recently proposed a new genus based partly on the structure of the mantle, viz. *Lecythoconcha*, Annandale, *Rec. Ind. Mus.* XIX, p. 114 (1920).

In considering the ornamentation of the shell both colour-pattern and sculpture can, therefore, be taken into account.

Ornamentation of the embryonic shell.

The ornamentation of the embryonic shell is almost uniform in pattern in all species of Viviparidae investigated, and the only important differences found are those in the degree to which the spiral sculpture is developed in different forms. Colour-pattern is usually absent, the shell being of a pale horny yellow or brown, with the protoconch darker and browner than the rest; but in those species in which the embryo has a comparatively large number of whorls before birth the dark spiral bands characteristic of some such forms begin to appear on the younger parts of the shell before it is set free from the egg-membrane.

The sculpture at this early stage is mainly periostracal, involving only the horny outer covering of the shell; but as this is not entirely so I propose to discuss the periostracal sculpture first and then that of the calcareous part of the shell or true test. It will be convenient to treat *V bengalensis* as a typical form in discussing the periostracal sculpture of the embryo.

The shell of this species consists at birth of 3½ whorls. Of these the apical whorl and a half constitute the true protoconch. They are flat, band-like and almost smooth, but with a strongly marked keel running round the outer edge of their upper surface in a spiral. Several faint, line-like spiral ridges, of which two are more prominent than the others, can also be detected on their surface under a high magnification. A single spiral row of extremely fine hair-like processes projects from the marginal keel, extending upwards to the tip of the apical half-whorl. Towards the base of the protoconch these processes become stiffer and are curved and retroverted at the extremity, the curvature of their tips being directed towards the mouth of the shell. They also become less crowded together. A little above the point at which the protoconch merges into the uppermost whorl of the younger part of the embryonic shell (*i.e.* that part in which the whorls begin to assume the essential characters of those of the adult), a second line of chaetae makes its appearance parallel to the first, and finally, on the penultimate embryonic whorl, a third. The oldest row, which I shall call in reference to its age and its position the FIRST or UPPERMOST ROW, is rather less developed than the SECOND or MIDDLE ROW. The THIRD or PERIPHERAL ROW, which continues to occupy the extreme periphery of the shell, is the largest and best developed of all. As the shell grows, however, and new whorls are added they destroy the chaetae that lie immediately above them by the pressure of their embrace.

Between the three primary rows of chaetae, above them to the left of the mouth of the shell, and particularly below them to the right (that is to say below the peripheral angle) there are other spiral lines on the external surface of the shell, running parallel to one another and to the rows of chaetae, but forming only very fine ridges with minute irregular processes or serrations. These I shall call the SECONDARY PERIOSTRACAL RIDGES of the embryonic shell. Finally, still finer oblique longitudinal or vertical lines can be detected under a powerful lens, running across the spiral lines in such a way as to form a delicate reticulation with rhomboidal meshes. That all this ornamentation is mainly periostracal can be proved by dissolving the calcareous matter of the shell with weak acid. The lines and chaetae remain intact.

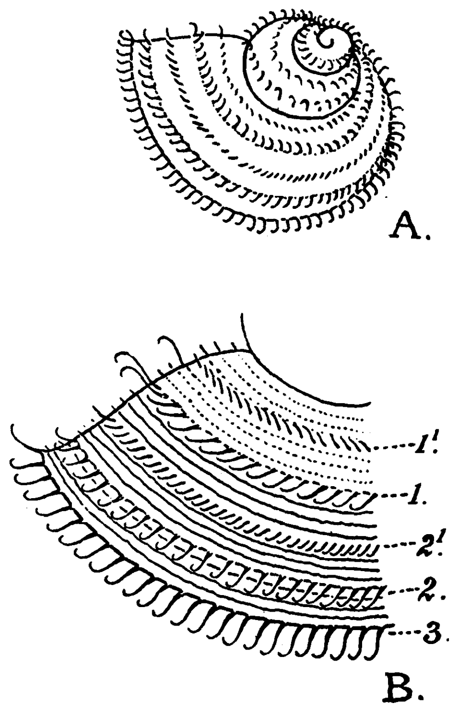


FIG. 10.—Embryonic shell of *Vivipara dissimilis* (Müller).

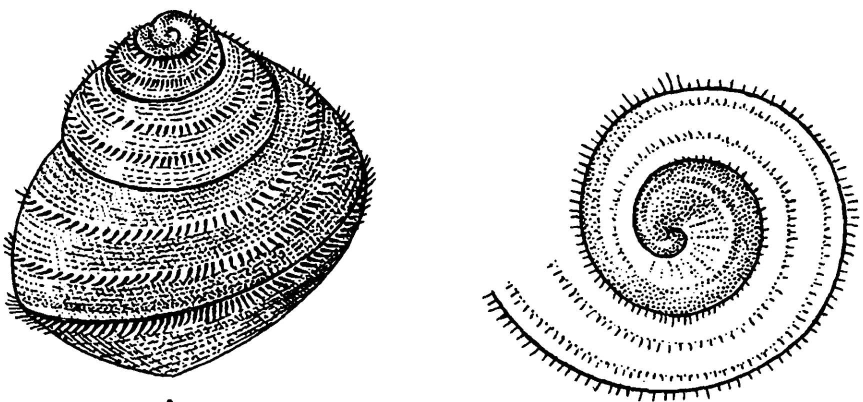
A. Oblique view of the whole shell at birth, showing lines of chaetae (magnified).
B. Part of the surface of the body-whorl of the same shell more highly magnified.

1 = uppermost primary row of chaetae;
2 = middle primary row of chaetae;
3 = peripheral row of chaetae;
1' 2' = secondary rows of chaetae.

In the other species of Viviparidae examined the periostracal ornamentation is essentially the same, but in several, the test-sculpture being more highly developed, the chaetae are given greater prominence. I will discuss this point later. In the embryonic shell of *V dissimilis* (fig. 10), two of the secondary periostracal ridges bear minute chaetae considerably finer and shorter than those of the three primary rows but essentially similar in structure. These secondary rows are situated between the first and second primary rows and above the latter.

In some species the periostracal ornamentation of the embryonic shell becomes obsolescent at an early age, but in all I have examined the peripheral row of chaetae is continued, at any rate in some individuals, on to the body-whorl of the full-grown shell, and the apparent disappearance of the chaetae of the other rows is more apparent than real. These structures are of extreme fragility and in a comparatively heavy organism such as an adult *Vivipara* are liable to be rubbed off at a touch. In a nearly full-grown *V. bengalensis*, in which the shell is receiving its final addition, I have found that the three rows of chaetae are still produced, but disappear almost as soon as they are formed. In *V dissimilis* traces of the embryonic periostracal sculpture are more persistent and the basis of the five rows of chaetae can frequently be detected in the form of fine punctures. Even in the adult of *L. lecythis* the periphery of the body-whorl is often surrounded by a line of extremely fine hairs representing degenerate chaetae. In the Siamese *V ciliata* (Reeve),[1] in which a larger number of secondary periostracal ridges probably bear chaetae than in *V dissimilis*, they persist throughout life on all the whorls of the shell, and in some individuals of the Chinese *V lapillorum* (Heude)[2] they are coarsely developed on the peripheral keel of the body-whorl.

In species of *Vivipara* such as *V bengalensis*, in which the embryonic shell is extremely thin and fragile, it is difficult to demonstrate the existence of any true test-sculpture as distinct from that of the periostracum, but by means of careful manipulation of lighting under a binocular microscope it can be seen that each of the rows of chaetae is situated on a slight elevation. This can be more readily demonstrated in such forms as *L. lecythis* (fig. 11), in which the test is much thicker at birth; while the chaetiferous ridges are conspicuous from the first in certain other species, such as *Margarya melanoides*,[3] *Taia intha*[4] and the peculiar Japanese *Heterogen turris*.[5] In these three species they are comparatively broad and blunt. In *V dissimils* and *V oxytropis*, although the embryonic shell is no thicker than in *V bengalensis*, they are more prominent than in that species, but thin and sharp. Generally speaking, a strong development of the three primary ridges in the embryonic shell is correlated with a coarse and well-developed spiral sculpture in that of the adult, but this is not so in *Heterogen*, in which it becomes gradually much less conspicuous on the younger whorls. In *H turris*, however, the only species of the genus known, as in the African *Neothauma*, Smith, and in many species



A. B.

FIG. 11.—Embryonic shell of *Lecythoconcha lecythis* (Benson).
A. Lateral view of the whole shell at birth (magnified).
B. Protoconch as seen from above (more highly magnified).

