STRUCTURE OF THE HEART OF THE ASCIDIAN *PYURA PRAEPUTIALIS* (HELLER)*

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The ascidian heart is an elongated, tubular structure which is attached along one side to the wall of the pericardium. In *Pyura praeputialis* it is located beneath the mantle immediately to the right of the endostyle and hence to the right of, and parallel to, the mid-ventral line of the animal's body.

The wall of the heart is an extremely delicate tissue which is easily damaged in dissection. Both in live and in fixed specimens it can be seen to have the configuration of a twisted tube. In other words it resembles, in external appearance, a piece of rope.

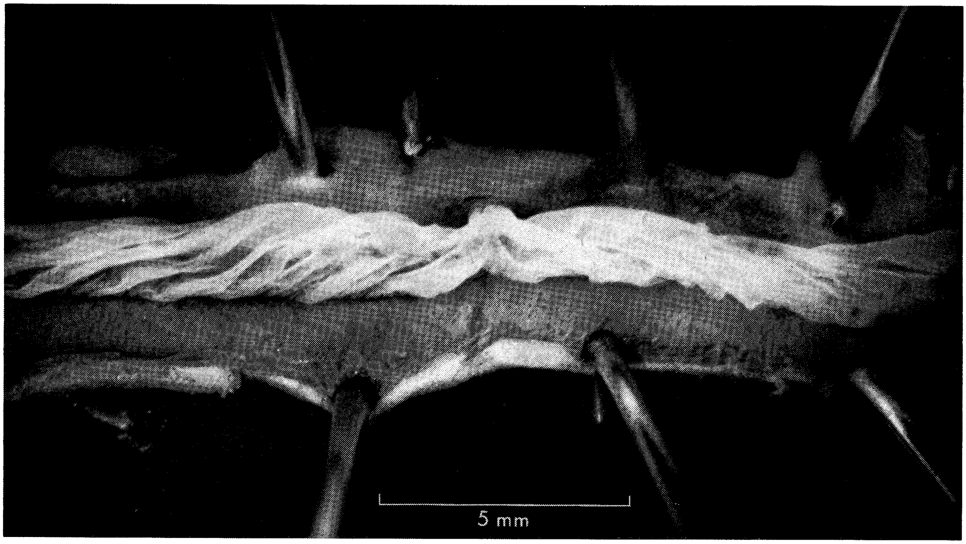

Fig. 1.—Heart of *P. praeputialis* after formalin fixation. Wall of pericardium pinned back dorsally and ventrally to show heart *in situ*, anterior to right. At right the spiral is clockwise relative to the anterior–posterior axis of the heart; at left it is anticlockwise. The flap of tissue which constitutes the "anchor connection" is clearly visible at the point where the spiral reverses direction.

The spiral pattern usually commences at, or close to, the anterior end of the tube but in some specimens it commences as far back as one-third the distance from the anterior end. From this point back to just past the middle of the heart (about one-half the length of the "twisted" portion) the tube has a clockwise spiral, i.e. clockwise with respect to the anterior–posterior axis of the heart (Fig. 1). At the latter point the spiral reverses direction, and for the remainder of its length the tube has an anti-clockwise spiral.

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At the point where the spiral reverses direction there is an interesting structural feature. A flap of tissue, part of the wall of the heart, is deflected upward (ventral to dorsal) and securely attached to the wall of the pericardium on the dorsal side of the heart. The attachment of this flap of tissue to the pericardium is clearly related to the spiral configuration of the heart.

The features described above can be interpreted as follows: A spiral structure is conferred on the heart by spiral arrangement of the fibrous elements of which it is built. This spiral reverses direction at a point located, in most cases, some little distance posterior to the middle of the heart. It is necessary to anchor the fibres at the point of reversal; if not anchored at that point contraction of the spiralling muscles would tend to straighten the tube and unravel the spiral, since the latter is pitched in opposite directions on the two sides of the point of reversal.

It is convenient to refer to the flap of tissue which anchors the fibres at the point of reversal as the "anchor connection". The role of this connection has been investigated by experimental manipulation. If the heart is exposed and mounted in sea-water, as shown in Figure 1, the normal functional pattern is upset. If the preparation is allowed some time (about 1 hr) to "settle down" it will begin to beat spontaneously: intermittent groups of peristaltic waves will pass over the heart. All waves of each group will commence at the same end and will travel the length of the heart. Each group of waves is followed by a more or less prolonged period of quiescence. The next group of waves may originate at either end; in other words the normal reversal of the direction of beat does not occur.

It is possible to induce "artificial" waves by prodding the ends of the heart. The mechanical stimulus causes a wave which commences at the point stimulated and travels to the opposite end. In fact, prodding at any point along its length will cause a wave to originate at that point and travel outward in both directions to the ends of the heart.

If the anchor connection is now severed the waves of contraction are not affected. Whether it arises spontaneously or is artificially induced, each wave travels the length of the heart. It traverses without difficulty the region of the anchor connection, even though the wall of the heart in that region is now extensively damaged.

The experimental evidence indicates, therefore, that the anchor connection is not essential for heartbeat. There is no obvious "unravelling" of the reversed spiral when the heart contracts. On reflection it becomes clear that the reversed spiral could not be unravelled because it is not maintained solely by the anchor connection: the fibres are also anchored by the suture which runs the length of the heart and attaches it to the pericardium.

Although the peristaltic wave is not obviously affected by destruction of the anchor connection, it is possible that without such a connection the effectiveness of the wave would be reduced. Stated differently, it seems possible that development of maximum force by the heart depends on a firm anchorage of the fibres at the point of structural reversal. This hypothesis explains the need for an anchor connection—given a reversed spiral structure—but it does not explain why a reversed spiral structure is necessary.

It is difficult to avoid the suggestion that the structural reversal is concerned, in some way, with the periodic reversal of beat. However, there is no obvious reason why the two phenomena should be related. Moreover, reversal of the direction of beat appears to be a general feature of the ascidian heart, whereas a reversed spiral structure may be peculiar to *Pyura*.

There is an extensive literature on the ascidian heart. Reviews have been published by Berrill (1950) and by Krijgsman (1956). More recent studies are summarized by Ebara (1971). The work of Hunter (1902) is noteworthy in that he reported a spiral arrangement of the nerves, muscle, and connective tissue fibres in the heart of *Molgula manhattensis*. Waterman (1943) noted "a spiral structure of the wall" of the heart of *Perophora*. However, there is no report, so far as the author can discover, of a *reversing* spiral structure like that described here.

There are persistent reports that the middle region* of the ascidian heart is both structurally and functionally "differentiated". Thus, Hecht (1918) reported a constriction located about one-third the distance along the heart of *Ascidia* and observed that both the pattern of contraction and the velocity of the peristaltic wave change when the wave passes this "node". Waterman (1943) observed a similar constriction at the middle of the heart of *Perophora*. Most workers agree that there are two pacemakers in the heart, one located at each end and controlling the peristaltic wave that starts at that end; however, contraction *may* start at the middle of the heart, producing waves which proceed to both ends (review by Krijgsman 1956).

The above observations suggest that the middle of the tunicate heart is more highly differentiated than casual observation reveals. The heart of *P. praeputialis* provides further evidence to that effect: the middle region shows a conspicuous reversal of structure and it remains to be seen whether this is related to the functional reversal which is so notable a feature of the ascidian heart.

References

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* The term "middle region" is intentionally imprecise. It implies all that portion of the heart from about one-third to about two-thirds its length.