

## Torsion in Gastropoda

### Definition:

Torsion (twisting) is the rotation of visceral organs in anticlockwise direction through an angle of  $180^\circ$  on the rest of the body during larval development. The phenomenon takes place in the free-swimming (veliger) larva of gastropods and converts the symmetrical larva into an asymmetrical adult.

Contraction of the larval retractor muscles and differential growth are possibly responsible for such rotation. Entire rotation results within few minutes. Asymmetry is encountered at the early stage in Veliger larva where the mesodermal bands develop asymmetrically. The mesodermal band on the right side is larger than its left counterpart.

The right band is composed of five mesoderm cells which elongate to form muscle cells. With the transformation of the muscle cells the visceral hump is displaced to the left side.

These cells on the right side converge and transform into the larval retractor muscles. The muscle cells are absent on the left side. Torsion of the visceral hump commences as soon as the larval muscle cells attain the power of contraction.

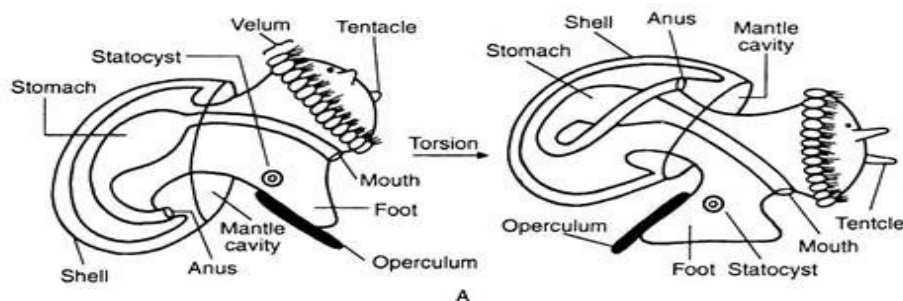


Fig. 16.71A: Figures showing the torsion of a free-swimming larva in a primitive gastropod (*Patella* sp.) (after Pechenik).

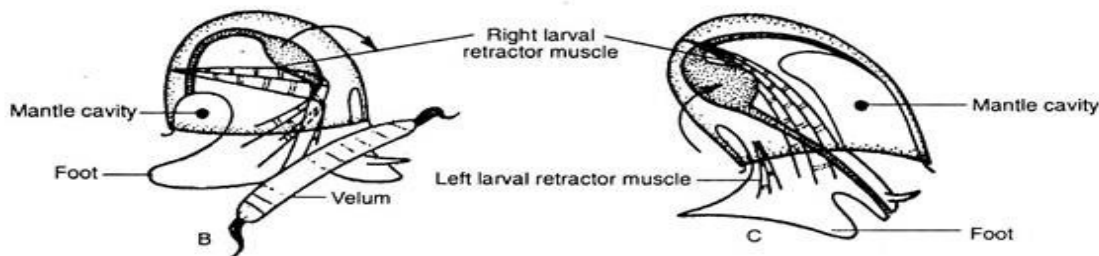


Fig. 16.71B, C: Diagrammatic representation of torsion in veliger larva of a prosobranch. B. Pre-torsional stage. C. Post-torsional stage (after Parker and Haswell).

### **Conditions before Torsion:**

1. The mantle cavity is situated at the posterior side containing the pallial complex.
2. The ctenidia and two nephridiopores are located posteriorly.
3. The alimentary canal is straight with the mouth at the anterior side and anus at the posterior side.
4. The auricles are placed behind the ventricle.
5. The nervous system is bilaterally symmetrical.
6. Firstly, the embryo is bilaterally symmetrical in the veliger stage when foot and a planospiral shell are formed first in this stage.