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[1] Reeve, *Conch. Icon.* XIV (*Paludina*), pl. vi, fig. 36 (1864).
[2] Annandale, *Mem. As. Soc. Bengal* VI, p. 314, pl. x, fig. 9 (1918).
[3] Kobelt on *Vivipara*, in new edit. of Mart. and Chemn., *Conch. Cab.*, pl. xxxvii, xxxviii (1909).
[4] Annandale, *Rec. Ind. Mus.* XIV, pl. xvii, fig. 7; pl. xviii, fig. 10 (1918).
[5] Annandale, *Mem. As. Soc. Bengal* VI, p. 400, figs. 1, 2. (1921).

of *Vivipara*, the third or lowest primary ridge remains conspicuous as a peripheral carina, even when the other two disappear or become obsolescent.

Ornamentation of the adult shell.

In the adult shell, as I have already pointed out, the periostracal sculpture is relatively unimportant. In many species of the family, including the great majority of those of *Vivipara*, the test-sculpture is not much more conspicuous. In *V bengalensis* the oblique longitudinal lines on the periostracum are impressed on the test and remain distinct through life. Indeed, they are coarser and more prominent in the younger whorls. In most races and phases of this species the spiral sculpture disappears almost completely on the body-whorl, but in some individuals of certain phases and races, such as the phase *halophila*, Kobelt (pl. II, figs. 9, 10), and the race *balteata*, Benson, the primary spiral ridges and also a few of those of the secondary order are slightly thickened on the body-whorl, while in the Burmese race (*doliaris*, Gould, pl. I, fig. 9) both the uppermost of the three primary ridges and the peripheral ridge are prominent, forming more or less sharp-cut angles in the outline of this whorl. In *V oxytropis* and a few other species of the same genus the peripheral ridge forms a prominent keel on the body-whorl, separating the shell into an upper and a lower region, while some or all of the other ridges remain more or less salient.

It is, however, in such forms as the more highly developed species and varieties of the genera *Taia* and *Margarya* that the sculpture of the test reaches its highest development in the adult shell. In *V oxytropis* [1] the ridges are smooth and sharp: in the more highly developed forms of the two genera mentioned they are broad and coarse and are broken up into numerous tubercles, scales or spines. Even in shells with a comparatively simple sculpture such as those of *Taia theobaldi* [2] or *Margarya melanoides* var. *mansuyi* [3] the ridges have not the unbroken surface of those on the shell of *V oxytropis* and other ridged forms of *Vivipara*.

In all the Viviparidae in which I have examined both embryonic and adult shells, the ridges of the test are grooved internally at first. They retain this structure in *V oxytropis* throughout life. In some other ridged species and races of *Vivipara*, however, with thicker shells, and also in all forms of *Taia* and *Margarya*, the internal groove becomes more or less completely obliterated by the deposit of nacreous matter on the internal surface.

In describing the ornamentation of the embryonic shell I have alluded briefly to the fact that in *Taia intha* and some other Vivi-

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[1] Hanley and Theobald, *Conch. Ind.*, pl. lxxvi, fig. 5 (1876).
[2] Annandale, *Rec. Ind. Mus.* XIV pl. xvi, fig. 1 (1918).
[3] Kobelt on *Vivipara*, in Mart. and Chemn., *Conch. Cab.*, new edit., pl. xxxvii, figs. 6, 7 (1909).

paridae in which the shell attains a relatively large number of whorls before birth, a colour-pattern appears on the lower whorls, while in *V bengalensis*, in which there are only $3\frac{1}{2}$ whorls at birth, this pattern appears later. It cannot, therefore, be regarded as belonging to the primitive shell. Generally speaking, the shells of the Viviparidae may be divided into two categories so far as colour is concerned.[1] The external surface in one category is of an almost uniform olivaceous colour, occasionally with irregular black longitudinal streaks. In the other type it is marked with dark spiral bands.

STRUCTURE OF THE MARGINAL REGION OF THE MANTLE.

By the phrase MARGINAL REGION OF THE MANTLE I mean the free edge of the roof of the branchial chamber and the immediate-

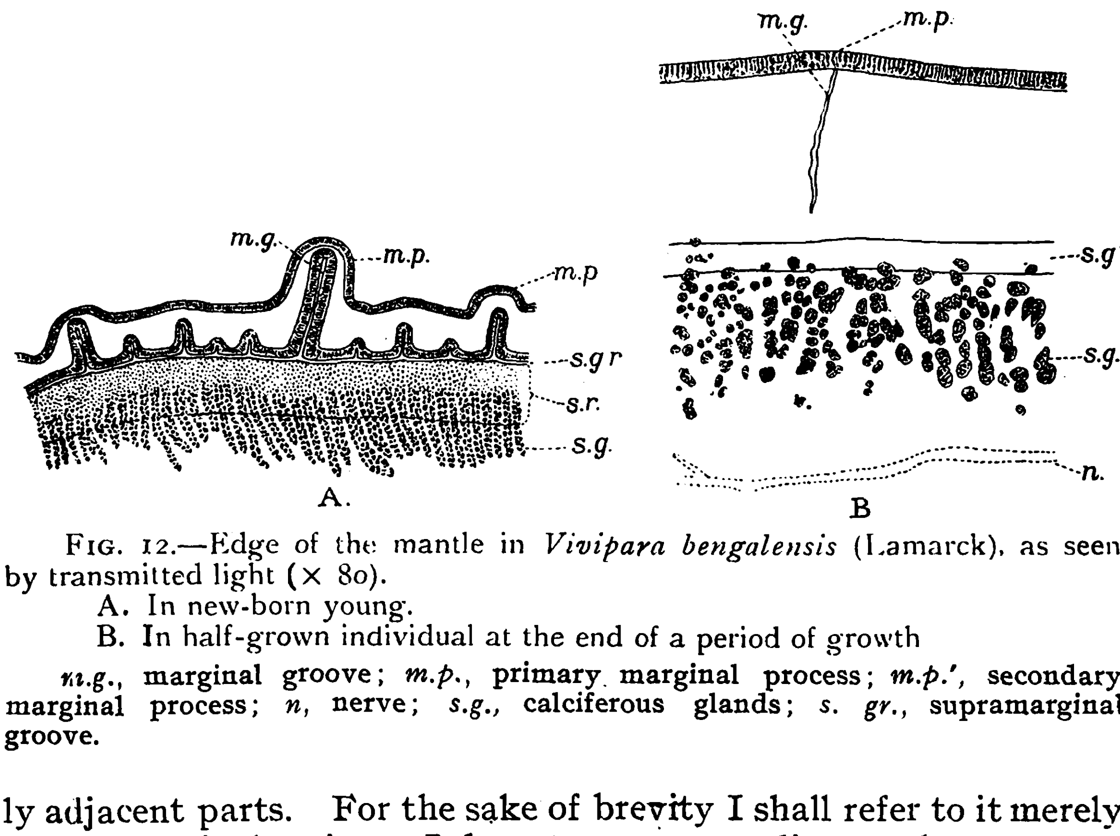

FIG. 12.—Edge of the mantle in *Vivipara bengalensis* (Lamarck), as seen by transmitted light (× 80).

A. In new-born young.

B. In half-grown individual at the end of a period of growth

m.g., marginal groove; *m.p.*, primary marginal process; *m.p.'*, secondary marginal process; *n*, nerve; *s.g.*, calciferous glands; *s. gr.*, supramarginal groove.

ly adjacent parts. For the sake of brevity I shall refer to it merely as the marginal region. I do not propose to discuss the structure of other parts of the mantle except in so far as it may be necessary to elucidate that of this region.

