

GASTROPOD PHYLOGENETIC TORSION – ARISING OF A CLASS

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ABSTRACT: In the paper the author reconsiders the problem of phylogenetic torsion, which has for more than a hundred years been a subject of interest of numerous malacologists, and is still unclear. The author briefly describes the present state of knowledge of the fossil record and ontogenetic torsion observed in the Recent gastropods. He points out that these two sources of information are still insufficient, which leaves room for speculations based on functional and comparative morphology. He discusses in detail the main questions that usually are asked when considering the phylogenetic torsion. He stresses that several data and problems, like the musculature (muscle scars), geometry of ancestor's shell, opercular profits, etc. are overestimated. He points out that the two phases of torsion must be considered separately. Finally, he presents a probable scenario of the process. The first, larval phase of torsion took place in an ancestor that fulfilled three (and not necessarily more) conditions: (a) a cyrtosomatid-type organization, (b) a benthonic and actively creeping adult, (c) a development with a free-swimming larva. These were necessary and sufficient to make the process both possible and inevitable, because of the larval problems with balance and with directional swimming, which had arisen when the foot/head development, caused by the active creeping of the adult, was so advanced that due to the growth of the ano-pedal flexure the larva became nearly semi-circular. Since any decrease in curvature would mechanically affect the mantle cavity of the veliger, the only way was to twist the visceral mass 90° in relation to the cephalopodium. Then, the second phase was simply a necessity for the settling larva to adapt itself to the benthic mode of life. After torsion was, the post-torsional gastropod proved better adapted and its range of possible adaptive radiation was much wider than that of its untorted ancestors whom it could later eliminate by competition, as the selective pressure grew.

KEY WORDS: first phase of torsion, cyrtosomatid, free swimming larva, balance problems, ano-pedal flexure, veliger

Folia Malacologica 5/1993 was originally published as No. 1462 of Scientific Bulletins of University of Mining and Metallurgy, Cracow. This digitalised version was prepared by the Association of Polish Malacologists and first published on-line on December 30th, 2016.

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Gastropod Phylogenetic Torsion - Arising of a Class

*But when the first new Veligers came home again to shore,
And settled down as Gastropods with mantle-sac afore,
The Archi-mollusc sought a cleft his shame and grief to hide,
Crunched horribly his horny teeth, gave up the ghost, and died*
Garstang, 1928

1. Introduction

Gastropoda are the class of the *Mollusca* that is most successful and rich in species and, in fact, one of the most successful classes within the whole animal kingdom. This means that the gastropod organization pattern must be very promising, opening a wide range of possible radiation. But how did it arise? The *Gastropoda*, along with their incredibly differentiated modes of life, organization patterns, habitats, and dimensions, are all characterized by only one (and no more) character: *torsion*. They can be simply defined as: *torted conchiferan Mollusca*. This seems to suggest their monophyly and, moreover, makes it possible to indicate precisely the moment they arose: when torsion occurred in their phylogeny.

Torsion is defined as the counter-clockwise rotation of the visceral mass in relation to the cephalopodium, reaching an angle of 180° (or somewhat less). After torsion the morphologically left side of the visceral mass becomes topographically right, and vice versa. Torsion influences several organ systems. The mantle cavity becomes anterior, with the ctenidia in front of the heart; the entire pallial organ complex is modified by torsion, which results in its asymmetry variously expressed in various gastropod groups: the *Archaeogastropoda*, especially, show a wide variety of organization patterns of the complex changed by torsion. Torsion has also caused streptoneury, and the U-shape of the alimentary tract, with the anus close to the head (Fig. 1).

It is believed that the *phylogenetic torsion* that occurred about 600 million years ago, in the Cambrian, had changed the untorted ancestor to the already torted but still most primitive gastropod. As a reminiscence of the process, the *ontogenetic*

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Ministry of Science
and Higher Education
Republic of Poland

This digitalised version of Folia Malacologica is funded by the Ministry of Science and Higher Education, Republic of Poland under the agreement no. 646/P-DUN/2016 allocated to the activities of disseminating science and by the courtesy of the Rector of the AGH University of Science and Technology, Cracow

torsion is observable in the development of almost all the gastropods. The majority of the Recent, adult gastropods can more or less twist their shell, including the visceral mass, in relation to the cephalopodium. This is known as the *physiologic torsion*. The above three types of torsion must be clearly demarcated in any debate on gastropod phylogenetic torsion - an arising of the class.

The literature on torsion is quite rich. From among the earliest hypotheses about its origin, mechanism and significance, the ones proposed by BOUTAN (1886, 1889), BÜTSCHLI (1887), LANG (1891, 1900), FISCHER & BOUVIER (1892), PELSENEER (1893, 1894), GROBBEN (1894), GOETTE (1896), PLATE (1896), SIMROTH (1898) and DRUMMOND (1902) can be mentioned. Some of these ideas are nearly fanciful (e.g. SIMROTH 1898), some others are based on purely biomechanical assumptions, and the remaining ones are strongly influenced by the Haeckelian idea of recapitulation. The latter have been fairly popular until quite recently (e.g. DeBEER 1958). One of the first complete theories (and, which is to be pointed out here, the one that still is present in numerous handbooks of zoology) is NAEF's (1911, 1913) theory: it is also under the strong influence of VERRILL's (1896) ideas of the veliger-like (Fig. 2) molluscan archetype. Also GARSTANG's (1929, 1951) idea of torsion being of decisive importance to the veliger protection/survival still impresses some malacologists (e.g. PENNINGTON & CHIA 1985, GOODHART 1987).

From among the other papers dealing with torsion there can be listed the ones by SMITH (1935), CROFTS (1937, 1955), EALES (1950), DODD (1957), MORTON (1958), CARLISLE (1962), FRETTER & GRAHAM (1962), GHISELIN (1966), BATTEN, ROLLINS & GOULD (1967), THOMPSON (1967), FRETTER (1969), STASEK (1972), UNDERWOOD (1972), GUTMANN (1974), SOLEM (1974), PURCHON (1977), LEVER (1979), VERDONK (1979), PEEL (1980), SALVINI-PLAWEN (1980, 1981), GIUSTI (1981), RUNNEGAR (1981), BANDEL (1982), STANLEY (1982), GRAHAM (1985), EDLINGER (1986, 1988a, b), VOLTZOW (1987), and HASZPRUNAR (1988a, b).

All the papers, although numerous, do not sufficiently explain all the basic problems connected with phylogenetic torsion. Hence, the aim of the present paper is to discuss the problem, and to propose some new view.

To begin with, I feel obliged to declare that personally I prefer the theory of punctuated equilibria (GOULD & ELDREDGE 1977) to the one assuming only a gradual, slow process of additive minor changes as the main mechanism of the macroevolutionary process. However, in the present paper I rather exploit the gradual-change-model as yet more widely accepted. On the other hand, the model presented below is not much in disagreement with GOULD's and ELDREDGE's ideas.

