Nervous System in Gastropoda

The nervous system consists of ganglia, commissures, connectives and the nerves to different organs.

(i) Ganglia:
A small compact mass of nerve cells and connective tissue is called ganglion.

The main ganglia are:

(1) One pair of roughly traingular cerebral ganglia situated on the dorsolateral sides of the buccal mass, one on each side of the head.

(2) One pair of pleuropedal ganglia placed below the buccal mass on the lateral side. Each pleuropedal ganglionic mass is more or less rectangular in outline and is formed by the fusion of pleural and pedal ganglia. The infraintestinal ganglion is also fused with the right pleuropedal mass.

(3) Visceral ganglion is very large and appears to be unpaired. It is a bilobed structure and is formed by the fusion of two separate ganglia. The visceral ganglion is placed posteriorly very close to the heart.

(4) A pair of buccal ganglia are situated on the buccal mass on the two sides of the oesophagus.

(5) A single supraintestinal ganglion is located near the middle of the left pleurovisceral connectives (Fig. 16.18).

ii) Commissures:
The nerve connections between two similar ganglia are generally called commissures. The ganglia are placed on the opposite sides of the body. Two cerebral ganglia are connected by a thick nerve cord, called the cerebral commissure. The buccal ganglia are also connected by a delicate buccal commissure. The inner sides of the pleuropedal ganglia are connected by a broad nerve, called the pedal commissure.

