ON THE STRUCTURE OF THE SNAIL'S HEART. By FRANCIS DARWIN, M.B. (Cantab.).

IN the important research "On the Behaviour of the Hearts of Mollusks[1]" by Dr Michael Foster, and Mr Dew Smith, the anatomy of the organs studied was necessarily rather briefly dealt with. Dr Foster suggested that I should undertake the investigation of the histology of the snail's heart; the present unfortunately very imperfect note gives the result[2].

The main anatomical fact stated by them is that the snail's heart is destitute of automatic nervous mechanism, and is not connected with the central nervous system in any way[3]. This statement I can, as far as my work goes, confirm; I have searched carefully, but in vain, for ganglion cells, both by staining with chloride of gold, and also with picrocarminate of ammonia, which brings out the nuclei of the ganglia of the central nervous system very brightly. Nor can I trace any nerve passing into the heart. The only reasons which render it at all probable that the heart may possibly have some kind of nervous mechanism, are the following[4]:

(i.) A nerve leaves the subœsophageal splanchnic ganglion and travels along the aorta towards the heart. I was unable to make out how this nerve terminated; the innumerable branching muscle-cells of curiously nerve-like aspect rendering the task difficult. It is possible that it may be merely distributed to the branches of aorta like a nerve described by Albany Hancock[5] in Ommastrephes (Loligo).

(ii.) A nervous supply to the heart is known to exist in some Mollusca: Keferstein[6] describes a nerve supplying the heart in *Tergipes edwardsii* (from Nordmann, 1845). Lacaze-Duthiers[7] describes a branch from the brancho-genital ganglion, supplying the heart in Pleurobranchus. Albany Hancock[8] describes and figures two ganglia at the apex of the heart in *Doris tuberculata*. The same

[1] *Proceedings of Royal Society*, No. 160.

[2] I have the pleasure of thanking Dr Klein for the kind manner in which he has helped me with his valuable advice and opinion.

[3] *Loc. cit.* p. 320.

[4] Mr Romanes has shown (*Proc. Roy. Soc.* No. 165), that in certain Medusæ the removal of the margin of the nectocalyx completely prevents the occurrence of spontaneous rhythm in the mutilated remnant; but that "the smallest atom of this (the margin) when left in situ is frequently sufficient to animate the entire nectocalyx." With this fact before us, we must be cautious how we build on the negative evidence which would declare the snail's heart to be devoid of nervous mechanism.

[5] *Annals and Mag. of Nat. Hist.* x. 1852, p. 8.

[6] *Thierreich*, B. III. Tab. 50.

[7] Quoted in *Thierreich*, B. III. p. 726.

[8] Albany Hancock, *Phil. Trans.* 1852.

author[1] describes a large ganglion on the pericardium in Ommastrephes (Loligo), which supplies the systemic heart and other parts of the vascular system.

My observations have been almost entirely confined to the heart of *Helix pomatia;* from what I have seen of that of the small garden snail I believe the structure to be the same in both. The superficially placed pericardial sac which contains the heart is situated between the kidney and the respiratory membrane. The pericardium is said by Keferstein[2] to be muscular, and is lined by a beautiful endothelial mosaic of cells. The heart consists of two cavities; a globular auricle which receives the pulmonary vein, and a conical ventricle, the apex of which is continuous with the main artery of the body or "aorta". The two cavities communicate by a small orifice guarded by a pair of very efficient semilunar valves, projecting into the cavity of the ventricle. The contractile tissue of the heart consists of unmistakeable striated muscle.

I was not aware until I had completed my research, that Gegenbaur[3] concluded that the tissue of the heart in the Pulmonogasteropoda is analogous with true striped muscle; he does not give any details on the subject, basing his opinion on general grounds. Leydig[4] however has described and figured the striated muscle composing the heart of *Paludina vivipara.* Keferstein[5] merely states that the snail's heart is composed of very granular muscle. Neither Weismann, Boll, Schwalbe, or Margo appear to have studied the heart of the Gasteropoda. The following instances of striated cardiac tissue in the Mollusca may be worth mentioning:—Müller[6] (quoted by Margo): branchial hearts of Cephalopoda (this tissue has been carefully described and figured by Boll[7]).—Margo[8]: heart of Anodon, faint striation.—Ray Lankester[9]: the extraordinary two-celled heart of Appendicularia.

To return to the snail's heart: the muscle is composed of elongated spindle-shaped cells closely superimposed and very intimately attached to each other. Without careful examination the cellular structure is not observable, and one merely sees

1 *Annals and Mag. of Nat. Hist.* x. 1852, p. 10.
2 *Thierreich,* Bd. III. p. 1206.
3 Siebold and Kölliker's *Zeitschrift,* Bd. III. p. 389.
4 Siebold and Kölliker's *Zeitschrift,* Bd. II.
5 *Thierreich,* Bd. III. p. 1206.
6 Siebold and Kölliker's *Zeitschrift,* 1853.
7 Max Schultze's *Archiv,* Bd. v. Supplement.
8 *Wien. Sitzungsb.* Bd. 39.
9 *Quart. Jl. of Micros. Sc.* 1874.

bundles of parallel-walled fibres of about ·0022 mm. in diameter. In Paludina, Leydig[1] points out the difference between the ordinary body muscles and those of the heart. In Helix also the fibres of one of the buccal-mass retractors (for instance) are much stronger, less granular, broader, and more easily isolated, than those of the heart.