### **Process of Torsion :**

1. The morphological phenomenon of bending on the ventral side which takes place in an antero-posterior sagittal plane about a transverse axis of the animal results.
  - (a) Firstly, the displacement of the mantle cavity towards the right side and then to the anterior end of the body but the head and foot remain fixed .
  - (b) The looping of the digestive tract and approximation of mouth and anus take place.
  - (c) The original saucer-shaped visceral mass and the shell become cone- shaped and finally become spirally coiled.
2. Simultaneous coiling up of these structures results in an exogastric coil.
3. Ventral portion of the visceral mass and mantle rotate about 180° or little more.
4. Twisting of dorsal mass occurs in such a manner that organs such as right gill and right auricle remain and corresponding parts on the left side are often lost.
5. During the completion of metamorphosis there is a lateral torsion subsequent to primitive ventral plexus with the result that the original coil of the visceral sac and the shell which was originally dorsal or exogastric becomes ventral or endogastric. So the lateral torsion leads to the attainment of condition of gastropods following certain changes in original organisation.

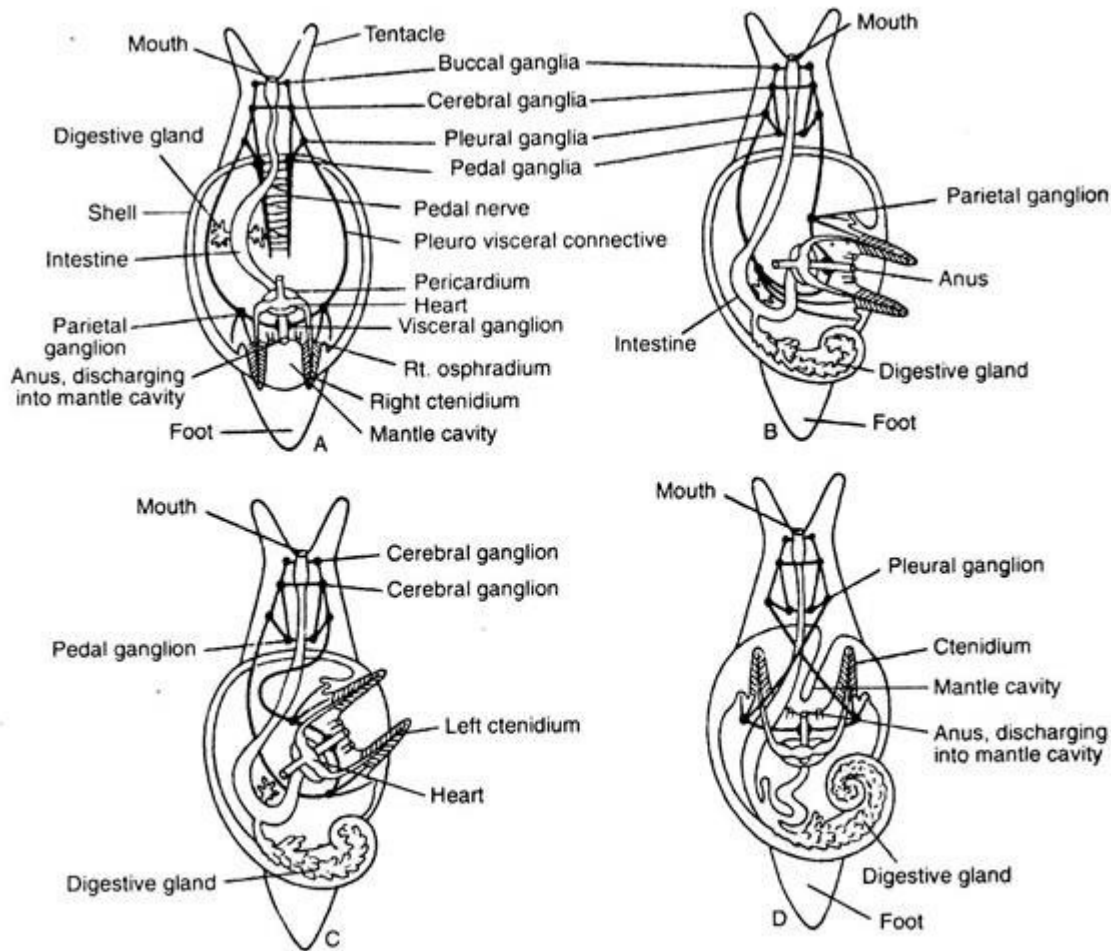
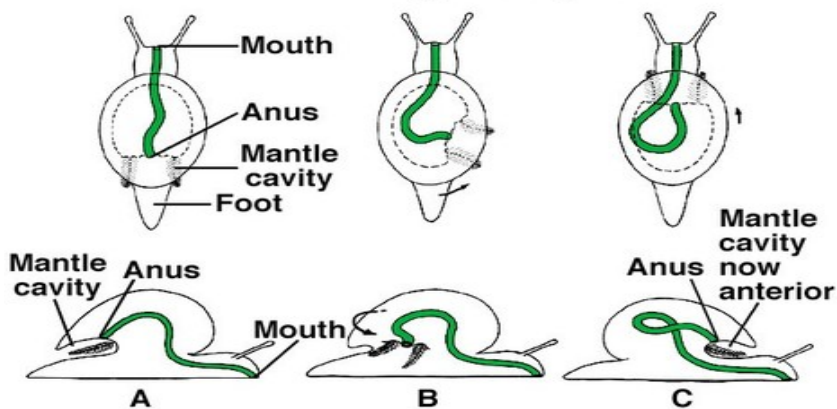