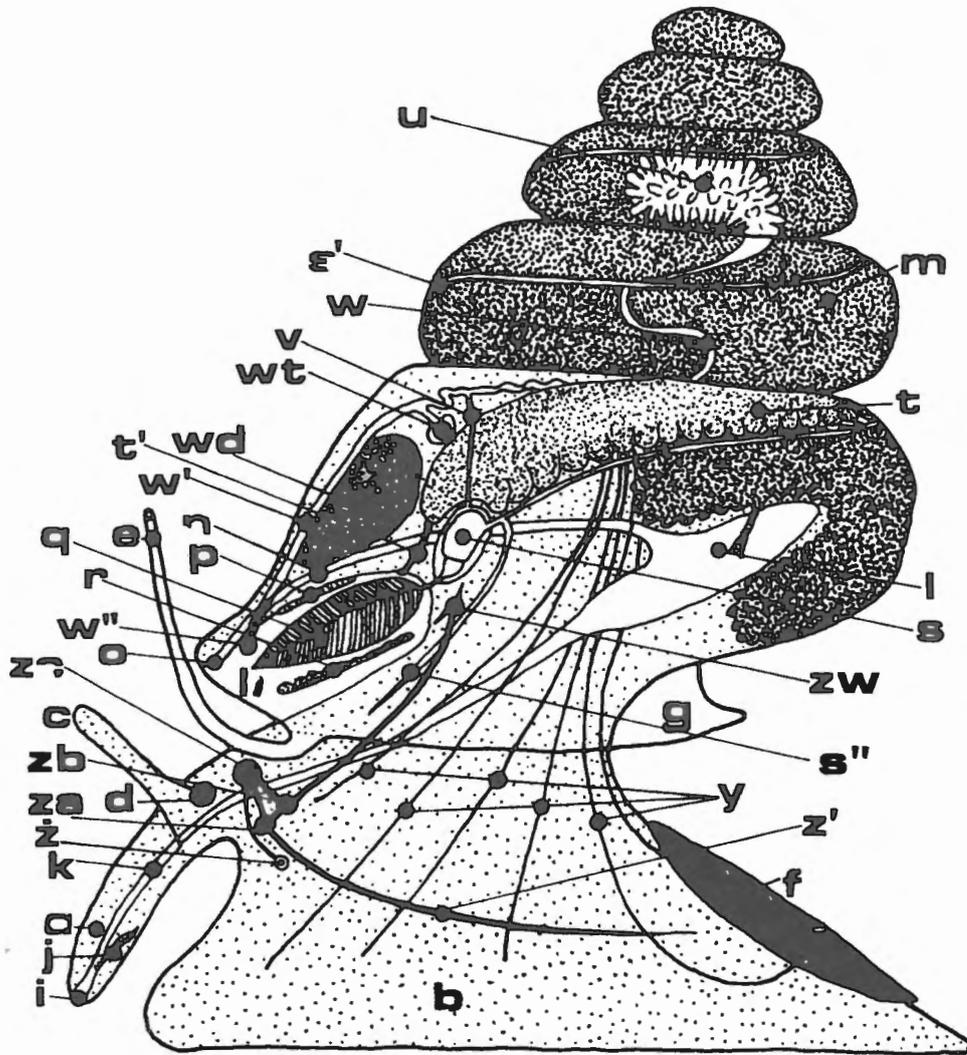


Fig. 1. Generalized organization of Recent monocardian female gastropod (after FALNIOWSKI 1989, modified from GÖTTING 1974): a - proboscis (snout), b - foot, c - cephalic tentacle, d - eye, e - siphon, f - operculum, g - mantle, h - mantle cavity, i - mouth, j - radula, k - oesophagus, l - stomach, m - hepato-pancreas gland (digestive gland), n - rectum, o - anus, p - hypobranchial gland, q - ctenidium (gill), r - osphradium, s - heart, s' - aorta posterior, s'' - aorta anterior, t - kidney, t' - duct of kidney, u - ovary, v - gono-pericardial duct, w - oviduct, w' - pallial section of oviduct, w'' - female gonoporus, wt - bursa copulatrix, wd - accessory glands of pallial section of oviduct, y - retractor muscles connecting cephalopodium with columella of shell, za - pedal ganglion, zb - pleural ganglion, zc - cerebral ganglion, zw - visceral ganglion (all are ganglia of central nervous system), z' - pedal nerve, z - statocyste

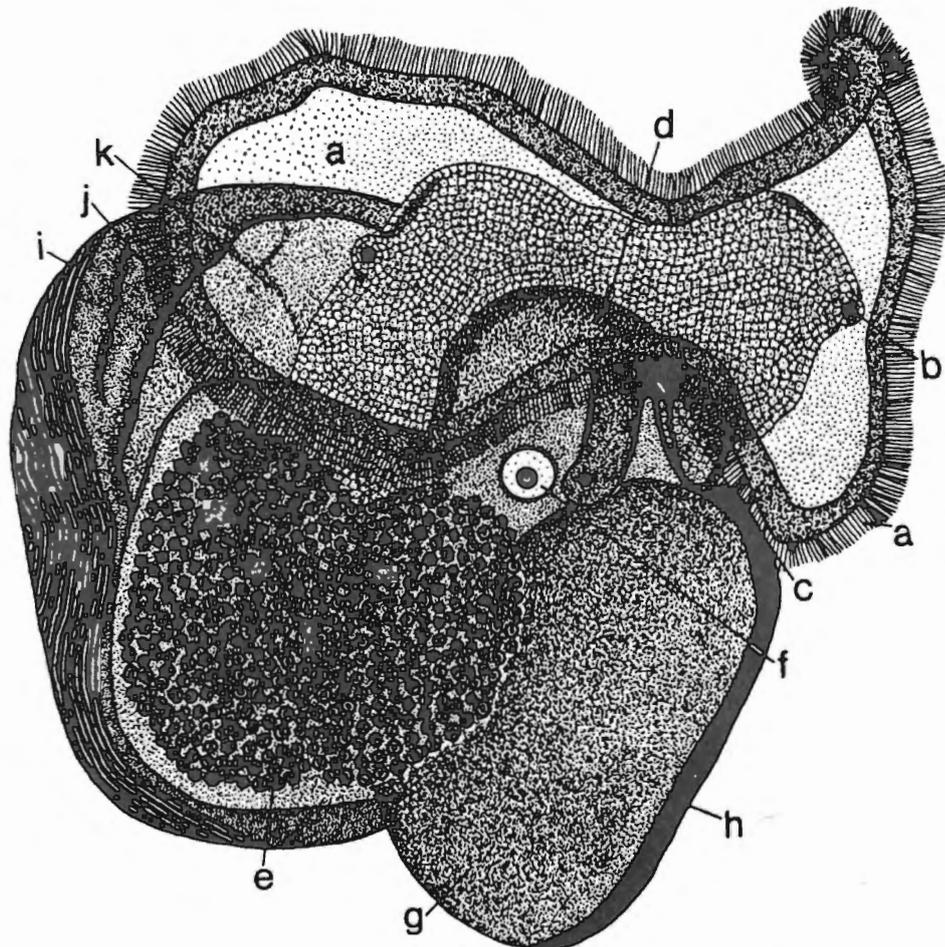


Fig. 2. Posttorsional, intracapsular veliger of *Theodoxus fluviatilis* (LINNAEUS) (after FALNIOWSKI 1989, modified from WESSENBERG-LUND 1939, after CLAPAREDE 1857): a - velum, a' - cilia of velum, b - eye, c - mouth, d - oesophagus, e - digestive gland and stomach, f - statocyste, g - foot, h - operculum, i - shell, j - mantle edge, k - mantle cavity

2. Main questions

(1) *Unusual, incredible mutation (hopefully such a positive one)?*

Several authors (e.g. YONGE 1947, EALES 1950, CROFTS 1955, DeBEER 1958, COX 1960, FRETTER & GRAHAM 1962, PURCHON 1977) point out that torsion was such an unusual, complex, and just incredible phenomenon that the only way, in which it would arise was by a similarly unusual and incredible mutation, which was so unusual as to occur no more than once in phylogeny.

It has to be stressed herein, that the above question is a methodological one. We have to realize that we are not able to ask: *how did it happen?* - but only: *what was the most probable way of the process?* And such a mutation - although rather improbable - cannot be excluded. But an interpretation of a poorly understandable phenomenon by an occurrence of an unusual and hardly probable mutation is nothing more than an interpretation based on the *incognito per incognito* rule. Therefore, as a one that does not contribute in our understanding of the process, this mode of interpretation has to be rejected when considering any phylogenetic problem.

