Torsion in Gastropoda

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Torsion is a process in larval gastropods whereby the visceropallium is rotated anti-clockwise through 180° from its initial position on the head-foot complex. The original mechanism by which torsion was brought about was probably the contraction of larval retractor muscles, the entire rotation being completed in a few minutes. In most of the gastropods in which torsion has been carefully studied, larval retractor muscles account for 90° of the rotation, differential growth for the rest.

Even in the very early veliger larva, the mesodermal bands develop asymmetrically. The right band is distinctly larger than the left and can be distinguished as five large mesodermal cells (Fig. 1). As these cells elongate to form muscle cells, they gradually displace the visceral hump to the left, emphasising the asymmetry. These cells converge on to the right side in the posterior region of the larval shell and are inserted into the anterior end of the body as larval retractor muscles (Fig. 2). There are no related muscle cells on the left side. As soon as the larval muscle cells have any contractile power, the process of torsion commences (Fig. 3). If the muscle contraction accounts for only 90° of rotation, the process usually lasts for a few hours. At the end of this first stage, the mantle cavity which originally lay ventrally and posteriorly now lies on the right side and the foot projects on the left.

Stage 2 of torsion is usually longer in duration, relying on differential growth. In general, the later the onset of torsion, the shorter the duration of stage 2, because of the more advanced stage of development when torsion begins.

It is possible to distinguish five ways in which torsion can be brought about (Thomson, 1958):

1. 180° rotation achieved by muscle contraction alone. This was probably the original mechanism and is known only for *Acmaea* (Prosobranchia, Archaeogastropoda, Acmaeidae).

2. 180° rotation achieved in two stages, an initial 90° movement by larval retractor muscle contraction followed by a slower rotation through the remaining 90° by differential growth processes. This is probably the commonest mechanism of present-day forms, e.g. *Haliotis* (Prosobranchia, Archaeogastropoda, Haliotidae), *Patella* (Prosobranchia, Archaeogastropoda, Patellidae).

3. 180° rotation achieved by differential growth processes alone, e.g. *Vivipara* (Prosobranchia, Mesogastropoda, Viviparidae).

4. Torsion achieved by differential growth processes, the change in the position of the anus being halted at a site appropriate to the adult state, e.g. *Aplysia* (Opisthobranchia, Anaspidea, Aplysiidae).

5. Torsion no longer recognisable as a movement of the viscerapallium, the organs being in the post-torsional position from their first appearance, e.g. *Adalaria* (Opisthobranchia, Acoela, Polyceridae).

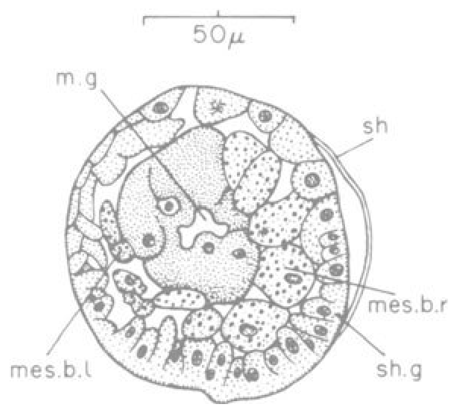

Fig. 1: Transverse section of early veliger of *Haliotis* to show the disproportionate growth of the right mesodermal cells. (*mes.b.l,* left mesodermal band; *mes.b.r,* right mesodermal band; *m.g,* midgut cavity; *sh,* shell; *sh.g,* shell gland)

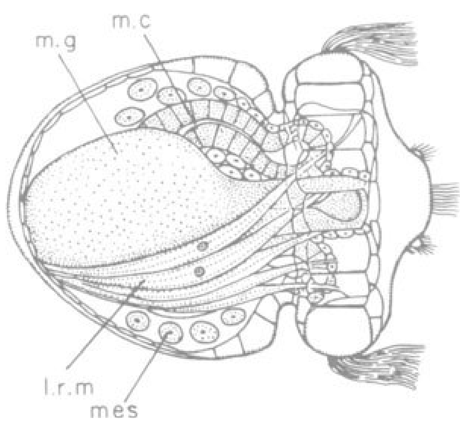

Fig. 2: 48-hour veliger larva of *Patella vulgate*. (*l.r.m,* larval retractor muscles; *m.c,* mantle cavity; *mes,* mesoderm; *m.g,* midgut)