EXTERNAL STRUCTURE.—The external structure of the marginal region is uniform in all the Viviparidae examined, so far at any rate as its main features are concerned, but exhibits certain minor generic and even specific characters, and differs in details at different periods in the life of the individual. The free edge is sharp at birth in *Vivipara* and *Taia*, blunt in *Lecythoconcha* and

[1] The only real exception I know to this rule is to be found in *V. helmandica* Annandale, from Eastern Persia, the shell of which is olivaceous with rounded pale spots, but there is often an obscure pale band round or just below the periphery of the body-whorl of the shell in forms of the *V. dissimilis* group.

also probably in *Margarya*, in which, however, I have examined only adult individuals. In the first three genera, and probably in all Viviparidae, it bears at this period three distinct finger-shaped processes,[1] one situated just above the snout near the middle of the edge, the other two to the right of this point. The left process, which marks a very important point in the orientation of the ornamentation of the shell, I shall call the PERIPHERAL PROCESS. It moves along, in the expansion of the animal, under the most prominent line of the body-whorl of the shell and is usually, but not always, a little longer than the others. The two processes to the right of the peripheral process may be called the first and the second process, the former lying the furthest to the right. These three processes correspond in position with the three primary rows of chaetae on the young shell (p. 250, fig. 13) and bear the same notation in my figures. The peripheral process, though usually the most conspicuous and the most important in the future history of the shell, is morphologically the youngest, while the first process, the least important of the three from this point of view, is the oldest. These three processes I call the three PRIMARY PROCESSES. They were first observed and figured in the embryo of *Vivipara vivipara* by Leydig,[2] but are omitted in the figures of more recent authors. I find them just as well developed in the fully formed embryo of the European *V contecta* as they are in Indian species.

In most other Viviparidae examined, at least traces of other processes between and to the left of the primary three can be detected at the same period. In *V bengalensis* (fig. 12) they are small and inconspicuous, but in *V dissimilis*, another common Indian species, four SECONDARY PROCESSES can be easily detected in fresh material, two of them being longer than the other two. The two longest secondary processes are situated one immediately to the right of the second primary process and the other to the right of the third. They correspond in position with the two secondary rows of chaetae on the embryonic shell (p. 248, fig. 12). The condition is similar in *V oxytropis*, but in *Lecythoconcha lecythis* only the three primary processes can be detected as such, even in fresh material.

Even the seven processes of *V dissimilis* and *V. oxytropis* are not all that actually exist, for between each pair associated with lines of chaetae two or three other minute projections occur, but can only be detected as projections if the mantle be examined in a fully expanded condition. These minute or TERTIARY PROCESSES correspond in position with the minute serrated ridges on the periostracum of the embryonic shell (p. 245, fig. 10). Both they and the secondary processes are probably present and functional, though often difficult to detect, in all Viviparidae.

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[1] It may be fixed in this condition by being subjected to gentle pressure between two glass slides as soon as it is removed, and treated with corrosive acetic solution while under pressure.

[2] Leydig, *Zeits. f. wiss. Zool.* II, pl. xi, fig. 16 (1850).

The external structure of the processes (be they primary, secondary or tertiary) is identical. They are not mere projections of the margin but organs with a definite form, position and function. When fully expanded in the living animal they are flattened dorso-ventrally and sharply pointed, but it is difficult to preserve them quite in this condition as they usually become blunter and thicker in preservations, as they do in life when the mantle contracts (fig 12). Along the external surface of each, from a point close to the tip, runs a narrow groove, and the whole of both surfaces, including the floor of this groove, is densely covered with long and powerful cilia. These extend also all over the edge of the mantle. Very often (fig. 12) the presence of a tertiary, or even a secondary, process is only indicated by the existence of this groove, which I shall call a MARGINAL GROOVE.

The marginal grooves run up the external surface of each process to a broader and rather deeper transverse groove that traverses the whole of the margin just above the bases of the processes and

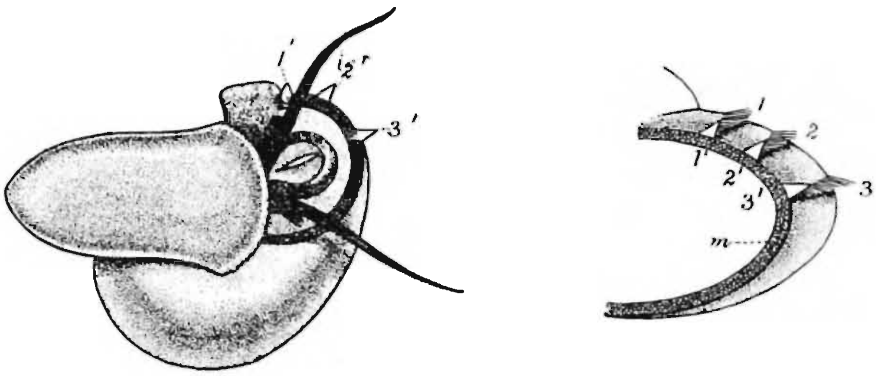

FIG. 13.—Living *Lecythoconcha lecythis* a fortnight old (magnified).
m., edge of mantle; 1, 2, 3, primary rows of chaetae on shell; 1,' 2,' 3' primary marginal grooves.

turns upwards for a short distance at the right extremity of the free edge. This groove I shall call the SUPRAMARGINAL GROOVE.

Immediately above the supramarginal groove on the external surface of the mantle is a broad and prominent ridge, which has been called the "white band" on account of its lack of epidermal pigment, but may be also known as the SUPRAMARGINAL RIDGE. Its surface is smooth and ciliated at birth in all the species examined at this period, and in *Lecythoconcha* its limits are not clearly indicated.

In the foregoing paragraphs I have described the external structure of the marginal region as it exists at the birth of the young mollusc, it remains to be seen how far it alters in the course of post-embryonic development. There is greater specific and generic variation in this respect than there is in the primitive structure, for while in some species and genera the marginal processes are greatly reduced in the adult, in others they retain their primitive condition, while in yet others they increase in proportionate development. I was under the impression that they disappeared completely in the adult of *V dissimilis* and *L. lecythis*, so long as I examined only preserved material; but at any rate the three primary processes can be quite easily detected in the largest living individuals of the former species, while in full grown specimens of the *Lecythoconcha*, at least traces of the peripheral process sometimes persist and probably remain functional throughout life. In *L. lecythis* (fig. 13) the primary processes are very conspicuous for at least a fortnight after birth on account of their bright yellow colour as well as their prominence. Major Sewell (p. 220) has shown that even when the processes have apparently disappeared in *V bengalensis* their position is apparently indicated by streaks of yellow pigment. In *V oxytropis* both the primary and the secondary processes increase in actual size with the growth of the animal. In the living adult they are not so easily seen as the primary processes in the young of *Lecythoconcha*, because they are usually retroverted inside the shell when the animal is expanded, but even in material preserved by immersion in strong spirit and killed in a highly contracted condition, they can be detected without difficulty as soon as the shell is removed.

The fact seems to be, therefore, that these marginal processes are characteristic of the Viviparidae as a family. They differ in position and structure, and probably in function, from the processes present on the mantle of certain genera of Melaniidae,[1] and I have failed to trace them on that of any Hydrobiid. Their presence is, however, frequently concealed by contraction and shrinkage in preserved specimens, and the extent to which they actually degenerate or persist in the adult differs in different species.

Other questions that remain to be answered are those concerned with differences in the system of marginal and supramarginal grooves and in the supramarginal ridge at different periods in the life-history of the mollusc. What I have said of the marginal processes applies with equal force to the marginal grooves, except that in the adult of *Lecythoconcha* the peripheral marginal groove is sometimes still more distinct than the peripheral process, but in considering the subsequent history of the supramarginal groove another factor must be considered, viz. that of periods of growth and of rest. These affect the groove indirectly by affecting the ridge that lies immediately above it and can be discussed most conveniently when considering the internal structure of this ridge (p. 252). One point that may be noted here is that the cilia disappear from the surface of the ridge at an early period in post-embryonic life and that when the glands in it are in a state of activity its surface is minutely ridged at right angles to its own axis. Further, in growing specimens of *Taia intha*, preserved in a half-expanded state, the ridge bears cushion-shaped swellings opposite to, but much broader than, the primary processes.

[1] See Benson, *Gleanings in Science* I, p. 21 (1830), and Annandale, *Rec. Ind. Mus.* XIX, p. 109 (1920).

