

GARSTANG'S HYPOTHESIS AND GASTROPOD TORSION

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ABSTRACT

Recent experiments purporting to show that torsion in gastropod veligers does not function defensively against attacks by planktonic predators are inconclusive. There is still much to be said for Garstang's suggestion that torsion is advantageous to the veliger in allowing it to withdraw head first in to the mantle cavity, sealing the shell aperture with the foot and operculum, and that the ability to do so may indeed have originated with a single gene mutation in evolution.

INTRODUCTION

Pennington & Chia (1985) have reported an interesting series of experiments designed to test the hypothesis first put forward by Walter Garstang (1929), that torsion of the gastropod veliger evolved as a result of the protection it provided against predation. They exposed both pre-torsional and post-torsional larvae of the archaeogastropod *Haliotis kamschatkana* Jonas, from the Pacific coast of North America, to predation by seven planktonic animals belonging to four different phyla. If proportionately more of the pre-torsional veligers were consumed, then this would have supported Garstang's hypothesis. This seems to have been the first attempt to validate the hypothesis by experiment rather than simply with argument, but its results must be regarded as inconclusive.

Of the seven predators tested one (a ctenophore) took practically none of the veligers offered, and for the four (a hydromedusan, another ctenophore, a copepod, and a young fish) which did consume a considerable number, the net predation was not significantly different before as compared with after torsion. There was however a large difference for the crab megalopa larvae, which took significantly more of the post-torsional veligers, and a smaller one for the hydromedusan *Aequorea* (*Mesonema*) *victoria* (Murback & Shearer), which took significantly fewer; these two balancing out so that

for all seven predators taken together there was no significant difference before and after torsion. However, the megalopas broke the shells of the veligers they ate, fragments of which were found on the bottom of the jar, so that torsion, which allows the veliger to withdraw into its shell, would anyway have provided no protection. Discounting the megalopas, differential predation by *Aequorea* might possibly have represented some small net advantage for torsion: but this would at best have been marginal, and can scarcely be claimed as support for Garstang. There must of course have been many other predators in the plankton capable of taking veligers, which were not tested.

GARSTANG'S HYPOTHESIS

Garstang explicitly based his hypothesis on the proposition that torsion would be advantageous to the veliger itself, and not necessarily to the adult snail, by allowing it to withdraw the head with its ciliated locomotory velum first into the mantle cavity, with the tail end of the foot (regarded as less vulnerable, and usually carrying an operculum to close the shell mouth) going in last, thus avoiding injury to the head when attacked by a predator. Before torsion, when the mantle cavity opens backwards, it is the tail which would go in first, and the head and velum last.

Garstang originally supposed that torsion was brought about by the left and right retractor muscles developing asymmetrically in the pre-torsional larva, with the right cephalic retractor being the larger and stronger and able to pull the visceral hump and mantle cavity round the full 180° in the course of a few hours. But Crofts (1937, 1955) later showed that the first muscular phase of torsion goes round only about half way, the full 180° being achieved by differential growth over the next 10 days or so. This however does not affect Garstang's argument since, in *Haliotis* at any rate, 90° of torsion is enough to

allow the head to be drawn fully in to the mantle cavity, and the shell mouth to be closed by the operculum, by the time the veliger sinks down out of the plankton.

An essential point of Garstang's hypothesis is that this muscular asymmetry is supposed to have originated as a single mutation, that is to say as a 'macromutation' leading to a major evolutionary advance in one step, and for this to have been preserved by natural selection it must have been of *immediate* benefit to the individual veliger in which it occurred. That would be so if the veliger could protect its head by withdrawing it in to a forwardly opening mantle cavity under the shell after torsion, as Garstang suggested. The operculum on the dorsal surface of the back end of the foot, which could serve no useful purpose before torsion, must have evolved later, and presumably not by a single mutation.