At this point, some more general, methodological notes seem to be unavoidable. As pointed out by RUNNEGAR & POJETA (1985), our knowledge of the Cambrian molluscs, pre-gastropods and early gastropods, is recently in rapid progress, and every theory dealing with phylogenetic torsion has to be compatible with the known facts. On the other hand, as it will be proved below, the interpretation of the fossil record is usually problematic and we rather cannot expect to obtain a complete series of intermediate forms to be interpreted with no doubts - especially as to their (crucial, in fact) soft parts - and, at last, to solve all the problems hopefully. Therefore, there still are both place and need for speculations.

On the other hand, the speculations should follow some rules of reasoning and consider all the known facts. That this is not always the case, it has been demonstrated by GHISELIN (1966) in his critique of various theories of phylogenetic torsion. In his paper, however, it is rather difficult to find too much positive suggestions concerning the problem. He orthodoxically follows the so-called synthetic evolutionism, as represented by MAYR (e.g. 1963). In my opinion, the latter weakens rather than strengthens his argumentation. Finally, he gives an appendix on logic, in which he lists the two predictions that are necessary for an evolutionary change: (1) ability to change, (2) an efficient cause for change. This needs comments. The ability to change is an obvious necessity, although we need not always exactly know all the real potential abilities of an organism. But to assume an efficient cause for change is nothing more than to follow rationalism and determinism in their nineteenth century form. As long as a change is possible it can take place. And, as long as it is not connected with a decrease in the selective value of an organism the effects of the change will not be eliminated. In general: everything possible is possible, but certainly not: only everything supported enough is possible. And, last but not least, we cannot eliminate some elements of the probabilistic/statistical mode of reasoning when considering any evolutionary process.

(2) *Ontogenetic torsion as the key to phylogenetic torsion?*

As mentioned above, ontogenetic torsion (Fig. 3) is observable in the development of all the *Gastropoda* (FRETTER & GRAHAM 1962). However, it is more or less modified, especially in the *Opisthobranchia* and *Pulmonata*

(e.g. THOMPSON 1958, 1962, BRACE 1977), which is due to a various degree of detorsion, yolk-rich development (e.g. CONKLIN 1897, DRUMMOND 1902, DELSMAN 1914, FRANC 1940, CREEK 1951), etc. The process of torsion may stop later - even at 270° (in *Neomphalus*: FRETTER, GRAHAM & McLEAN 1981, McLEAN 1981), which seems to be connected with adaptations to the special mode of filter-feeding life - or much earlier, after not much more than the first 90° (*Nudibranchia*: THOMPSON 1962). The process is best observable in the so-called *Archaeogastropoda*, which are generally believed to be the most primitive gastropods. Ontogenetic torsion was a subject of interest of numerous malacologists (e.g. BOUTAN 1886, PATTEN 1886, CONKLIN 1897, DRUMMOND 1902, ROBERT 1902, DELSMAN 1914, SMITH 1935, CROFTS 1937, 1955, FRANC 1940, THORSON 1946, CREEK 1951, DODD 1957, THOMPSON 1958, 1962, CARLISLE 1962, FRETTER & GRAHAM 1962, KESSEL 1964, FRETTER 1969, UNDERWOOD 1972, MANLY 1976, VERDONK 1977, BANDEL 1982, VOLTZOW 1987, HOLYOAK 1988a, b). In fact, the ontogenetic torsion, unlike the phylogenetic one, can be observed and must to some extent reflect certain patterns of the phylogenetic process (GOULD 1977). But the question is: to what extent?

To the present knowledge (e.g. BANDEL 1982) the gastropod/cephalopod ancestor was characterized by a direct development. Then, an arising of a free-swimming planktonic larva made the torsion possible (necessary? - see below). However, it has to be pointed out that CHAFFEE & LINDBERG (1986) questioned the possibility of occurrence of a pelagic (planktonic) larva in the Early Cambrian molluscs, because of their small body size: too little space within the shell for the gonade to produce the number of eggs that would be big enough for the planktonic development. To me, it is not convincing. Firstly, it would not be a problem, when considering the gastropod origin, if YOCHELSON's (1976) opinion on the Late Cambrian origin of the *Gastropoda* were correct. Secondly, all CHAFFEE & LINDBERG's (1986) assumptions are based on Recent observations: not everything that is the rule in the Recent must have been the rule in the Cambrian. Thirdly, if a larva is not free-swimming and feeding it must be lecithotrophic (at last, it must eat something); at the same time the lecithotrophic larva must be placed in an egg that must be much bigger than in the planktotrophic case; this means that the lecithotrophic eggs have to be much fewer than in the case of the free-swimming larva; since small dimensions are hardly a prerequisite for ovoviviparity, all the problems with survival caused by predators and pointed out by CHAFFEE & LINDBERG are not less serious for a few lecithotrophic eggs than for a few hundreds of planktonic larvae (even not considering the far higher possibilities of expansion in the latter case). In fact, there are no Recent *Archaeogastropoda* having free and feeding (planktotrophic) larvae, therefore a non-feeding larva seems an ancient character in the *Gastropoda*.

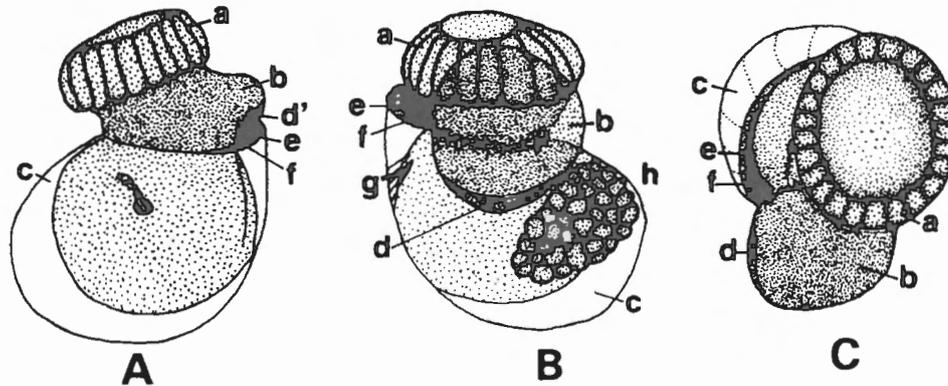


Fig. 3. Larval torsion in *Gibbula cineraria* (LINNAEUS) (after UNDERWOOD 1972): A - pretorsional veliger, B and C - veliger after first 90° of torsion; a - velum (locomotory cilia omitted), b - foot, c - shell, d - operculum, d' - opercular rudiment, e - mantle cavity, f - mantle fold, g - site of attachment of larval retractor muscle, h - digestive gland

However, in archaeogastropods there are many species with a non-feeding but free-swimming larva, and in one group of closely related archaeogastropod species some representatives may develop passing through a free-swimming larva stage while some others may develop directly [HADFIELD & STRATHMAN (1990): they point out that it is impossible to distinguish the protoconchs of snails with a free-swimming larva from those of snails with an intracapsular development, questioning the importance of JABLONSKI's (1986) theories of the evolutionary significance of planktotrophic versus nonplanktotrophic development]. As long as we are looking for some reflection of phylogeny in the ontogenetic patterns we observe, and as long as we could extrapolate from the Recent archaeogastropods to the Cambrian primitive gastropods, some other peculiarity seems noteworthy. In archaeogastropods with a free-swimming larva, the larva hatches very early, at its trochofore-like stage, to escape from the bottom to the water. This early escape may have been due to the mortality rate being much higher on the bottom at that time. Probably the benthic predators were abundant much earlier than the pelagic ones or filtrators.

Ontogenetic torsion in the *Archaeogastropoda* is not a continuous process, but consists of two phases: if it occurs after hatching, which is known in not many species (e.g. *Haliotis*), phase I (the first 90° rotation of the visceral mass) will go on in the planktonic larva (Fig. 3). Then the process stops, and phase II will start not earlier than after the larva has settled on the bottom. This interval, combined with some characters of the phase-I-torted larva that seem profitable to the planktonic life (see below), indicate that phylogenetic torsion must have consisted of two phases, too. Consequently, the backgrounds of those two phases must be

different. Several theories based solely on the potential profit of only one stage (larva or adult) - many of them based, moreover, on improbable morphological/palaeontological assumptions - have therefore to be rejected (e.g. NAEF 1911, 1913, GARSTANG 1929, 1951, EDLINGER 1986, 1988a and b).