It has not been necessary to say much about the edge of the mantle between the processes, the external structure of which offers no particular feature of interest at any time of life in most species. The difference between its conformation in *Vivipara* and *Taia* on the one hand and *Lecythoconcha* and *Margarya* on the other, already noted in the young (p. 249), is accentuated with the growth of the individual. It is, however, somewhat exaggerated in highly contracted or shrunken specimens. Another important generic difference, not following the same lines of division, may now be noted. It has a much more direct bearing on the special object of this section of our paper, as it is evidently correlated with the glyptic ornamentation of the shell. In *Vivipara* and *Lecytho-concha* the edge when fully expanded is straight, or rather curved in a wide arc outwards. It is, indeed, capable of considerable

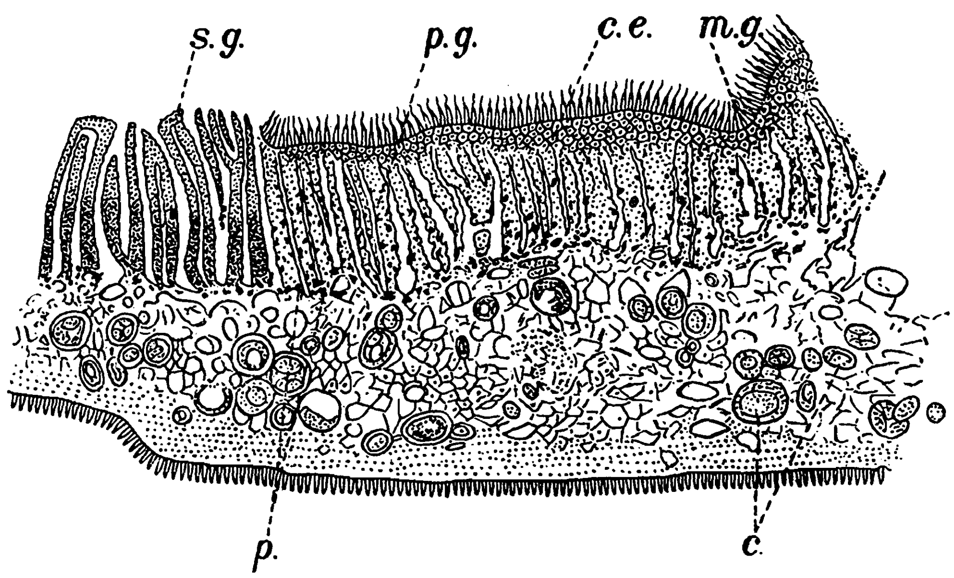

FIG. 14.—Horizontal transverse section through part of the edge of the mantle at the base of a primary marginal process of an adult *Vivipara oxytropis* (Benson), highly magnified and slightly diagrammatic.

c, calcareous concretions; *c.e.*, ciliated epithelium; *m.g.*, marginal groove of primary marginal process; *p.*, pigment granules; *p.g.*, periostracal glands; *s.g.*, calciferous glands.

change of shape and may become distinctly sinuate; but the irregularities of outline are mere irregularities without definite position or apparent function. This is also so in *L. lecythis*. It is unfortunate that I have not had an opportunity of examining either *Taia* or *Margarya* in a living condition in this connection, and in contracted specimens of these genera preserved in alcohol I can find no peculiarity of the edge of the mantle. In young examples of *Taia intha*, however, which were paralysed with menthol and fixed in 5% formalin without being fully contracted, a broad lobular projection can be detected at the base of the terminal scale-like projection on the peripheral ridge of the shell, proceeding for a short distance into the anterior cavity of the projection.

EPITHELIUM.—The epithelium of the extreme edge of the mantle is, as already stated, provided with long and powerful cilia. The cells are relatively deep and narrow and have large, deeply-staining nuclei. Unicellular glands do not occur among them. Epithelium of this type extends over both surfaces of the marginal processes and over the floors of the marginal and supramarginal grooves. Above the latter it gives place, but not abruptly, to non-ciliated epithelium containing unicellular glands. The change is gradual, the cells becoming shorter and stouter and the cilia more feeble and finally non-existent. On the surface of the supramarginal ridge, however, epithelium is usually absent after birth, the underlying glands being exposed on the surface.

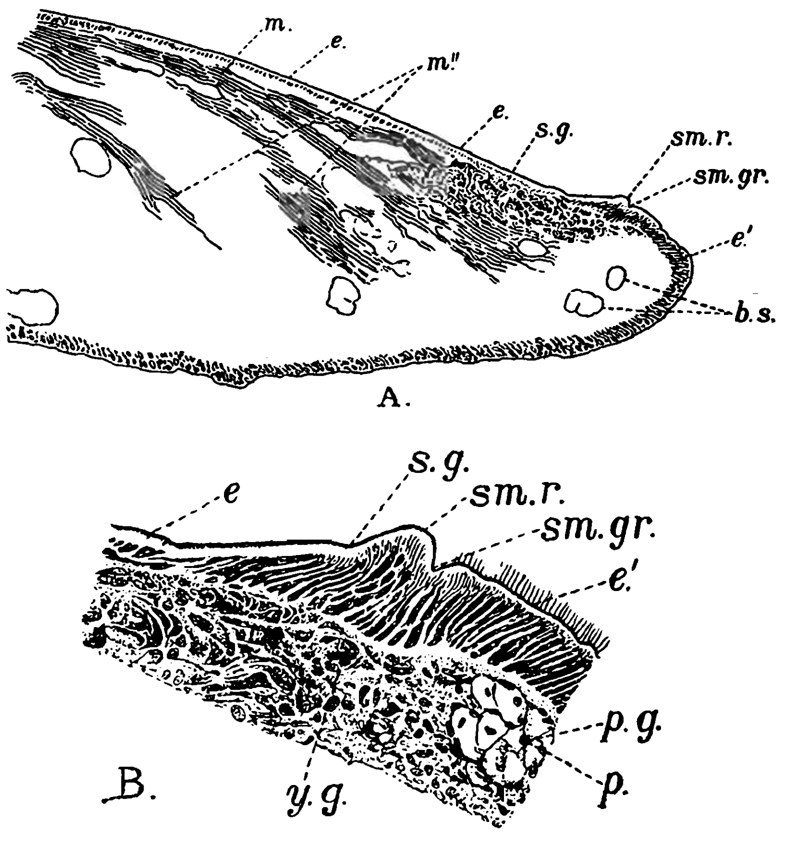

FIG. 15.—Vertical section through the edge of the mantle in the adult *Taia elitoralis*, Annandale, in a period of arrested growth.
A. The whole structure (×80).
B. Region of the supramarginal groove more highly magnified.

b.s., blood-sinus; *e.*, non-ciliated epithelium; *e'.*, ciliated epithelium; *m.*, external retractor muscle; *m''.*, muscular network; *p.*, pigment granule; *p.g.*, part of periostracal gland; *s.g.*, degenerate remains of shell-gland; *sm. gr.*, supramarginal groove; *sm. r.*, supramarginal ridge; *y.g.*, yellow granules.

CONNECTIVE TISSUE.—Two kinds of connective tissue can be distinguished in the marginal region of the mantle of the Viviparidae. The bulk of the roof of the branchial chamber consists of a peculiar kind of cells closely resembling that of which the adipose fins of fishes are mainly composed and identical with those of the foot of the molluscs. These cells are of very large size and of polygonal outline (pl. iii, fig. 3). Their walls are thick, their nuclei very small and they are gorged with a gelatinous substance evidently not protoplasmic. Immediately under the epithelium of both surfaces of the mantle a thin layer of undifferentiated connective tissue can also be distinguished. It is thicker at some places than at others but has no particular feature of interest.

MUSCLES.—The muscular system of the mantle is complex in all genera of the family, but more so in some than in others. In *Vivipara* it is comparatively simple. In this genus a relatively thin sheet of longitudinal fibres extends down the external surface as far as or nearly as far as the upper limits of the supramarginal ridge. This may be called the EXTERNAL RETRACTOR OF THE MANTLE. In a corresponding position on the internal surface a few fibres of a similar nature can be distinguished, but they are poorly developed. In the neighbourhood of the supramarginal ridge a strand of oblique or nearly transverse fibres runs along parallel to