Haliotis is one of the few prosobranchs whose pre-torsional larva is free-living, if only briefly, and so exposed to the sort of predation against which the ability to withdraw its head in to the mantle cavity after torsion might be supposed to be advantageous. Other examples include patellid limpets and some trochids, but in the large majority torsion is completed before hatching, the larva emerging either as a post-torsional veliger or as a juvenile snail lacking the velum altogether. The European *Haliotis tuberculata* L. lives planktonically for no more than a few days (Crofts, 1938), after emerging from the egg membranes about 9 hours from fertilization. The first 90° of torsion starts some 18-20 hours later, after which it stays in the plankton for a little over 30 hours as a non-feeding post-torsional veliger, before starting to sink down to the bottom. The second 90° phase of torsion usually does not begin until the veliger has ceased to be planktonic, and it is not completed for at least a week. The veliger cannot crawl properly until torsion is fully completed, but it is still able to swim until the velum is eventually resorbed some 10 days after fertilization, after which the metamorphosed snail lives for many years crawling about on the bottom of the sea.

Pennington & Chia (1985) used a different species of *Haliotis*, for which the same times do not seem to have applied, since at 8-10°C they cultured the pre-torsional veligers for about 48 hours, as compared with 120 hours for the veligers after torsion. So that alone might have accounted for the net predation by crab megalopas having been twice as much after torsion as before. Indeed, the observation that for most

of the other predators tested torsion appeared to have no significant effect could be taken as evidence that torsion *did* provide some protection, if net predation was related to the length of time exposed. But the effect was a small one, and hardly enough to argue convincingly in favour of Garstang.

Although *Haliotis* larvae are planktonic for no more than a few days as compared with years of benthic life, so that differential selection by planktonic predators before and after torsion must be relatively unimportant, many other marine prosobranchs do live in the plankton for weeks or even months before descending to the bottom. Probably all of these will have completed torsion before hatching, and many of them have a large ciliated velum, often extended by long pre-oral lobes on either side of the head and used for planktotrophic feeding as well as for locomotion. The head and velum of many of these can certainly be withdrawn in to the mouth of the shell, which must surely provide protection against predators, as envisaged by Garstang. It is true that Thompson (1967) has questioned the validity of Garstang's assumption that the head of a veliger would be more vulnerable than the posterior end of the foot, having observed that attacks by small carnivores on any part of the cephalopodal mass, and not only on the head, are invariably lethal to veligers of the opisthobranch *Aplysia*. But there are so many other creatures, for example tubicolous polychaetes, bryozoans, calyptoblast hydrozoans, etc., which do withdraw their heads and feeding apparatus in to shells or tubes when danger threatens that it seems not unreasonable to suppose that at least some gastropod veligers should gain an advantage from the same habit. Thompson's other point, that the veliger's head is withdrawn in to the shell rather than the mantle cavity, the mantle itself often being retracted from the shell aperture, does not really affect the argument since the shell, which is secreted by the mantle, opens forwards only after torsion, to allow the head to go in first as required by Garstang's hypothesis.

Most prosobranchs with planktotrophic larvae do not hatch until after torsion has been completed, so, if this had been evolved through selection against larvae which had not undergone torsion, it must have operated in some ancestral form which did have a free-living pre-torsional larva. Garstang saw torsion as having been advantageous specifically for the veliger, and not necessarily for the fully metamorphosed adult; but if it had resulted from a single mutation in a pre-torsional larva, as he

supposed, what is important is that this should have increased the *lifetime* fitness of the individual in which it occurred, which would be so even if it had benefitted only the later post-torsional veliger, or indeed the adult snail. And in fact torsion could not only be advantageous to planktotrophic veligers in allowing them to withdraw the velum in to the mantle cavity for protection, but also to the benthic adult retreating head first in to its shell.