On the other hand, as in any animal group, the "recapitulation rule" has to be used carefully. Firstly, recent ontogenetic stages may provide *some* information on the *ontogenetic* stages of the ancestors, but not on the adult ancestors. Secondly, larval development is often (or, more precisely: usually) more or less modified. Thirdly, the recent free-swimming pre-torsional veliger is a very short, and very early stage, and then its simple structure provides very little information on the ancestor. Even the mantle cavity usually appears later in the development; also the visceral loop of the nervous system, although most strikingly affected by torsion, is formed not earlier than after phase I of torsion has been completed (HASZPRUNAR 1988a). It has to be added that such a situation is not surprising - similarly, a trochophore-type larva, although generally regarded as the one that is basic for the *Mollusca*, and widely acknowledged as a basis for phylogenetic speculations, has been found in only a few archaeogastropod species and, moreover, it is not exactly of the annelid trochophore type, but is only a modified (derived?) *trochophore-like-larva*.

Therefore, such experiments as the one of PENNINGTON & CHIA (1985) testing an adaptation of a pretorsional and posttorsional larva against predation, even if acceptable methodologically (as shown by GOODHART 1987, the experiment of PENNINGTON & CHIA is not acceptable from this point of view) seem simply pointless. We have to realize that both pretorsional and posttorsional larvae are sufficiently well adapted, since both have existed for millions years. And the only way to obtain information on phylogenetic torsion by studying the ontogenetic process is not to compare the recent, living pretorsional veliger with the posttorsional one, but to try to realize what would happen with the pretorsional veliger if torsion *did not* occur.

(3) *The benefit of the adult gastropod as the reason for torsion?*

One of the first attempts to explain phylogenetic torsion as something that had been profitable to the adult animal was the one of LANG (1891, 1900). His hypothetical "pra-snail", having an enormously high, cone-like, slowly narrowing tubular shell, was hardly imaginable as one that had been able either to appear or to survive. Although LANG pointed out that in his drawings the shell was much longer than he had assumed, which was just to better demonstrate the problems, any conical tube-shaped shell high enough to have caused those problems with locomotion/respiration was hardly imaginable in a hypothetical "pra-snail". And, last but not least, any shell of this shape could occur only in a sedentary animal or a shell-dragger (LINSLEY 1977, 1978), in which case it

would be kept on one side of the cephalopodium, and either the posterior or the anterior position of the mantle cavity of the animal would be equally functional. Anyway, it was the first complete theory, in which attention was paid to the mechanical antagonism between the cephalopodium and the visceral mass covered with the shell as the possible cause of the phylogenetic torsion.

Several authors (e.g. NAEF 1911, 1913, MORTON 1958, FRETTER & GRAHAM 1962, GHISELIN 1966, UNDERWOOD 1972, LEVER 1979) discussed the advantage the adult gastropod may gain from torsion. Indeed, a torted gastropod seems to be better adapted to the benthic life (nothing seems to indicate any pelagic gastropod ancestor, as suggested by NAEF 1911, 1913), and - which is perhaps more important - presents a far wider range of possible radiation than an untorted gastropod-like creature.

The latter, with its mantle cavity located posteriorly, would have to cope with serious problems with the ventilation of the mantle cavity. In a creeping animal water movements not only are of no help in cleaning the cavity, but they even bring substrate particles into it. It is SOLEM (1974) who stresses the importance of the problems of circulation within the mantle cavity as the reason for torsion. Moreover, the osphradium must work insufficiently as a sense organ, since anything in front of the animal has to be felt later than in the case of the anteriorly situated mantle cavity of a gastropod. This is pointed out by MORTON (1958) who also explains the detorsion observed in opisthobranchs by the diminishing significance of the mantle cavity functions in those gastropods. Finally, an untorted animal would withdraw itself into the shell with the foot first and the head last, and thus the functioning of the operculum would be problematic (STANLEY 1982).

All the above disadvantages were probably as serious as to have eliminated (or strongly restricted) such untorted forms, when competing against the "true" gastropods, yet the untorted animal might have been able to live, if its shell had been limpet-like (or even coiled, but with an extreme dominance of the body whorl: Fig. 4). This meant that a possible morphospace range for such forms was markedly restricted, which resulted in very limited radiation possibilities. A survival of an untorted, benthic animal with a coiled shell - either planispiral or turbospiral - is much unlikely. Such a form when creeping, would have to plough the substrate with its mouth, the mantle cavity getting filled with substrate particles, while the spire would push the head, pressing it against the substrate. On the other hand, the above mechanical problems might have been not so serious since the earliest gastropods (and, therefore, their ancestors) were most probably very small forms (1...3 mm: e.g. RUNNEGAR & JELL 1976, 1980, YOCHELSON 1978, RUNNEGAR & POJETA 1985, CHAFFEE & LINDBERG 1986, HASZPRUNAR 1988a, b).

Anyway, it would have been unjustified to create such a hardly survivable benthic creature, to be "saved" later from extinction by the beneficial torsion, the latter being probable as much as the existence of such a poor monster. It seems

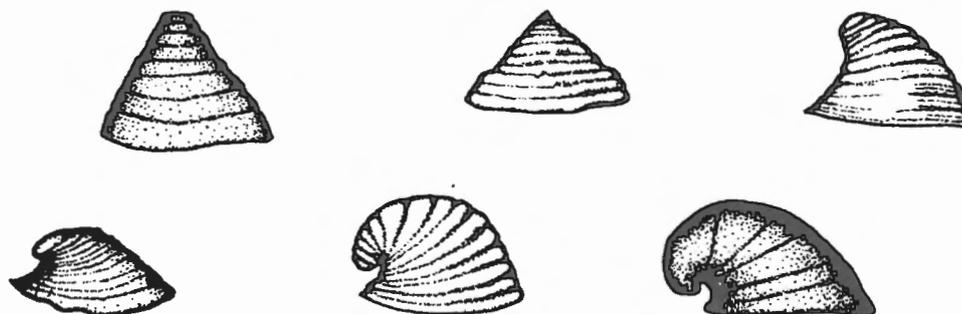


Fig. 4. Early Cambrian conchiferan (monoplacophoran or early gastropod) shell shape variety (after CHAFFEE & LINDBERG 1986)

highly improbable even to enthusiasts of the "hopeful monsters" concept. Our understanding of evolutionary processes suggests another picture: the untorted gastropod ancestor was actually worse adapted to the benthic life than the torted gastropods and, moreover, its radiation range was strongly restricted, to limpet/nearly limpet-like form having small dimensions. Torsion became a progressive preadaptation of supreme importance, enabling the animal to be better adapted for the benthic life and facilitating the creation of as wide a radiation range as we observe in the Recent gastropods. It has to be pointed out, however, that during the Late Precambrian and Early Cambrian the selective pressure was low (e.g. COWIE 1967, but CHAFFEE & LINDBERG 1986 disagree with this viewpoint) and torted gastropods occurred commonly with untorted tryblidiaceans (monoplacophorans).

LEVER's (1977) arguments, based on BERKNER & MARSHALL's (1965) opinion that the atmosphere was poor in oxygen at that time, which made any animal life at depths below about 10 m impossible and exposed molluscs to a strong wave action, which consequently favoured the conical shells of the torted animals, seem not convincing. Especially in the light of the palaeontological record, which showed a rather wide variety of shell forms of either torted or untorted gastropod-like molluscs of that period (Figs 4 - 7) the hypothesis cannot be maintained. But later, when the selective pressure had grown the torted animals turned out to be fitter, in general. This clearly explains the extinction of the untorted pre-gastropods as a result of a strong competition, and a rapid spread of the torted gastropods, but tells us nothing about the possible mechanism of torsion.