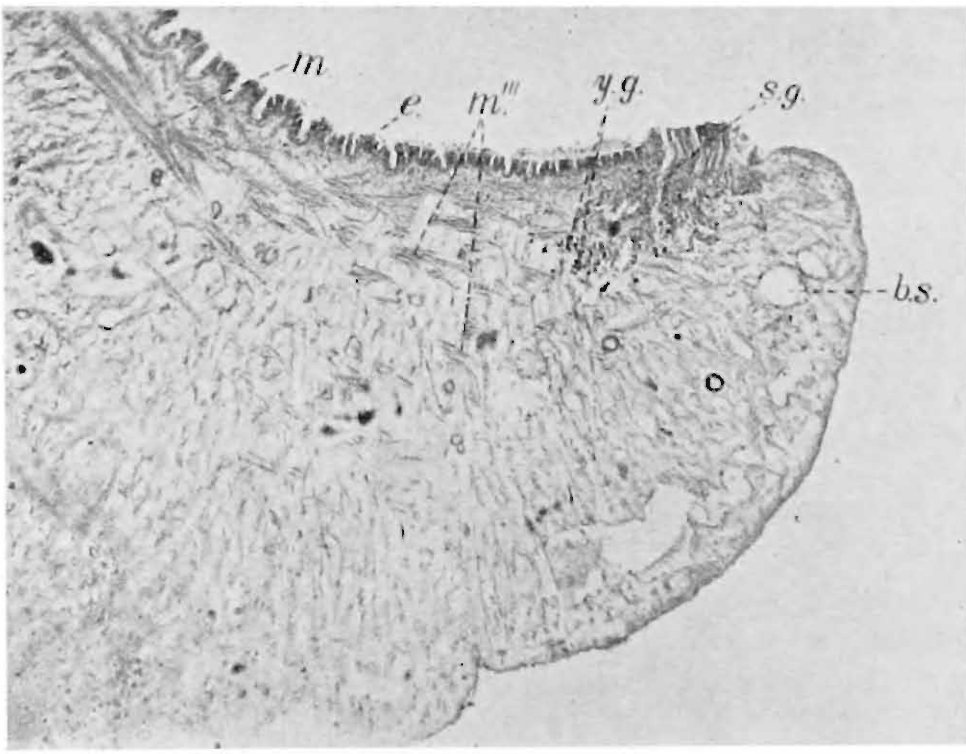

FIG. 16.—Microphotograph of vertical section through the edge of the mantle in *Margarya melanoides* var. *carinata*, Neumayr. The ciliated epithelium has been removed from the surface below the shell-glands.

b.s., blood-sinus; *e.*, epithelium; *m.*, external retractor muscle; *m'''.*, muscular network; *s.g.*, calciferous gland; *y.g.*, yellow granules.

the margin rather deeper in the tissues and forms the SPHINCTER OF THE MANTLE. Its structure is simple in this genus and it is not powerfully developed. Finally, the external retractor sends numerous fine branches obliquely into the thickness of the mantle, in which they ramify and anastomose to form a loose MUSCULAR NETWORK.

In other genera the same elements of musculature are found, but variously developed. In *Taia* and *Margarya*, in which the sphincter is still more feebly developed, the muscular network is closer and has much smaller meshes and the individual strands are finer. In *Margarya*, in which the mantle is greatly thickened, it is better developed than in *Taia*.

It is, however, in *Lecythoconcha*, in which also the mantle is thick, that the muscles are the most powerful among the forms examined. The external retractor and its branches are both very coarse, but the latter are not numerous and the muscular network is not well developed. The sphincter, however, is both thick and complex, consisting of several strands which run obliquely in the midst of the shell-glands. Their position in reference to the edge of the mantle differs in different states of expansion and retraction (figs. 3, 4, pl. iii).

NERVES.—I have not attempted to work out the nervous system of the marginal region in detail and have not observed any external sensory organs. The whole of the roof of the branchial chamber is supplied by nerves arising from the parietal ganglia (Sewell, p. 240). In the marginal region a fairly stout transverse nerve can be readily distinguished, pursuing an irregular course above the supramarginal ridge, some parts of it being much nearer the margin than others. From it finer nerves run down at irregular intervals among the shell-glands. Their position is not definitely correlated with that of the marginal processes (fig. 12 B, p. 248).

VASCULAR SYSTEM.—The marginal region of the mantle is highly vascular in all species of Viviparidae examined. Definite blood-vessels can be seen entering it, but for the most part the blood is contained in irregular sinuses without definite walls. These reach their maximum development in the primary marginal processes of *Vivipara oxytropis* (pl. iii, fig. 5), in which the connective tissue has a strictly cavernous structure. A vascular system of this type cannot be investigated in detail without careful injection. This method I have not attempted to adopt as it is quite sufficient for my purpose to know that the processes, and indeed the whole of the edge of the mantle, are erectile rather than muscular, though their erectility is doubtless correlated with the action of the muscles of the roof of the branchial chamber.

SHELL-GLANDS.—A most important part of this investigation refers to the structure, position and function of the glands that secrete the substance of the external layers [1] of the shell and their relation to the external structure of the marginal region of the mantle and the ornamentation of the shell. The main facts about these glands have long been known and certain important points were made clear by Leydig,[2] Mer and Longe [3] and Moynier de Villepoix,[4] but I have failed to find in zoological literature any discussion of their comparative anatomy and functions in any one family of Gasteropods. As my own observations are in general agreement with those of the authors cited I will give an account of what I have myself seen without further historical discussion.

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1 I do not propose to deal with those that secrete the internal nacreous layer.
2 *Zeits. f. Wiss. Zool.* II, p. 123 (1850).
3 *Comp. Rendus* XC, p. 882 (1880).
4 *Comp. Rendus* CXIII, p. 317 (1891) and CXX, p. 512 (1895).

The glands (fig. 14, p. 252) concerned with shell-sculpture in the Viviparidae belong to two distinct series, differing in structure, position and function. We may call them respectively CALCIFEROUS and PERIOSTRACAL GLANDS in reference to the nature of their secretions.

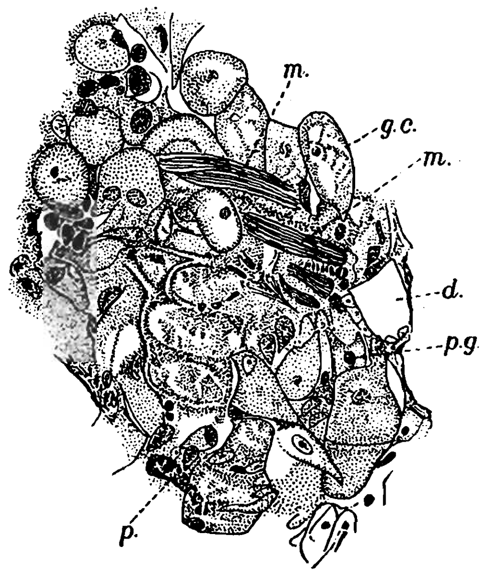

FIG. 17.—Vertical section through part of the periostracal gland in an adult *Vivipara contecta* (Millet) towards the end of a period of growth (× *ca.* 333).

d., duct of gland; *g.c.*, gland cell; *m.*, fibres of sphincter of the mantle; *p.*, suffused black pigment; *p.g.*, black pigment granule.

The periostracal glands are the smaller, less conspicuous and nearer to the free edge of the two series. They lie opposite the bases of the marginal processes and extend both upwards beneath the calciferous glands and downwards into the processes, at the base of which they open into the supramarginal groove by a series of very minute pores, one for each gland (pl. iii, fig. 1). In the young molluscs at birth each gland is a simple tubule formed of a single layer of gland-cells and more or less twisted in its course, which is tangential to the free edge and lies amidst the thick-walled cells of the interior of the marginal region. Later the glands become contorted and the cells proliferate to form an irregular mass (pl. iii, fig. 3). A definite duct is then developed, lined with very minute flat epithelial cells. It makes its way to the external pore from a small reservoir lying in the substance of the margin and also lined with minute flattened epithelial cells. Into this the secretion of the gland is evidently poured. The gland-cells (fig. 17) are relatively small and ovoid in outline. Their contents do not stain deeply except at birth and they become very inconspicuous in periods of arrested growth. In those species of Viviparidae that have dark-banded shells, such as *V bengalensis*, *V oxytropis*, *V contecta*, and the young of *Taia intha* and *T elitoralis*, very minute granules of black pigment are found in the cells and lining the ducts of the glands, but they are absent or very scarce in species with unicolorous shells, such as those of *V dissimilis* and *L. lecythis*, except at the end of growth-periods, when dark pigment may become widely suffused among the interior cells of the mantle and is then by no means confined to the immediate vicinity of the periostracal glands.