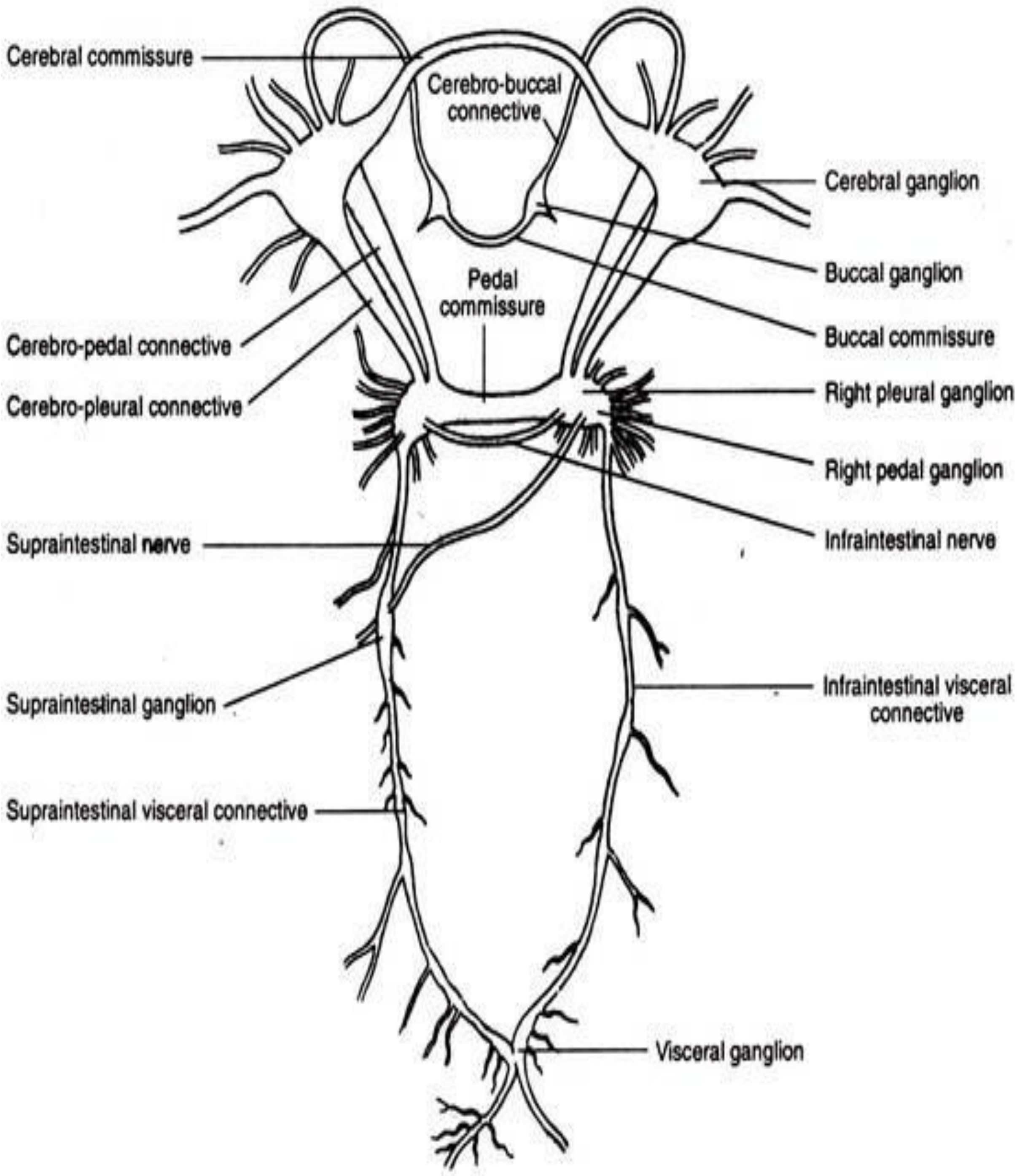

Fig. 16.18: Nervous system of *Pila.*

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(iii) Connectives:

The nerve connections between two dissimilar ganglia are usually called connectives. The ganglia may be situated on the same or opposite sides of the body. The cerebral ganglia and the buccal ganglia are connected by cerebrobuccal connectives.

The pleuropedal ganglia are connected on each side with the cerebral ganglion by cerebropedal and cerebropleural connectives. That the pleuropedal ganglia are formed by the fusion of separate pleural, and pedal ganglia is indicated by the presence of an indistinct constriction and the existence of two separate connectives joining the cerebral ganglia.

The pleural ganglion is connected with the visceral ganglion by a pleurovisceral connective on each side. The right pleurovisceral connective lies below the level of the oesophagus and is generally designated as infraintestinal visceral connective and the left pleurovisceral connective is situated above the level of the oesophagus and is termed as supra-intestinal visceral connective.

The supra-intestinal ganglion is connected with the right pleuropedal ganglion by an oblique nerve placed above the oesophagus, called supraintestinal nerve. A very slender nerve, called the infraintestinal nerve, is present connecting the two pleural ganglia of two sides.

Nerves to the different parts of the body:

Each cerebral ganglion innervates the eye, the snout and the tentacles on its side. The statocyst is also innervated by a slender nerve arising from the cerebral ganglion. The pedal ganglion gives out numerous nerves to the foot and the pleural ganglion supplies the mantle.

The supraintestinal ganglion supplies nerves to the ctenidium and the pulmonary sac. The visceral ganglion sends nerves to kidney, genital organ, pericardium and intestine. The buccal ganglion innervates the buccal mass.

Torsion in Gastropoda

Definition:

Torsion (twisting) is the rotation of visceral organs in anticlockwise direction through an angle of 180° 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 (Fig. 16.71 A, B, C). 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. 16.71 A, B, C).

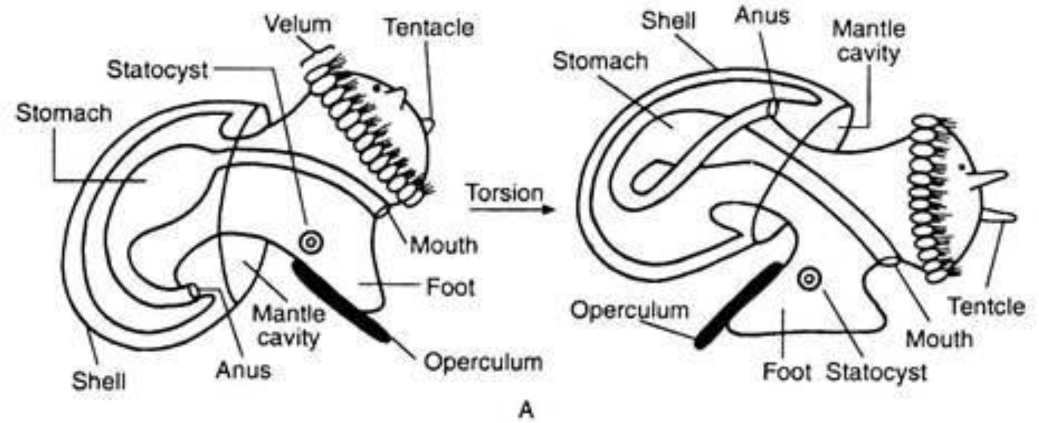

Fig. 16.71A: Figures showing the torsion of a free-swimming larva in a primitive gastropod (*Patella* sp.) (after Pechenik).