(4) *Advantages given to the larva as the reason for torsion?*

Numerous authors point out the advantages that torsion have given to the veliger larva. Usually the properly functioning larval operculum as a result of the process is stressed (e.g. BANDEL 1982, HASZPRUNAR 1988a and b), but the opercular question will be discussed below in detail. GARSTANG (1929, 1951)

presented a theory that torsion was a larval mutation enabling the veliger to withdraw itself totally into its shell, the velum and head first, so it was directly as profitable to the larva as to have an *immediate* selective value. Later, his theory strongly influenced numerous malacologists, although for a long time nobody tried to study the actual differences in retraction capabilities between the pretorsional veligers and the posttorsional ones. The theory seems convincing, but it is not in agreement with the facts. As could be expected, the head would be withdrawn into the mantle cavity only if the latter were attached to the shell mouth edge, which obviously is not the case in all the gastropods.

It was THOMPSON (1967) who demonstrated that the head was always retracted into the shell cavity and the mantle cavity was not simply folded during the retraction of the animal into the shell. As is shown by BANDEL (1982), some pretorsional veligers can withdraw into their shells totally. On the contrary, UNDERWOOD (1972) described the veliger of *Gibbula cineraria* (LINNAEUS) (Fig. 3) completely unable to withdraw itself, as well before as after torsion. Also the importance of head versus foot protection seems questionable, since THOMPSON (1967) demonstrated no histological difference between the two regions of the veliger, along with the letality of any injury to either the foot or the head of the veliger larva attacked by decapod larvae, ciliates, coelenterates and chaetognathes. This also weakens STANLEY's (1976) arguments. And once more we have to consider COWIE's (1967) data on the low selective pressure and predators probably lacking in the Pre-Cambrian and Early Cambrian period. Therefore, it seems obvious that the adaptive value of the operculum as the reason for phylogenetic torsion is overestimated. GHISELIN (1966), UNDERWOOD (1972), SALVINI-PLAWEN (1980, 1981) and HASZPRUNAR (1988a and b) point out that torsion is possibly of much importance to the larva to cope with problems connected with balance and directional swimming.

The latter seems crucial for the understanding of the larval torsion process. The gastropod veliger, as all the mollusc larvae, shows the ano-pedal flexure characteristic of this phylum. This results in the more or less arcuate habitus of the molluscan larvae. As long as the mantle cavity and the shell are both peripedal, the flexure is slightly marked. But if the shell, like in all the *Cyrtosoma* (including *Gastropoda* and *Cephalopoda*: see below) is restricted to the visceral region only, the flexure will become more and more pronounced. As long as both the head and foot are relatively small, the problem is not serious. The development of the cephalopodium, connected with the progressive evolution of benthic forms, caused this part to gain proportionally bigger dimensions earlier in the ontogeny. So, we can imagine some level of cephalopodium evolutionary development, some point, when the larval ano-pedal flexure became too strong. This has been coupled with the asymmetry that is observed in the *Cyrtosoma* from the very beginning of the embryonic development (e.g. RAVEN 1958, VERDONK 1977)

and always precedes the moment of ontogenetic torsion. The direction of this asymmetry determines the direction of rotation at torsion (RAVEN 1958).

It must be pointed out here that the problem does not concern cephalopods, as their development is direct, with no pelagic larva. But within the "pre-gastropod line" there must have been a stage in the cephalopodium development, at which the larva became as much bent (just semi-circle-like) as to be simply unable to control its balance, and which was even more problematic, any directional swimming. Any type of further growth that increased the curvature, was simply lethal, while any growth decreasing curvature had to affect the mantle cavity and, therefore, several physiologic processes. The 90° rotation of the visceral mass in relation to the cephalopodium solved the problem - further growth, as not increasing the flexure, did not affect the mantle cavity. Therefore, to the larva, torsion was not only profitable; it was just absolutely necessary to its survival.

(5) *Time and ancestor*

The origin and the early stages of evolution of the *Mollusca* are purely hypothetical. All the subphyla and some classes were already present at the very beginning of the Phanerozoic. It is generally (although not always) believed, that the most primitive, stem group of molluscs are the *Aculifera*, with the more primitive *Aplacophora* and the more advanced *Polyplacophora* (e.g. WINGSTRAND 1985, HASZPRUNAR 1988a, SCHELTEMA 1988).

The representatives of the subphylum *Conchifera*, apparently more advanced and including nearly all the Recent *Mollusca*, are known also from the Precambrian. WINGSTRAND (1985) listed 11 synapomorphies of the conchiferans, the monophyly of which seemed undoubtedly demonstrated. The *Tryblidiida* (see the note below and the note on the Cambrian *Monoplacophora*) known from the Precambrian to the Recent, are widely accepted as a basic group for all the other conchiferan classes.

In the Precambrian (or the upper Cambrian) two classes evolved from the *Conchifera*: the *Diasoma* (= *Ancyropoda* = *Loboconcha*), which then branched themselves into the classes *Scaphopoda*, *Bivalvia* and fossil *Rostroconcha*, and the *Cyrtosoma* (= *Visceroconcha* = *Rhacopoda*). The latter branched then into the *Gastropoda* and *Cephalopoda* classes.

The *Cyrtosoma* share a couple of synapomorphies sufficiently indicating the separateness and monophyly of the group, out of which the mantle and shell restriction to the visceral part of the body is most striking, and most important if the phylogenetic torsion process is considered. The originally peripodal mantle cavity - as known, for example, in chitons, bivalves or tryblidiids - is here restricted to the visceral part only, leaving the head and foot free. This is most probably a result of adaptation to the active, mobile, benthic mode of life.

Such a cyrtosomatid ancestor, probably very small (1...3 mm) and having a direct development, in the Cambrian branched into the *Cephalopoda* (with a

chambered shell, untorted, and still having a direct development) and *Gastropoda* (torted cyrtosomatids). Anyway, undoubtedly torted gastropods are known already from the Cambrian, about 600 million years ago. On the other hand, YOCHELSON (1978) considers both the *Helcionellacea* (Figs 6A, B, and 7B) and *Pelagiellacea* (Fig. 7A) as untorted non-gastropod representatives of extinct classes and shifts the beginning of the *Gastropoda* from the Early Cambrian to the Late Cambrian, about 500 million years ago. To the best of my knowledge, the problem will remain open, unless new fossil records and new interpretations appear.