The calciferous glands are larger, more numerous and more conspicuous, and occupy a higher and more superficial position on the mantle than the periostracal glands. They undergo, moreover, greater changes in the course of post-embryonic life and show a greater range of structural difference in different genera. I shall first describe them as they occur in the young of *Lecythoconcha lecythis* at birth, for they are greatly hypertrophied at the time in that species, occupying practically the whole of the external layer of the roof of the branchial chamber, lying immediately or almost

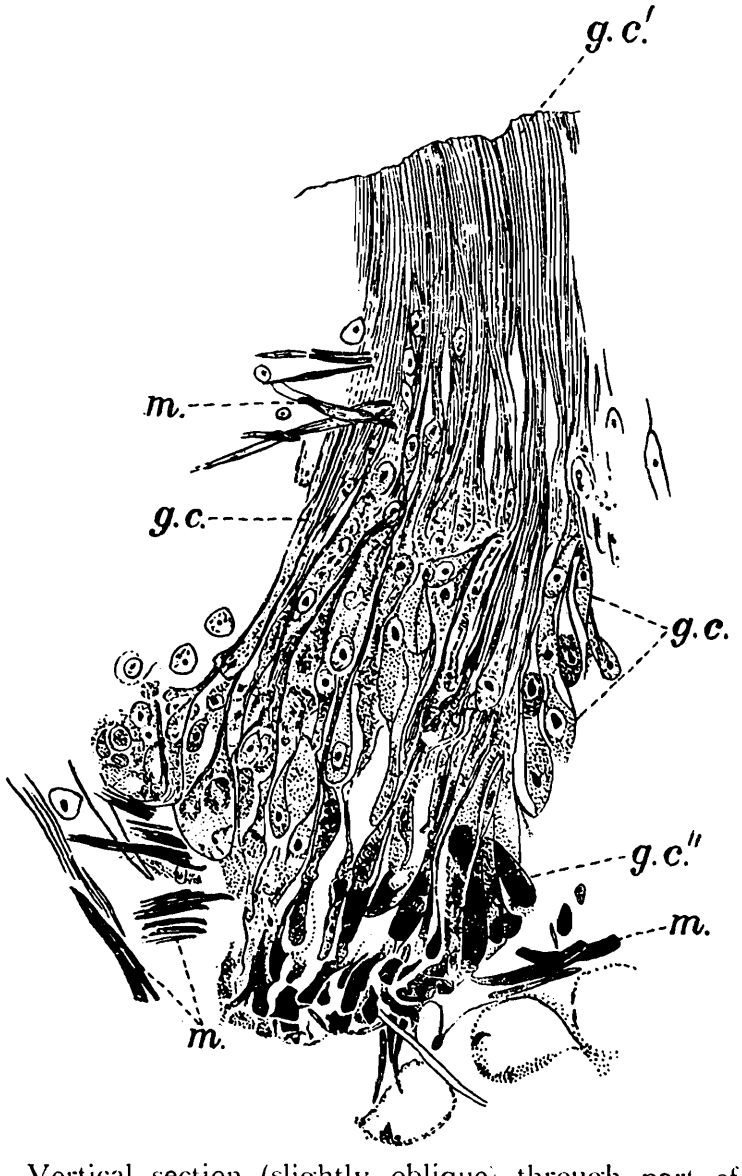

FIG. 18—Vertical section (slightly oblique) through part of a calciferous gland of the same individual as figured in fig. 17 (same magnification).

g.c'., necks of gland-cells opening on the external surface of the mantle; *g.c''.*, degenerating gland-cells. Lettering otherwise the same as in fig. 17.

immediately beneath the external epithelium and extending downwards into the substance of the mantle for nearly half its thickness.

In a vertical section of the mantle passing through the peripheral marginal process (pl. iii, figs. 1, 2) the tissues can thus be separated at sight under a low power of the microscope into an external glandular area and an internal vascular layer. It is with the former we are at present concerned. At the extreme margin, in the substance of the process, the periostracal glands can be distinguished, lying in the external part of the vascular layer. External to them, and not extending quite so far downwards or entering the process, the calciferous glands occupy the whole of the glandular area. These latter glands form in sections of the kind a series of minute tubules with their main axis at right angles to the surface, but a careful examination of a series of sections indicates that the tubules are not really separate but form a continuous or almost continuous tube with numerous closely adpressed loops. The uppermost loops are already degenerating and do not stain well and those quite near the margin are not closely adpressed and have their cells smaller and probably not yet functional. In the upper part of the marginal region, however, the glands are well

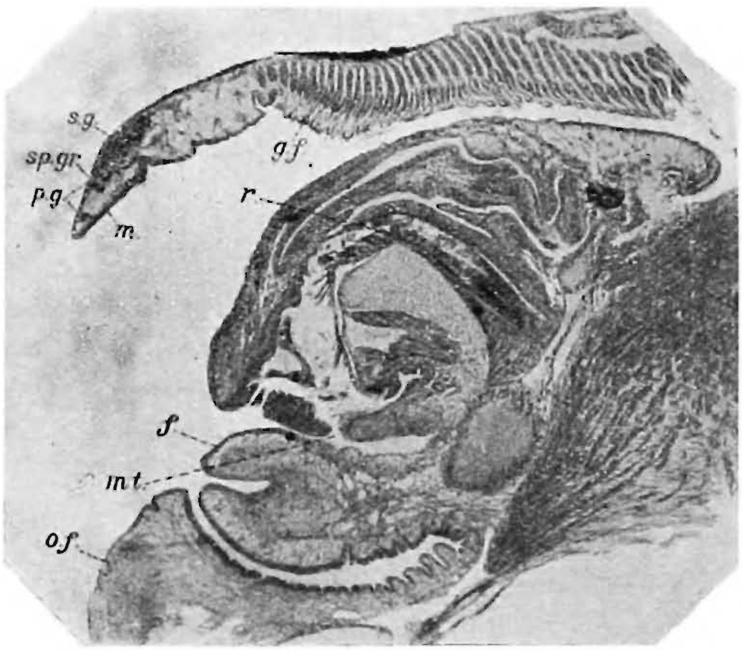

FIG. 19.—Microphotograph of a vertical section through the anterior part of the body of a young *Vivipara contecta* just before birth, to show general position of shell-glands.

g.f., gill-filaments; *f.*, foot; *m.*, mantle; *mt.*, mouth; *p.g.*, periostracal land; *gr.*, radula; *s.g.*, calciferous gland; *sp. gr.*, supramarginal groove; *o.f.*, operculiferous lobe of foot.

developed and evidently functional. Here they consist of large deeply staining cells arranged in parallel rows from just below the external epithelium inwards to the base of the glandular layer.

In the young of other species (fig. 19) the structure of these glands is not essentially different, though they do not occupy nearly so large an area and are relatively much smaller. Their tubular conformation and the adpressed loops of the whole gland are just as well marked and the cells are similar in form and appearance.

At subsequent growth stages, however, a considerable change takes place. The cells are greatly reduced in numbers but increased in size and become ampulliform with extremely elongate "necks" and swollen proximal parts. The loops of the primitive gland, moreover are converted into groups of cells of the kind, each arranged round a small and ill-defined space. Their swollen proximal extremities lie buried in the mantle, while their necks extend outwards, closely pressed together, and reach the external surface.

In a vertical section they have in the mass a fibrous appearance which renders them liable to be mistaken for muscle fibres unless differential stains are used, and as the main axis of the cells is not quite at right angles to that of the surface, sections have to be slightly oblique to show their structure in detail.

The extent to which degeneration of the calciferous glands takes place in the rest-periods that succeed those of active growth differ in different species and probably in different circumstances, but they never completely disappear and even when completely degenerate form a conspicuous feature of sections of the marginal region of the mantle even under low powers of the microscope. Generally speaking, the degeneration appears to be greater in forms from a colder climate than it is in tropical species, probably because the alternate periods of growth and rest are more absolute in the former. Major Sewell's observations on the rate of growth in *Vivipara bengalensis* in Calcutta (p. 280) seem to show that growth may be, if not absolutely continuous, at any rate very readily revived at any time of year, whereas in *Taia intha*, which lives at an altitude of 3000 feet in a much colder climate, few shells were observed in early spring that appeared to be in a state of active growth. I find that the European *V contecta* agrees with this species and its congener *V elitoralis* from the same lake and also with *Margarya melanoides* (fig. 16, p. 254), which lives at greater altitudes in Western China, in having the glands very degenerate in periods of rest, whereas in *V bengalensis*, *V dissimilis*, *V oxytropis* and *Lecythoconcha* it alters little in structure.

In those species in which the glands become most degenerate in periods of rest, as for example in *Taia elitoralis* (fig. 15, p. 253), the periostracal glands practically disappear, while the calciferous glands are reduced to an amorphous mass in which the cell-limits are distinguished with difficulty. This is most marked in their "necks," which fuse together to form a structureless or almost structureless layer on the external surface. When this occurs the flat epithelial cells of the upper part of this surface encroach to some extent on the area previously devoid of epithelium, while the ciliated columnar cells of the extreme margin apparently become more vigorous but do not extend upwards beyond the position of the supramarginal groove, which practically disappears as such. In preserved specimens in this condition I am unable to detect any trace of the marginal processes and grooves, but possibly they may be still present in the living animal.