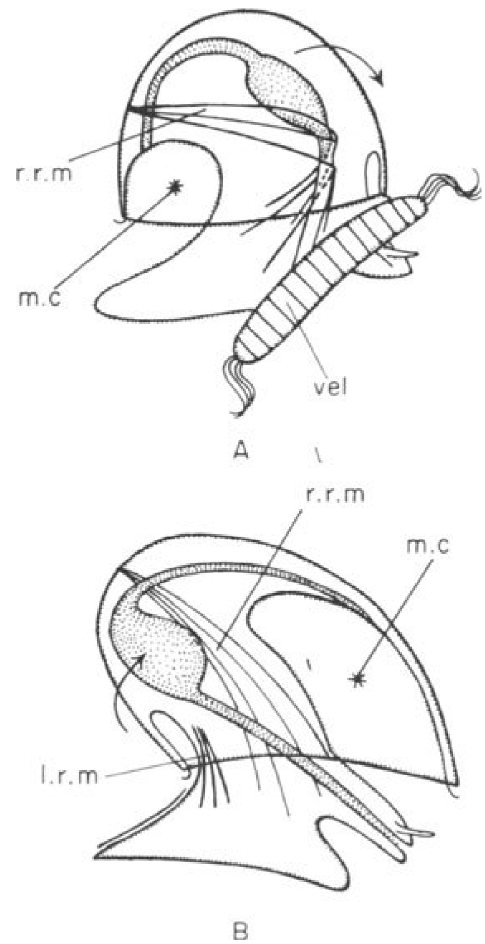

Fig. 3: A diagrammatic representation of torsion in a prosobranch veliger larva. A, pre-torsional; B, post-torsional. (*l.r.m,* left larval retractor muscles; *m.c,* mantle cavity; *r.r.m,* right larval retractor muscles; *vel,* velum)

Whatever the mechanism involved, the post-torsional larva now has its mantle cavity placed anteriorly and whatever organs are developed will be affected in some way, particularly in their spatial relationship with each other. It must be emphasised that by the time torsion is complete many organ systems, e.g. pallial organs and nervous systems, are represented only by rudiments, if at all. Nevertheless, as development proceeds, the organs will develop in their new positions, resulting in such phenomena as looped and crossed pleura-parietal nerve connectives.

Significance of torsion

Torsion is a fundamental feature of gastropods and represents their greatest departure from the primitive molluscan plan. There are two rather different views on torsion. One, put forward by Garstang in 1928, confines itself largely to a discussion on the advantages of torsion to the larval mollusc. The later view, propounded by Morton in 1958, seeks to convince us of the value of torsion to the adult gastropod, not merely to the larva. In brief, these two views are:

1. The anterior location of the mantle cavity in the larva resulted in greater protection for the head and its associated parts by providing them with a cavity into which first they, and then the foot, could be withdrawn at the approach of danger. With a posterior mantle cavity, it would be a case of foot first, vital head structures last.

While the withdrawing of the vulnerable organs into the shell would offer the larvae no protection against large, predatory fish, it would protect them against their known main enemies, the predatory planktonic animals.

Garstang held that the adaptive value of torsion was useful primarily to the larva. The adult gastropod was thus a flow on of an evolutionary investment for a brief requirement of ancestral larval life.

2. Morton holds the view that because the mantle cavity is such an important and dominating feature of molluscs, its position may be just as important to the adult as to the larva, but that its advantages in an anterior position may be quite different for the adult and for the larva.

The anterior mantle cavity which opens forward, contains, in the adult, three important structures. The most important are respiratory in function and it is clearly to their advantage to be placed in the face of an on-coming water current. The second are sensory and test the incurrent water stream chemically and for sediment; again, it is an advantage to test what is coming rather than what has gone. The chemoreceptive sense has become highly developed in some of the carnivorous gastropods, many of which have an inhalant siphon which can function as a movable 'nostril'. The third structures, the anal and renal apertures, are somewhat unfortunately placed. In a symmetrical mantle cavity, the respiratory current would be Ushaped, entering one side, leaving via the other, dumping the faecal waste on the head as it passed. This problem has been solved in various ways in the Gastropoda, partly because the mantle cavity tends towards asymmetry and as we shall see, this asymmetry can arise just as much from coiling as from torsion.

Detorsion

In some molluscs, reversible changes take place in torsion to a certain extent during the larval stages. This reversion is known as detorsion. It is very characteristics of the whole group of the Euthyneura. In such situations twisting of visceral mass is not necessary. As a result, nervous system becomes symmetrical and not twisted in the shape of 8. Pallial complex travels backwards. Ctenidium travels backwards or to the lateral side. Auricle moves behind the ventricle. Visceral loop and intestine become straightened.

Detorsion takes place partially in Pulmonata (*Acteon*, *Bulla* etc.) in which visceral loop remains partly twisted and the anus and ctenidium are directed laterally. In Opisthobranchia (*Aplysia*), total detorsion is accompanied by a reduction or disappearance of the shell. The gills are directed laterally but lie posterior to the heart and the body becomes symmetrical. In *Pterotrachea coronata* (floating sea slug) the shell, mantle and visceral sac are lost and hence the body becomes symmetrical and worm-like. Nudibranchs (*Eolis* and *Doris*) also undergo detorsion due to the loss of shell. *Doris* has symmetrical rhinophores and anal gills on the posterior side. The sea slugs, *Eolis* and *Iolidia* are symmetrical animals because they have undergone detorsion due to the absence of shell.

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