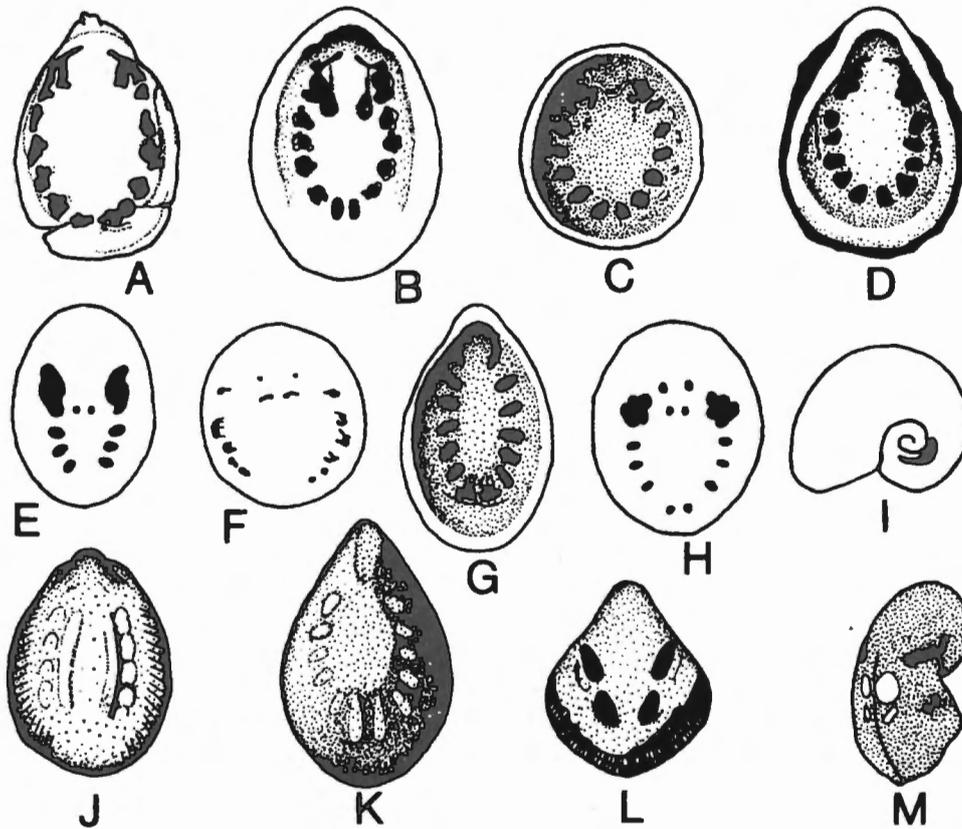


Fig. 5. Shell outlines and muscle scars in some tryblidiids and related (possibly gastropod) forms (after WINGSTRAND 1985: A - H - from inside, I - M - from outside of the shell): A - *Pilina cheyennica* PEEL, B - *Pilina unguis* LINDSTROM, C - *Archaeophiala*, D - *Tryblidium*, E - *Kirengella*, F - *Scenella*, G - *Drahomira*, H - *Lenaella*, I - *Bellerophon*, J - *Bipulvina*, K - *Propilina*, L - *Cyrtoneilla*, M - *Cyrtolites*

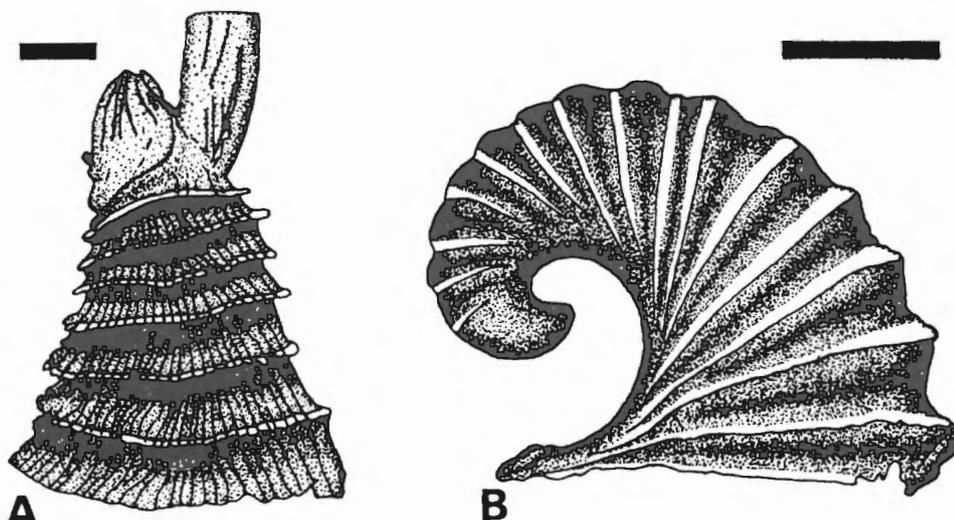


Fig. 6. Early Middle Cambrian helcionellacean monoplacophorans (silica replicas): A - *Yochelcionella ostentata* RUNNEGAR et JELL, bar equals 1 mm; B - *Latouchella accordionata* RUNNEGAR et JELL, bar equals 200 μ m (drawn after photographs in RUNNEGAR & POJETA 1985)

(5') *A note on the Tryblidiida*

I use the name *Tryblidiida* after WINGSTRAND 1985, SALVINI-PLAWEN 1980 and HASZPRUNAR 1988a, as "*Monoplacophora s. stricto*", to point out the narrow understanding of the rather descriptive term *Monoplacophora* as created by WENZ (1940) and followed by LEMCHE (1957). YOCHELSON (1978) pointed out serious problems with distinguishing the monoplacophorans in the fossil record and doubts as to the more than exceptional, sporadic occurrence of any coiled forms within the class. The *Monoplacophora* include numerous fossil records of variously shaped shells (Fig. 5). As demonstrated by RASETTI (1954, 1957), KNIGHT & YOCHELSON (1958) and several other authors, some of them might have been gastropods. Especially some of the coiled Palaeozoic forms were probably already torted gastropods. On the other hand, the extant tryblidiids presented some advanced characters and could hardly be assumed to be "living fossils" and interpreted as ancestral forms of the *Gastropoda*. Therefore, to consider the ecology and behaviour of the Recent *Vema*, as described by LOWENSTAM (1978), as being representative of the ones of the Palaeozoic *Monoplacophora* seems, to my understanding, pointless.

(5'') *Cambrian Monoplacophora: fossil record*

The crucial position of apparently the most primitive Early Cambrian (already Precambrian) *Tryblidiida* in the phylogeny of all the other conchiferan classes seems well demonstrated. On the other hand, the direct ancestors of gastropods

need not have been uncoiled as tryblidiids. In fact, in the light of comparative and functional anatomy, the gastropod ancestor might have been uncoiled, limpet-like. On the other hand, recently we have numerous fossil records that point to the existence of a few lineages of the Cambrian coiled *Monoplacophora*. To our understanding, they were untorted and also showed a nearly continuous, gradual change in whorl number. We can accept them as possible candidates for gastropod ancestors. Therefore, I have to describe those records briefly.

There are numerous papers (e.g. HORNY 1965a, b, RUNNEGAR & POJETA 1974, 1985, MATTHEWS & MISSARZHEVSKY 1975, POJETA & RUNNEGAR 1976, RUNNEGAR & JELL 1976, 1980, PEEL 1977, 1980, BERG-MADSEN & PEEL 1978, YÜ WEN 1979, JIANG 1980, STINCHCOMB 1980, DZIK 1981, RUNNEGAR 1981, 1982, 1983,) dealing with the problem. All but one (*Scaphopoda*), the conchiferan classes had evolved by the end of the Cambrian, but obviously the early evolution and differentiation of the *Mollusca* must have taken place already in the Precambrian, since in the oldest Cambrian they came into sight abruptly (e.g. RUNNEGAR & POJETA 1985). We know over 450 Cambrian species described, although some of them must be synonyms (RUNNEGAR & POJETA 1985). In fact, the first mass radiation of the *Mollusca* took place in the Late Cambrian/Early Ordovician (RUNNEGAR 1983), but for the first gastropods the Early Cambrian must have been crucial.