The degeneration of the gland-cells is correlated with the secretion of certain yellowish granules of variable size and irregular shape, which are formed in them and finally become very conspicuous, even when the mantle is examined whole as a transparent object under a low power of the microscope (fig. 12, p. 248).

REFRACTILE BODIES.—Throughout the vascular parts of the anatomy of the Viviparidae, and especially in the mantle, numerous small refractile bodies can be distinguished under a low power of the microscope. They are spherical or occasionally ellipsoidal in form and become more numerous in the half-grown and adult animal than they are in the young. Their size varies in different species and they are largest (among the forms examined) in *Lecythoconcha lecythis*. Unstained they are colourless, but they absorb stains such as haematoxylin and borax carmine readily and these stains, if the bodies are cut in sections, penetrate throughout their substance. They dissolve, however, immediately in acid and therefore disappear in a technique in which the use of free acid is involved, leaving open spaces that may easily be confused with small blood-sinuses. Their position is extracellular, but they occur in the peculiar gelatinous tissue described above. When the mollusc is in a state of active growth they congregate in large numbers between the shell-glands and the internal surface of the mantle (fig. 14). Externally they are perfectly smooth. Their internal structure is lamellar and concentric, but the lamellae of which they are composed are not numerous.

The structure of the shell-glands of both series is essentially similar in the Melaniid genera *Melanoides* and *Acrostoma* to that here described in the Viviparidae. As de Villepoix[1] has shown that it is also similar in *Helix*, we may assume that it is of a type widely distributed among the Gasteropod molluscs. It will therefore be worth while, before discussing the function of the glands and of the marginal region generally in relation to the ornamentation of the shell, to summarize the description already given so far as its main points are concerned. I have been able to find no detailed account of the external structure of this region, which probably differs greatly in different forms, in any other family. Even if certain features are peculiar to the Viviparidae, parallel, if not precisely analogous, features probably exist in other families.

SUMMARY ACCOUNT OF THE ORNAMENTATION OF THE SHELL.

The ornamentation of the shell in the Viviparidae is partly periostracal, partly impressed on the outer calcareous layers. In the embryonic shell, including the protoconch, both horny and testaceous structures are already concerned, but the periostracal ornamentation, when magnified proportionately, is the more conspicuous.

The periostracal ornamentation is, at any rate in some species, both glyptic and coloured. Its sculpture is minute and consists of spiral rows of horny chaetae, fine spiral ridges and still finer oblique longitudinal lines. These are best developed in the fully-formed embryo and as a rule disappear or become obsolete (with the exception of the longitudinal lines, which tend to become more

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[1] de Villepoix, *Comptes Rendus* CXX, p. 512 (1895).

prominent) in the full-grown shell. Three primary rows of periostracal chaetae can be distinguished, the best developed of which runs round the periphery of the whorls, while the other two are situated above it. The peripheral row, though the most important of the three, is the latest to be formed and only the first or uppermost row extends to the apex of the protoconch. In some species (e.g. *Vivipara dissimilis*), two additional rows of chaetae are present on the embryonic shell, one between the peripheral and middle row and one above the first row. These chaetae are, however, smaller than those of the three primary rows. They are homologous with two of the fine spiral ridges on the shells of other species.

In those species in which the shells are ornamented with bands of dark pigment the colour-pattern is periostracal in origin, though the calcareous matter may be slightly stained. The bands correspond in position with the rows of chaetae and spiral ridges.

The test-sculpture (*i.e.* that of the outer calcareous layers of the shell) also corresponds in position with that of the periostracum. In shells of the family in which it is highly developed, it consists mainly of prominent spiral ridges. These ridges may be smooth and uninterrupted (as in *Lecythoconcha lecythis*) or broken up more or less distinctly into series of tubercles (as in some individuals of *Taia naticoides*), scale-like projections (as in the most highly developed shells of *Taia* and *Margarya*) or even spines, as in the fossil *Rivularioides.*[1] They may be hollow as in *V oxytropis* or solid as in the Chinese *V lapillorum.* In practically all shells of all types the most prominent and most highly developed ridge corresponds with the peripheral row of chaetae, and in a large proportion those that correspond with the two other primary rows of chaetae are better developed than any others. Moreover, each ridge corresponds either with one of the primary rows of chaetae or with a secondary ridge of the periostracum.

SUMMARY ACCOUNT OF THE STRUCTURE OF THE EDGE OF THE MANTLE.

We may summarize the structure of the distal part of the mantle in the Viviparidae as follows:—

The free edge of the mantle is membranous, but much thicker in some genera (e.g. *Lecythoconcha*) than in others. The margin bears at least three digitiform processes, which are better developed in some species (e.g. *Vivipara oxytropis*) than in others, and are usually obscured by contraction and shrinkage in preserved material. In addition to those three primary processes other, smaller processes are present, probably in all cases, but are still more difficult to detect except in the living animal and may perhaps become vestigial in the adult of certain species. These primary and secondary processes correspond in position with the

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[1] Annandale, *Rec. Geol. Surv. Ind.* L, pl. xxxiii, figs. 7–12 (1919).

periostracal sculpture. Immediately above the processes a groove runs transversely across the external surface and from it short longitudinal grooves are given off at right angles and run to the tip of the processes. Above the transverse supramarginal groove and running parallel to it, a convex ridge, varying in breadth and prominence at different stages of growth, can usually be traced. For it I have proposed the name of supramarginal ridge. The margin, including the grooves, is covered with columnar ciliated epithelium as far up on the external surface as the lower edge of the supramarginal ridge. Except at a very early stage in free life (*Lecythoconcha*) the epithelium is degenerate on the ridge, and above it consists of non-ciliate cells.

The substance of this part of the mantle is composed mainly of a peculiar kind of connective tissue consisting of polygonal cells with small nuclei, rather thick walls and gelatinous contents, in the main non-protoplasmic. It is cavernous in structure, including numerous ill-defined blood-spaces without cellular walls as well as true blood-vessels. Longitudinal muscles, sometimes powerfully developed, run down the mantle under the external epithelium, and certain oblique strands can also be followed out near the margin, forming a sphincter round the aperture of the branchial chamber. A fine network of muscle fibres also extends inwards from the outer layer. The musculature is much more highly developed in some genera than in others.

The nervous system of the margin has not been worked out in detail, but an irregular transverse nerve, some parts of which are nearer the edge than others, runs above the supramarginal ridge, and sends down fine longitudinal strands at intervals to the calciferous glands.

The glands whereby the greater part of the substance of the shell is secreted lie just above the edge of the mantle and are of two orders, the periostracal glands, which secrete the periostracum or epidermis of the shell, and the calciferous glands, which secrete the calcareous matter. The former are true multicellular glands of a vermiform shape, consisting of contorted tubules and opening to the surface by ducts with cellular walls. They lie some distance below the external surface in a transverse series along the extreme margin, for the most part beneath (*i.e.* distad of) the calciferous glands and with the main axis of each gland at right angles to the margin. Their ducts open into the supramarginal groove. The calciferous glands are much more bulky and differ considerably in structure. They occupy the supramarginal ridge and as a rule extend slightly beyond it both above and below, lying only a short distance beneath, or actually on, the surface and having no cellular ducts. Like the periostracal glands they form a transverse series, though the main axis of each gland is at right angles to the margin. Each gland is at first an elongate cylindrical tubule of gland-cells forming a large number of closely adpressed loops in the external margin of the connecting tissue. The cells are large and do not appear to have any very intimate organic connection *inter se.* The lumen of the tubule has no special lining. At this stage ducts, perhaps of a temporary nature, can be detected in sections, but they form mere gaps in the epithelium, leading out from ill-defined spaces beneath it (fig. 2, pl. iii). Later the gland-cells become greatly enlarged and elongate and open direct on the external surface; while the tubular character of the gland disappears.

The calcareous matter secreted by the calciferous glands is apparently derived from concretions scattered through the connective tissue of the mantle and foot but congregated in large numbers immediately beneath the glands at times of active growth.

The secretion of the nacreous layers, probably affected by unicellular glands scattered over the whole of the upper part of the mantle, is not discussed here.

Function of the different parts of the Marginal Region in reference to the Shell.