In some specimens the striation is perfectly clear, distinct light and dark bands alternating with each other with perfect regularity. In others again the muscle cells appear simply granular with Hartnack No. 8 and 9. Between these two extremes intermediate conditions, faintly striated and half-granular half-striated, may be found. These cells exhibit the transition from smooth to striped muscle which was, I believe, first pointed out by Bowman[2], and has been well described by Boll[3]. The muscle elements contain an oval nucleus occupying the broadest portion of the cell. I have not observed the "Axen-strang" or axial chain of granules figured by Boll[3] in the cardiac muscle of Octopus, nor have I made out the branching of the fibres mentioned by Leydig[4].

In the muscles of Anodon, Margo[5] has shown that the striation depends, as in vertebrate muscle, on the alternation of isotropous and anisotropous substances. Through the kindness of Dr Klein I have been enabled to examine the snail's cardiac muscle with polarised light. I did not attempt to repeat Margo's observation, but the examination of unstained sections between crossed Nicolls proved distinctly that the muscle of the snail's heart resembles vertebrate muscle in being uniaxial, with the axis parallel to the direction of the muscle cells.

The arrangement of the larger bundles into which the muscle is massed, offers no points of interest. The ventricle laid open shows them passing in all directions, and interlacing in an elaborate and irregular manner. The valves are attached to the opening by the continuity of their fibres with those of both chambers of the heart.

The connective tissue of the organ presents a few points of interest. The substance which unites cell to cell stains brightly in chloride of gold, and also comes out with nitrate of silver;

[1] *Loc. cit.* [2] *Cycl. Anat. and Phys.* III. 514, 519.
[3] *Loc. cit.* [4] *Loc. cit.* [5] *Loc. cit.* (*Wiener Sitz.* 39).

portions of the valve stained with this reagent exhibit the elongated muscle cells marked out with dark lines.

Sections of the heart stained with hæmatoxylin present a curiously dotted appearance under a low power; this is chiefly due to the connective-tissue corpuscles with which the muscle abounds. These bodies are about ·009 mm. in diameter, and contain a large nucleus embedded in a scanty protoplasmic body which stains in chloride of gold. They are often pyriform in shape, and may be seen *in profile* projecting from the side of a muscular bundle; or sending fine processes to be intimately distributed among the muscle cells.

The connective tissue is remarkably developed towards the periphery of the heart. If the external surface is stained with nitrate of silver, a mosaic work of polygonal cells becomes apparent. In sections or teased preparations this structure is found to consist of closely packed pyriform connective-tissue corpuscles, whose larger extremities are directed outwards. Dr Foster and Mr Dew Smith mention this structure as an "external tesselated epithelium[1]." The cells composing it are firmly attached to each other, and can be torn off in strips which do in fact exactly resemble a tesselated epithelium. Leydig[2] describes and figures the heart of Paludina as covered by an epithelium of simple rounded cells. In Helix the constituent cells differ from those described by Leydig in being connected together by their processes. In some sections I have observed a kind of honeycomb-tissue, the bodies of the cells having fallen out of the meshes in which they were contained.

If one of the epithelium-like strips torn from the external surface be examined with its internal surface upwards, the curious arrangement of the muscles at the periphery of the heart may be observed. Muscular bundles are seen fraying out into beautiful fans, the fibres losing themselves among the mosaic of cells. I am unable to say what the exact connection between the cells and the muscle fibres is; I have never seen them actually terminate in the processes of the connective-tissue cells in the manner described in the frog's tongue[3]. From the fact of their losing themselves among the cells it is clear

[1] *Loc. cit.* p. 320. [2] *Loc. cit.*
[3] *Handbook for the Physiolog. Laboratory*, p. 62.

that the muscles do not all form loops at the periphery of the heart, as analogy would have led one to expect.

In what manner the internal surface of the heart is limited I cannot say. The pulmonary vein is lined with a regular endothelium; according to Keferstein, an "epithelium" coats the inner surface of the aorta. Analogy would suggest that the cavity of the heart is limited internally by the same membrane that lines the vessels continuous with it. The valves are certainly covered with a somewhat irregular pavement of cells, but I cannot make out such a structure in other parts of the heart.

Dr Michael Foster and Mr Dew Smith describe a remarkable kind of physiological insulation which exists between the auricle and ventricle, and suggest the explanation that a ring of connective tissue, penetrated by no nerves, separates the two portions of the organ. This statement I can hardly confirm; the muscles at the region of the junction are apparently rather more intimately permeated by connective tissue; but I can find nothing which can be supposed to insulate the two portions of the organ. At the point of junction many fibres from both auricle and ventricle enter the valve, but this arrangement can hardly be efficient in insulating the two chambers from each other. I have convinced myself, by making longitudinal sections from hearts hardened in osmic acid, that there is muscular continuity between the auricle and ventricle; so that I can offer no anatomical explanation of the above mentioned fact. The appearance of a ring of connective tissue might easily be given by a section passing through the peripheral layer of connective tissue covering the narrow neck between the auricle and ventricle, and which at the same time included muscle fibres from both chambers of the heart. These would be cut obliquely, and would be separated from each other or even seem to arise from a region where they were replaced by connective tissue. Dr Foster and Mr Dew Smith[1] describe the curious waves of contraction which can be made to traverse the ventricle in any direction; it is remarkable that this should be the case in muscular tissue which seems to contain a considerable quantity of connective tissue. But the anatomical relations corresponding to physiological conduction and insulation are no doubt at present obscure or unknown.

[1] *Loc. cit.* p. 329.