The majority of the Cambrian *Mollusca* remained small (e.g. RUNNEGAR & JELL 1976, RUNNEGAR 1982, 1983, RUNNEGAR & POJETA 1985) - about one millimetre, rarely up to 2...3 mm in diameter. Also their generic and specific diversity remained low and nearly constant through the Cambrian. RUNNEGAR (1982; also RUNNEGAR & POJETA 1985) connects the small dimensions of those early molluscs with the low oxygen content in the atmosphere at that

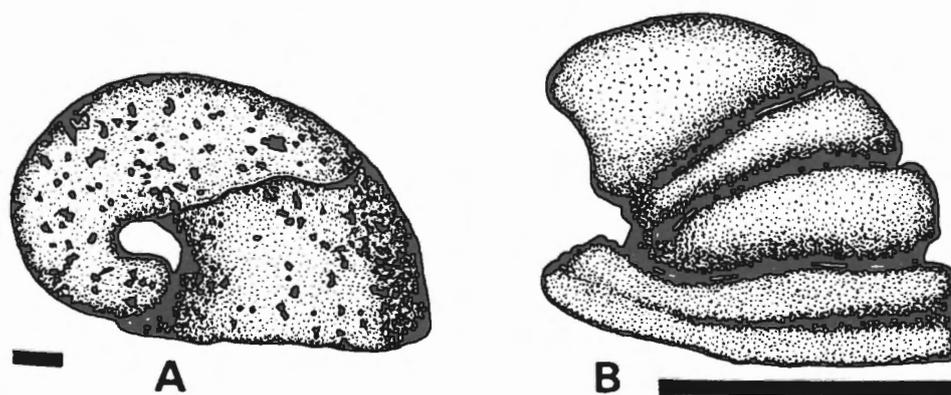


Fig. 7. Early Cambrian monoplacophorans (phosphatic internal molds): A - pelagiellid *Pelagiella* cf. *subangulata* (TATE), South Australia, left side, bar equals 100 μ m; B - undescribed helcionellid from Parara Limestone, Yorke Peninsula, Australia, bar equals 1 mm (drawn after photographs in RUNNEGAR & POJETA 1985)

time. However, this seems not quite convincing: first, in the Cambrian all the oxygen was produced by sea cyanophytes and other primitive algae; therefore we can conclude that all the oxygen in the atmosphere was the one released from saturated (or nearly saturated) sea water, so the oxygenation of the shallow littoral water might have been similar to that of the Recent seas. Secondly, assuming either the nemertean or annelid grade of organization of the molluscan ancestor, we can expect the existence of vasculatory/respiratory organs. Therefore, the small dimensions of the ancestor were probably not connected with the possible low oxygenation of the water.

In the earliest Cambrian there occurred limpet-shaped tryblidiids (e.g. RUNNEGAR & POJETA 1974, 1985, POJETA & RUNNEGAR 1976, YÜ 1979) similar to the extant *Neopilina* and *Vema* (Fig. 5). BATTEN, ROLLINS & GOULD (1967) pointed out the existence of Cambrian *Cyrtolites*-like cyclomyans (HORNY 1965a, b, ROLLINS 1969), many of which had been symmetrically coiled, had had multiple muscle scars symmetrically arranged, and some of them had also had an anal sinus; the general tendency of the lateral muscles towards reduction and fusion was observed within the group (Fig. 5). In the Cambrian there were two lineages of non-tryblidiid monoplacophorans, which had died out till the end of that period: *Cyrtonellida* (including *Helcionellacea*) and *Pelagiellida* (RUNNEGAR & POJETA 1985). The former lineage (Figs 6A, B, and 7B) included forms with curved conic shells, from smooth or wrinkled (Figs 6B and 7B) to laterally compressed or snorkel-bearing (Fig. 6A). They were bilaterally symmetrical (nearly symmetrical) and had one or two pairs of gills. Later on - in the Middle Cambrian - within the lineage planispirally coiled but still symmetrical forms developed (RUNNEGAR & JELL 1976, BERG-MADSEN & PEEL 1978), which possibly were the ancestors of the Late Cambrian/post-Cambrian *Bellerophonitida* discussed below.

The second lineage - *Pelagiellidae* (Fig. 7A) included asymmetrically coiled monoplacophorans, some of them dextrose. They still were untorted, although some of them had possibly undergone a few degrees of torsion (RUNNEGAR 1981), regulatory in character. They had one pair of shell-inserted muscles and one or two pairs of gills. However, LINSLEY & KIER (1984) include the *Pelagiellidae*, together with the strongly coiled and turriform *Onychochilidae*, into the *Paragastropoda*, a rather paraphyletic class of gastropod-resembling molluscs, whose adult problems with the posteriorly situated mantle cavity were solved not by torsion but by anisostrophy.

The above data, although showing the real range of monoplacophoran diversity, are not too much useful when the gastropod origin is concerned. The two major lineages of gastropods appear abruptly at the same time, in the earliest Cambrian strata. First of them, including *Aldanella* (Fig. 8A), a minute, *Valvata*-like shelled gastropod from the Early Cambrian strata of Siberia, Europe and eastern

North America (RUNNEGAR & POJETA 1985), can possibly be acknowledged to have been the ancestor of pleurotomariids. *Aldanella* had neither a slit nor a sinus, but these structures were unnecessary in such a small gastropod. The second lineage, including *Yuwenia* (Fig. 8B), was characterized by ultradextral shells. There was a clear gradation from its earliest representatives to the operculate Ordovician macluritaceans. The lineage ancestors could be pelagiellids or some other Early Cambrian dextrally coiled monoplacophorans. According to RUNNEGAR (1981) the transition from dextral to ultradextral coiling could have resulted in torsion. This idea, however, is not in accordance with HADFIELD & STRATHMAN's (1990) observations. Therefore, the *Gastropoda* may be diphyletic, since the two lineages evolved independently.

The latter evolution of early snails is differently interpreted by various authors (e.g. RUNNEGAR 1981, 1983, DZIK 1983, RUNNEGAR & POJETA 1985). The second, ultradextral lineage may represent the ancestors of the major lineage of one-gilled archaeogastropods (RUNNEGAR & POJETA 1985) and, possibly, of more advanced meso- and neogastropods, as well as opisthobranchs and pulmonates, the latter two also known to occur already in the Palaeozoic (e.g. KOLLMANN & YOCHELSON 1976, SOLEM & YOCHELSON 1979).

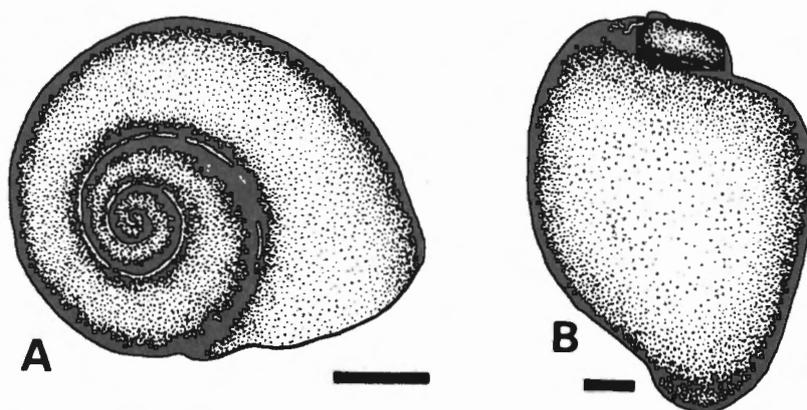


Fig. 8. Early Cambrian gastropods (internal molds): A - *Aldanella attleborensis* (SHALER et FOERSTE), bar equals 1 mm; B - ultradextral *Yuwenia bentleyi* RUNNEGAR, bar equals 100 µm (drawn after photographs in RUNNEGAR & POJETA 1985)

(6) *Opercular question: is the operculum actually a post-torsional structure?*

The appearance of the larval operculum is widely regarded as at least one of the most important (if not the most important one) advantages of torsion, which are *immediatelly* beneficial for the larva (e.g. GARSTANG 1929, 1951, FRETTER & GRAHAM 1962, PURCHON 1977, SALVINI-PLAWEN 1980, BANDEL 1982,

GOODHART 1987, HASZPRUNAR 1988a). Indeed, the operculum is the second (while torsion the first) and the last synapomorphy of the *Gastropoda*. Its significance for the larva seems to be obvious, since it is present in all the *Gastropoda* that have a free-swimming larva and even in those which have their adult shell limpet-like.