We are now in a position to discuss the function of the edge of the mantle in relation to the ornamentation of the shell. The first structures in the soft parts to be considered in this connection are the marginal processes. They are not organs of secretion but, at any rate when hypertrophied as in *V oxytropis*, perhaps accessory breathing organs. They are closely correlated in position with both the periostracal sculpture, the colour-pattern and the sculpture of the test. The connection between them and the periostracal sculpture can be traced without difficulty. They mould this sculpture, apparently as erectile rather than muscular organs. The horny matter that will form the thin outer cuticle of the shell is poured in a liquid condition into the supramarginal groove, in which it is kept in motion by the cilia of the epidermal cells. It runs down the longitudinal grooves on the external surface of the processes and by them is deposited on the edge of the lip of the shell, over which they are retroverted as it consolidates. The three primary rows of chaetae are thus formed by the three primary processes, and in such forms as *Vivipara dissimilis* in which there are more than three rows, those of the secondary rows by the best developed of the secondary processes. The upright form of the chaetae is due to the greater length of these processes. This enables them to project well beyond the lip and be curled up over it. The hooked tips of the chaetae are due to the fact that the tips of the processes are curved at the moment of formation of the chaetae. The fine subsidiary ridges of the periostracum, which when first formed project horizontally from the edge of the lip as fine hairs, are similarly produced by the subsidiary processes, their orientation being due to the fact that the moulding processes are short and cannot be curved upwards over the lip.

In those shells which like *Vivipara bengalensis* have a pattern of dark spiral bands in the periostracum, the dark pigment is also poured out along the grooves on the external surface of the marginal processes. This is proved not only by the position of the bands and their arrangement on the shell but also by the close correlation of dark pigment with the periostracal glands in such species and by its absence from the margin in those species the shells of which are not marked with dark spiral bands. We may presume that, after the secretion of the horny fluid to form the chaetae and ridges, the pigment is poured out in a similar manner along the processes and deposited by them on the surface of the lip. The chaetae themselves are not coloured by it, and I do not think that the ridges are either, though this point is difficult to observe with certainty, because the dark bands do not appear until the shell has become fairly opaque and the ridges project very little from the surface.

To return to the periostracal sculpture, the fine vertical lines are evidently due to a pouring out of horny matter direct from the supramarginal groove, with which they correspond exactly in orientation, each representing, so to speak, a separate act of secretion.

The sculpture of the test also corresponds closely in position and arrangement with that of the periostracum and, indeed, so far as the minute sculpture is concerned, is practically a cast of it from which the upright chaetae are necessarily omitted, just as single upright hairs cannot be represented in a plaster cast. In most forms of *Vivipara bengalensis*, and indeed in most Viviparidae, there is nothing more to be said on this point, but in those species which have highly sculptured shells, and even in some phases and individuals of *V bengalensis*, a further exposition is necessary.

The highly sculptured shells among the Viviparidae fall into three categories, viz. (1) very thin shells with uninterrupted, *hollow* spiral ridges; (2) thicker shells with uninterrupted, *solid* or almost solid spiral ridges, and (3) shells, thick or thin, with ridges that are more or less distinctly broken up into nodules, scales or spines.

Of the first type, which is the scarcest of the three, V *oxytropis* is an excellent example. The shell, in spite of its large size, is exceptionally thin and fragile and the ridges upon it though prominent are very little thicker than the intervening spaces on account of the well-marked concavity of their internal surface, which forms a regular groove. No peculiarity of the calciferous glands has been observed in connection with these ridges on the shell, and none is necessary to explain them, for they lodge the greatly hypertrophied marginal processes, the mere presence of which on the internal surface of the shell while the calcareous matter was soft is sufficient to account for their presence.

On shells of the second type with solid uninterrupted ridges no satisfactory direct observations have been possible, owing to imperfect preservation of the material available, but the marginal processes are not hypertrophied as in *V oxytropis* and it may perhaps be assumed that the ridges are due to a certain slight hypertrophy of the calciferous gland in a position on the mantle corresponding with them on the shell. This is indicated by the facts that even in smooth shells of *V bengalensis* the dark spiral bands are slightly thickened and that at the end of a growth-period the calciferous glands are often a little larger immediately above the primary marginal processes than at other points on the periphery. It is clear, however, that some of the matter which occupies their base is nacreous, and we know that on the internal surface of the shell nacre can be deposited by almost any part of the mantle after the external ornamentation is complete.

The third, most highly sculptured type of shell is the most interesting of the three, not only because of its peculiar facies but also because it has appeared and become dominant among the Viviparidae[1] on different occasions and in different places and different geological epochs. The test sculpture, even in this type of shell, corresponds closely in fundamental pattern with the primitive periostracal sculpture of the embryo of *V bengalensis*, that is to say that it consists essentially of spiral ridges bearing prominences and that these ridges have fundamentally a definite number and position on the shell exactly similar to that of the three rows of chaetae and the secondary ridges of the embryonic periostracum, and that the most prominent ridge corresponds with the peripheral row of chaetae. It follows that the interrupted ridges of the test in this type of Viviparid shell are correlated at least in position with the marginal processes of the mantle, but the connections between the structures on the shell and those on the soft part are certainly not so close as in the periostracal sculpture and cannot be stated with the same precision. Here again, however, we know that the test sculpture is not correlated as in *V oxytropis* with any hypertrophy of the marginal processes of the mantle, which are small in both *Taia* and *Margarya*, and also that the processes show no essential difference of structure in individual shells of the former genus in which the sculpture is less and more highly developed.

If the mode of construction of the projections on the peripheral and other ridges of the more highly developed shells of the genera *Taia* and *Margarya* can be explained, that of the remainder of the ridges is a simple matter. They cannot have been formed, so to speak, in the air (or rather in the water) but must have been built up in continuity with the edge of the lip. In the fossil *Rivularioides* they may be nearly half as long as the diameter of the whole shell. Their form suggests that they must have been moulded by some comparatively broad projection of the mantle edge. In contracted specimens of *Taia* and *Margarya* no trace of any such structure can be detected, and the extreme margin differs little from that of *V dissimilis*, which has a very smooth shell. It is unfortunate that I made no observa-

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[1] Annandale, *Rec. Geol. Surv. Ind.* L, *p.* 209, pl. xxxi, figs. 8–11 (1919).

tions on the living *Taia* that would have thrown any light on this point, but I have been able to examine some well-preserved specimens of *T intha* in which the animal is partially expanded and the mantle not completely retracted. In those in which the growth-period was completed when they were killed I can find no peculiarity in the margin of the mantle, which is either quite smooth or undulates gently, but in several specimens in which the extreme thinness of the lip proves that growth was still in progress, the base of the youngest scale-like projection of the peripheral ridge is still hollow and contains a broad lobe of the mantle-edge, evidently temporary in nature.

The projections on the shell, however, are not only of considerable length when highly developed, but contain a relatively large amount of calcareous matter. In both *Taia* and *Margarya* the calciferous glands degenerate greatly in the periods of rest and in full-grown individuals become very uniform all along the edge of the mantle, but in a young growing specimen of the *Taia intha* I find that immediately opposite the peripheral ridge there is a cushion-like thickening of the supramarginal ridge due to the greater depth of the glands at this point. In the individual in which this observation was made a scale-like projection was in the process of formation. In others, in which this was not so, the glands at the same point were not hypertrophied to any appreciable degree.

It follows, therefore, that the projections are formed owing to periodical hypertrophy of the calciferous glands in the part of the mantle that lies immediately beneath the ridge on the shell, and moulded into shape by temporary lobes of the mantle edge. The difference between the smooth ridges on the shell of such species as *Vivipara lapillorum* and the interrupted ridges, often with relatively long projections, of such forms as *Taia intha* or the var. *carinata* of *Margarya melanoides* is probably, therefore, due to the local hypertrophy of the calciferous glands being in one type of shell permanent, and in the other temporary. Elongate projections on the ridges of the most highly sculptured shells of the family are secreted thus and are modelled into shape by the temporary lobes. It is noteworthy that whereas the muscles are not so coarse, and the transverse fibres distinctly less well-developed, in the marginal region of the mantles of *Taia* and *Margarya* than in the smooth-shelled *Lecythoconcha lecythis*, the two former genera have a regular network of muscles pervading almost the whole mantle in a manner not observable in *L. lecythis* or any other species of the family examined. This may doubtless assist in the projection of temporary lobes from the edge of the mantle.

The secretion of the periostracal glands probably mixes to some extent with that of the calciferous glands and forms the organic basis of the shell.

The dark margin of the mouth of the shell to be noticed in many species of *Vivipara* when the growth-period is complete is probably due to a general suffusion of black pigment correlated with its accumulation in the tissues at such periods.