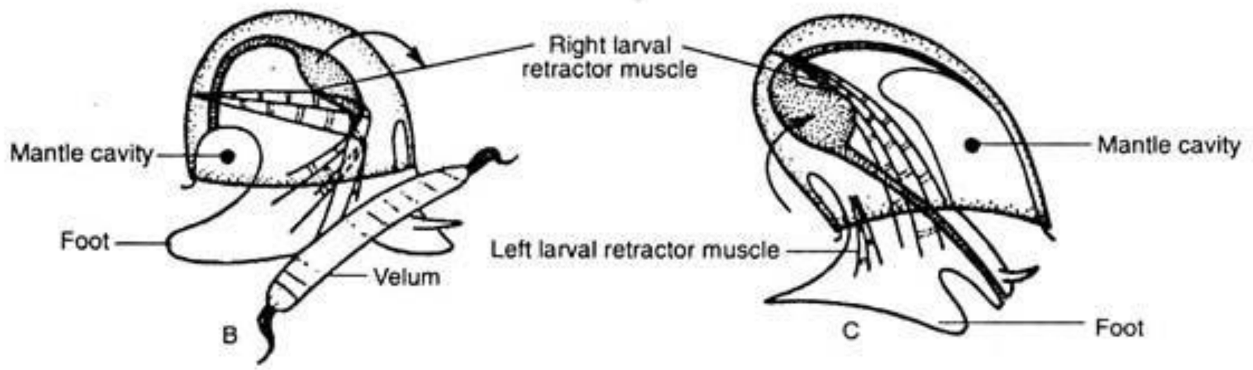

Fig. 16.71B, C: Diagrammatic representation of torsion in veliger larva of a prosobranch. B. Pre-torsional stage. C. Post-torsional stage (after Parker and Haswell).

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.

Remarks:
Torsion is not the coiling of the shell and all the evidences indicate that the shell evolved before torsion.

How Torsion Occurs:

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 (Fig, 16.72).

(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 plexux 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.