Fig. 16.72: Diagrammatic representation of torsion in Gastropod. A. Hypothetical ancestral stage with symmetrical arrangement of structures. B. Displacement of the mantle cavity to the right side. C. Showing 90° torsion. D. Showing complete torsion.

## Torsion in gastropods



### Cause and Significance of Lateral Torsion:

1. Lateral torsion is due to arrested growth of one side and active expansion of the other. Generally the growth of the right side becomes retarded so that the mantle cavity and pallial complex gradually pass down to the right side and to the anterior side on account of the better growth of visceral mass towards the left.

2. This is necessary for protection, compactness and provision for continuous growth. This is the response with necessity in life of animal for best adaption.

### **Effect of Torsion and Shuttling of Pallial Complex:**

#### **1. Displacement of mantle cavity:**

The mantle cavity was originally posterior in position but after torsion the mantle cavity opens just behind the head and its associated parts shifted forward.

#### **2. Changes in relative position:**

Before torsion the anus and ctenidia are pointed backwards and auricles are situated behind the ventricle. After torsion the anus and ctenidia come forward and the auricles come to lie in front of ventricle.

#### **4. Origin of chiastoneury:**

Crossing of the pleuro-visceral connectives is due to the fact that the pallial complex must have changed its position from the posterior to the anterior part of the body and become twisted in the form of 8. The right connective with its parietal ganglion passes over the intestine called the suprainestinal and the left connective passes below the intestine called the infraintestinal.

#### **5. Endogastric coil:**

The coil of visceral sac which was primarily dorsal or exogastric becomes ventral or endogastric after torsion. The coiling of the shell is not associated with the torsion and was a separate evolutionary event and the shell remained a symmetrical spiral.

#### **6. Loss of symmetry:**

It is due to displacement of anus towards right side of the mantle cavity and loss or reduction of paired parts of the primitively left or topographically right side.

**In majority of the gastropods torsion, is resulted in two stages, viz., Stage-I and Stage-II:**

#### **Stage-I:**

The contraction of the larval retractor muscles account for 90° of the rotation of the visceral hump. This process usually lasts for only a few hours. At the end of Stage-I, the mantle cavity (which was initially situated ventrally and posteriorly) comes on the right side with the foot projecting on the left side.

#### **Stage-II:**

The rest of the torsion is the result of differential growth and is usually longer in duration. Actual mechanism of torsion in gastropods is not properly known and it is difficult to give a generalised account of torsion in gastropods.

## **Significance of Torsion in Gastropods:**

### **(a) Garstang's view:**

Garstang (1928) advocated that torsion is an adaptive feature and useful to the larvae (veliger larva) for protection of soft parts against enemies but of little direct use to the adult.