Several other explanations besides Garstang's have been suggested to account for the evolutionary origin of gastropod torsion, mostly based upon its presumed advantages in the adult snail rather than for the veliger larva, and these are well summarized in a review by Lever (1979). The first was that of Lang (1900), who supposed that the ancestral benthic gastropod had been bilaterally symmetrical, with a posteriorly opening mantle cavity protected by a conical shell which covered also the dorsal visceral mass. As this elongated it became unbalanced and tended to flop over and, since there are serious disadvantages for it having done so either directly forwards or backwards, the best solution was for it to point out sideways asymmetrically at right angles to the main body axis, leading to the first 90° of torsion. The long conical shell will later have become coiled, making it more compact and manageable, which will eventually have produced the full 180° of torsion with the mantle cavity opening directly forwards. Naef (1911), on the other hand, thought that shell coiling may have preceded torsion, in a bilaterally symmetrical planktonic form with a dorsal exogastric shell, similar to *Nautilus*, which later adopted a benthic way of life for which an exogastric shell is unsuitable so that it tended to flop over sideways resulting in asymmetry, and ultimately in torsion. More recently Ghiselin (1966) and Underwood (1972) have emphasized the significance of torsion as an adaptation for crawling on the bottom, in balancing the coiled visceral hump by bringing it over the mid-line of the body, so that the shell could be dragged along with the spire pointing backwards, and more or less streamlined. This was thought to have happened at an early stage, when the larva was settling down to benthic life, although having a balanced shell would be equally advantageous to the adult. And Morton (1958) pointed out that a forwardly opening shell has other advantages besides possibly providing protection for the head, in facilitating respiration and the disposal of waste products, for example. However Lever himself, believing that torsion must have been preceded by some

sort of asymmetry, which he thought might have been evolved as an adaptation to the hydrodynamic forces to which the early snails were exposed in their life on wave-beaten shores, was inclined to regard torsion as no more than an incidental consequence of this asymmetry, which may initially have had no specific function at all.

This is all very well, but although some of these explanations are consistent with the existence of the full 180° torsion characteristic of prosobranchs and pulmonates, none of them would seem positively to require it: after all, many opisthobranchs crawling about on the sea bottom must be faced with much the same problems as are prosobranchs, and yet they get on well enough with a greater or lesser degree of secondary detorsion. The merit of Garstang's hypothesis, of a single mutation producing an asymmetry in the development of the retractor muscles, is that it shows how torsion could have been achieved early on in development in one step, which would have been of immediate advantage in enabling the veliger to protect its head by withdrawing it first in to the mantle cavity, for which complete torsion is necessary. Whether or not it really happened like this in evolution, it certainly does so in the development of many living prosobranchs, and forms showing less than complete torsion result from secondary detorsion and cannot therefore be regarded as representing possible intermediate stages in the evolution of full torsion.

It is interesting to see that cephalopods also have the mantle cavity opening forwards, and with it the shell in nautiloids and ammonites in to which the head and tentacles could be fully retracted (though not in to the mantle cavity itself), the shell mouth being closed by an operculum or aptychus. But this is brought about by symmetrical ventral folding of the body and, although there is no embryological evidence as to how this could have happened, one can see how intermediate stages of partial ventral folding, as for example in nautiloid orthocones, might have been advantageous; which would not have been so with the asymmetrical torsion in the horizontal plane characteristic of gastropods.

Garstang long ago produced a plausible hypothesis to show how this might have happened in evolution. It is of course purely speculative, and unsupported by any direct palaeontological evidence but, although it could perhaps be falsified experimentally, this would seem not to have been done by the work of Pennington & Chia discussed above, and Gar-

stang's Hypothesis may still be deserving of serious consideration as a solution to the difficult problem of the evolutionary origin of torsion in gastropods.

CONCLUSION

The hypothesis first put forward by Walter Garstang in 1929, that torsion in gastropods originated by a single gene mutation causing asymmetrical development in the two retractor muscles of the pre-torsional veliger larva, of immediate advantage to it in allowing the head to be withdrawn first in to the mantle cavity for protection, should not be regarded as having been falsified by the recent experiments of Pennington & Chia (1985), comparing the net predation rates on pre-torsional and post-torsional veligers, the results of which are in fact inconclusive. It would still seem to provide a plausible explanation for the origin of asymmetrical torsion in the horizontal plane, making it unnecessary to postulate any intermediate stages in the evolution of full torsion, the selective advantages of which would not be at all apparent.

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