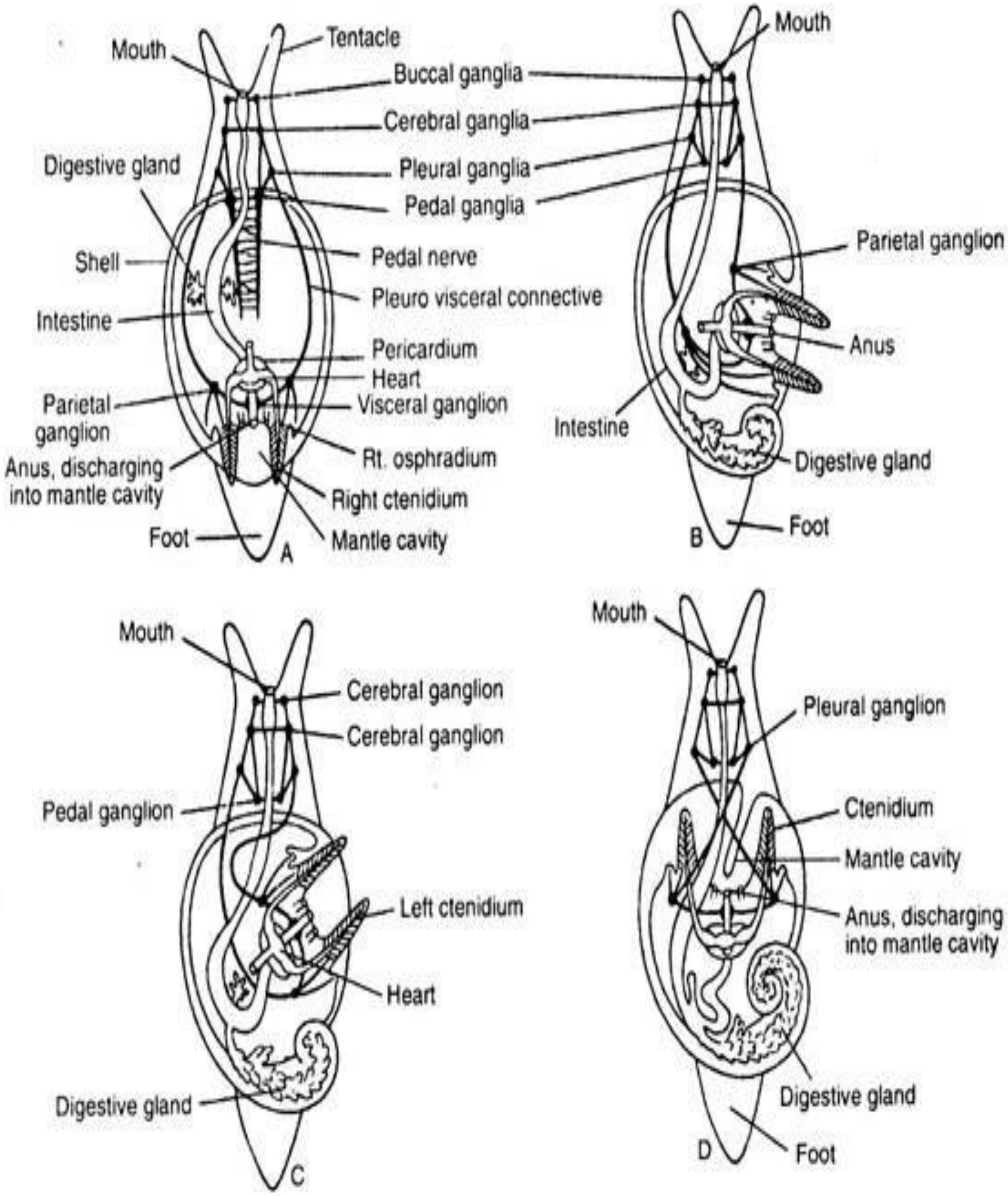

Fig. 16.72: Diagrammatic representation of torsion in Gastropod. A. Hypothetical ancestral stage with symmetrical arrangement of structures. B. Displacement of the mantle cavity to the right side. C. Showing 90° torsion. D. Showing complete torsion.

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.

3. Twisting of alimentary canal:
The alimentary canal which was primarily straight is twisted in the form of a loop and approximation of mouth and anus takes place.

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 arid become twisted in the form of 8. The right connective with its parietal ganglion passes over the intestine called the supraintestinal 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, as already stated, 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 proper y known and it is difficult to give a generalised account of torsion in gastropods.

However, Thomson (1958) distinguished five possible ways by which torsion has resulted in gastropods:
They are:
(a) 180° rotation of visceral hump is achieved by muscular contraction alone. This mechanism is seen in Acmaea and is regarded to be the original way of torsion.

(b) The commonest way of torsion (180°) as encountered in Haliotis, Patella, etc., is achieved in two subsequent stages.

(i) The initial 90° rotation is caused by the contraction of the larval retractor muscle and

(ii) The remaining 90° is effected by differential growth. The first phase occurs at a faster rate, while the next phase is slower.

(c) In some gastropods as exemplified by Vivipara, complete (180°) rotation is achieved exclusively by growth processes.

(d) In Aplysia, torsion is resulted by differential growth and the change in position of anus is halted at a region appropriate to the adult stage.

(e) In Adalaria, torsion of the visceropallium is not recognisable. The different organs appear as in the post- torsional position.

Whatever be the cause of torsion in gastropods, a post-torsional larva possesses an anteriorly placed mantle cavity and all the developing organs are severely affected.

With the completion of torsion many organ systems (e.g., Pallial organs, nervous system) become greatly affected. Formation of loop and crossing of pleuroparietal connectives are a common occurrence in the nervous system in gastropods, especially protobranchia.

Views on the Significance of Torsion in Gastropods:
Torsion is a characteristic feature of gastropods. The significance of such torsion in gastropods is not clear. Several contrasting views are extant on this issue.

They are:
(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 Pennigton and Chia (1985) does not support Garstang's view.

Objections:
The theory was criticised for several reasons such as:
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.

Detorsion:

Acquisition of secondary symmetry observed in some Opisthobranch Gastropod is regarded as the result of detorsion. The distortion means the reversion to the changes that have occurred during torsion. As a result of detorsion the pallial complex travels towards the posterior end along the right side.

The ctenidia are pointed backwards and the auricles come behind the ventricle. The visceral loop becomes untwisted and symmetrical. In this way a secondary external symmetry is established again. Detorsion is always associated with the loss of shell and the liberation of gills (ctenidia) from their enclosing case.

The gills become exposed and subjected to external current. Different gradations of detorsions are encountered in the different members of opisthobranchs. In Acteon and Bulla detorsion is partial, and complete detorsion is observed in Aplysia. In some nudibranchs (e.g., Doris, Apolidia, etc.), the shell and mantle cavity are absent and the body becomes secondarily bilaterally symmetrical.