He suggested that before torsion the untwisted larva swimming the sea was subjected as an easy prey to its predators because the mantle cavity was at the posterior position and there is no place into which delicate head and velum can be withdrawn at the time of danger so it is disadvantageous to the larval life.

But after torsion the mantle cavity is brought around the anterior end of the larva which provides the space for head and velum and the larva gives the greater protection of the head and associated structures. At danger the larva is able to withdraw its head and velum into the mantle cavity. Then the beating of cilia stops and the larva falls to the sea bottom. In this way they avoid the predators. This view is widely supported by Yonge (1947), Barnes (1980), Ruppert and Barnes (1994) and Anderson (1998). But the recent experiment by Pennington and Chia (1985) does not support Garstang's view.

### **Objections:**

1. There are many pelagic larvae of lamellidens which are not twisted but still survive in pelagic larval life.
2. The cilia of some gastropods are under nervous control and these could be stopped by simpler means than withdrawing them into the mantle cavity.
3. In *Haliotis* the shell rotates in two phases – firstly through 90° and secondly then through 180° but the animal is only pelagic at the first stage while the head is unable to retract into the mantle cavity. The larva does not complete its torsion (180°) till it has settled in the bottom.

### **(b) C.M. Yonge's theory (1947):**

1. Primitive Gastropods were not twisted and the gills were attached posteriorly inside the mantle cavity. The cilia of the gills draw the respiratory current from behind the mantle which is in opposite direction of the current produced by the locomotion of the animal and the weak current of the sea itself, thus producing disadvantage in respiration and locomotion.
2. If the animal once twists all the currents would follow in the same direction, thus aid the flushing of mantle cavity with freshwater and thus torsion becomes advantageous for ventilation of mantle cavity.
3. The twist brings the anus anterior, so there is some chance of interaction between the discharged faecal matter and respiratory current.

### **To avoid this, at least three adaptations are found:**

- (a) Shell develops a fold or series of folds. The anus retracted and respiratory currents sweep over the gills, e.g., *Haliotis*.
- (b) One of the gills and its associated auricles are lost, so that the respiratory current sweeps laterally through the mantle cavity.

(c) Gills are either reduced or lost. The respiratory surface in the mantle cavity which in some cases develops pallial gills, e.g., Patella.

**(c) Ghiselin's view (1966):**

According to him, the primitive gastropods developed a conical shell on the dorsal surface for protection instead of shield-like shell. To maintain the balance of body the shell of the gastropods prolonged anteriorly. But for the crawling purpose it was disadvantageous bearing such anteriorly prolonged shell. The shell containing anterior- prolonged side rotated into the posterior through 180° during torsion. So it has become advantageous in the adult stage. Stasek (1972) and Purchon (1977) have also supported that torsion is advantageous during adult stage.

**Coiling:** The ability of withdrawal of the head-foot complex into the anterior mantle cavity due to torsion increases the efficiency in locomotion, feeding and sensory function in gastropods. The head-foot complex retains its bilateral symmetry. The visceral hump together with the protecting shell becomes coiled to economise the volume.

## DETORSION

Detorsion is reversal of torsion which takes place when during evolution shell is lost or a type of shell evolves that has openings on the opposite sides. In such situations twisting of visceral mass is not necessary. Hence, detorsion takes place during the larval stage and the animal again becomes bilaterally symmetrical. 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 in Pulmonata, such as *Acteon* and *Bulla* in which anus and ctenidium are directed laterally. In *Aplysia* (Opisthobranchia), detorsion takes place owing to the loss of shell. The gills are directed laterally but lie posterior to the heart and the body becomes symmetrical.

In *Pterotracheacoronata* (floating sea slug) the shell, mantle and visceral sac are lost and hence the animal becomes symmetrical, worm-like with a long proboscis for feeding.

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. They move with the help of a ventral foot and breathe with respiratory cerata that are present all over the body.

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