In the torted mollusc the operculum is highly functional; STANLEY (1982) stresses its being of vital importance along with the impossibility of its existence as a non functionless structure in untorted monoplacophorans. Moreover, the operculum is produced asymmetrically to be asymmetrical: the direction of the spiral coiling of the operculum is always the same as the direction of torsion, which is not the case when the shell is concerned; the coiling direction of the latter is not necessarily the same as the direction of torsion (e.g. HASZPRUNAR 1988a). All the above facts indicate that the operculum is a posttorsional structure, but its rudiment appears in ontogeny before torsion (Fig. 3 A). On the other hand, nothing is known about the possible mechanism of its arising during/immediately after (?) torsion. If the larval operculum appeared due to torsion and were profitable to the larva, the adult operculum that occurs in the majority of prosobranchs would then be of a paedomorphic origin. At the same time, we know about an extinct class (?) of molluscs (?), the representatives of which (e.g. *Joachimites* belonging to the *Hyolithida*: YOCHELSON 1978, 1984; RUNNEGAR & POJETA 1985, on the other hand, consider the *Hyolithida* as a sister group of the *Mollusca*) had an apparent, big, calcified operculum. However, nothing can be assumed as to their torted morphology (YOCHELSON, 1984). The operculum, therefore, need not be as characteristic of torted gastropods as it is usually thought.

It is STANLEY (1982) who considers the operculum to be a structure, which is functionally possible only after torsion and decisive to gastropod success. He stresses that the diversity of the operculum-less so unprotected *Monoplacophora* had been declining throughout the Palaeozoic so that in the late Paleozoic they became definitely uncommon, contrary to the operculate so protected gastropods being able to survive under the growing pressure of predation. But this does not explain, for example, the lack of operculum in the Recent pulmonates. Also his opinion that "...it is virtually impossible for any other part of the body [than foot - A. F.] to secrete an operculum..." can hardly be accepted. To start with, the structure of the operculum resembles the one of the shell, and surely such a structure can be secreted by the mantle, for example. Secondly, there is no reason to reject the possibility of secretion of an operculum-like plate by the foot dorsally and close to the head (posteriorly to the head) - such a possible operculum would be functional in an untorted animal. Thirdly, probably the most primitive condition for both shell and operculum was an uncalcified, purely conchiolinous structure. Such an operculum, widely known also in Recent gastropods, would not be present in the fossil record, so we can only hypothesize on the presence/absence

of opercula in coiled monoplacophorans. And, as long as limped-like forms are concerned, there is no difference between the gastropod limpets and the monoplacophoran ones: they both have no operculum.

Anyway, the origin of the operculum remains enigmatic. As long as we consider - as a gastropod ancestor - any gastropod-like, coil-shelled-creature, untorted but having a big and massive shell and foot (the existence of which, as pointed out above, seems highly doubtful) the presence of any not functionless operculum in such an ancestor must be excluded. But we can imagine an untorted, limpet-like mollusc with a relatively small foot and a functioning operculum. Indeed, such an untorted ancestor would not be able to withdraw itself into its shell as rapidly as the gastropods do, but it would be able even to cover its shell mouth by its operculum, at least in part. Therefore, it seems that the operculum, its position, formation, appearance and functioning strikingly affected by torsion, was not necessarily absent or functionless in the gastropod untorted ancestor.

Is there anything similar/possibly homologous to the operculum in other *Conchifera*? To our present knowledge, there is not, but if we assumed the cephalopod siphon to be the only cephalopod structure of a pedal origin (IHERING 1877, DIETL 1878, YOUNG 1965, 1971, SALVINI-PLAWEN 1980, HARSZPRUNAR 1981a, ZELL 1988: some more data on the structure and homology of the cephalopod arms), and if we made some minor alterations to the reconstruction of the soft parts of the *Ammonoidea* that is commonly accepted in the literature (Fig. 9), then a homology between the gastropod operculum

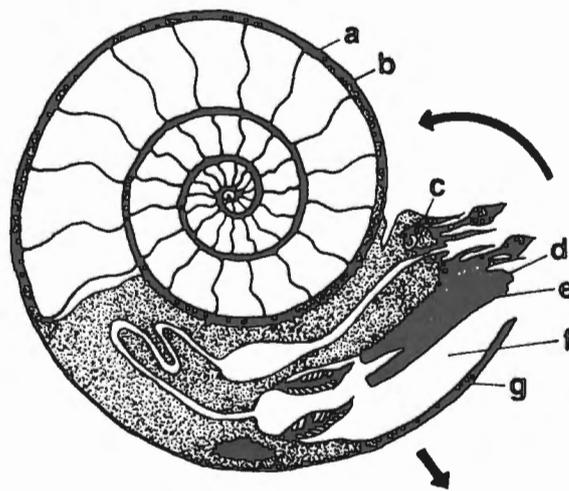


Fig. 9. A possible modification of reconstruction of ammonoid soft parts: a - shell, b - siphon, c - head with tentacles and eyes, d - funnel, e - paired aptyches (or single anaptyche), f - mantle cavity including gills, g - mantle edge; arrows indicate possible directions of the soft parts movement during retraction into the shell and covering it with the operculum

and ammonoidean aptyches would be very probable. The ammonoidean calcite aptyches (formed by the foot in such case) were paired and closed the mouth of the shell of those untorted molluscs. Perhaps the gastropod ancestor had the same structures. Then, after torsion, the aptyche-like plate was completely reduced on one side, while on the opposite side it was developed. The latter is still present in gastropods as the operculum. It must be noted, however, that in some representatives of the *Ammonoidea* there is a single anaptyche instead of paired aptyches.

(7) *Planispiral or turbospiral shell of the ancestor?*

There is a rich literature dealing with this problem. Usually the turbospiral shells of the torted gastropod are contrasted with the planispiral shells of the untorted cephalopods (*Nautiloidea*, *Ammonoidea*). It is believed (e.g. FRETTER & GRAHAM 1962, SALVINI-PLAWEN 1980) that the larval torsion itself has to cause at least a little asymmetry in the shell coiling, a strictly planispiral shell being therefore hardly possible in a torted animal. There are also functional arguments: the planispiral shell seems suitable for the pelagic, swimming cephalopod, while the more compact and mechanically resistant turbospiral one is better adapted to the benthic conditions of life.

The above arguments seem valid, but not of much importance. There are a few examples of strictly planispiral gastropod shells [e.g. *Omalogyra atomus* (PHILIPPI), *Valvata cristata* O. F. MÜLLER], and numerous examples of gastropod shells resembling the planispiral ones (e.g. *Planorbarius*, *Planorbis*). The latter have an ortho- or hyperstrophic protoconch, but the adult shell is functionally planispiral but still adapted well enough to the benthic mode of life. On the other hand, there are numerous examples of nautiloid shells being uncoiled but straight or arched, or coiled only in their initial part. There also are known some ammonoids having a turbospiral shell (e.g. *Turrilites*), and fossil gastropods, like *Orthonychia*, which had the shells slightly coiled, horn-like. BANDEL (1982) has shown that the trochospiral shell coiling has nothing in common with the ontogenetic torsion, since after torsion the shell is still symmetrical.

In my opinion the problem of the planispiral/turbospiral ancestor's shell does not exist in reality, since it concerns our mode of thinking rather than actually biologically different structures. Indeed, this is a problem of geometrical abstraction. The geometrical form of the shell ranges from conispiral, orthostrophic, through planispiral (=isostrophic), to conispiral, hyperstrophic. Within this wide range the planispiral shell is only one clearly defined point. The relatively small number of planispiral-shelled gastropods is therefore perfectly understandable: simply the possible radiation range of the conispiral (=turbospiral) shells is very wide, while the one of the planispiral shells is extremely narrow. Therefore, we would rather reject the sequence: planispiral shell - torsion - turbospiral shell.

The untorted gastropod ancestor could be either plani- or turbospiral; the same concerns the first gastropods, already torted.

Anyway, there are actually some functional differences between the planispiral shell and the turbospiral shell. The latter seems more convenient for a benthic animal, especially when having numerous whorls thus being more compact. It is also more resistant mechanically, for example, against the attacks of crabs. On the other hand, the high proportion of planispiral/nearly-planispiral-shelled cephalopods is understandable, since in these actively swimming animals any better marked asymmetry in shell coiling would have to affect their swimming efficiency: the hydrodynamic drag of such an asymmetrical shell would be higher, and serious problems with directional, straight-lined swimming would arise. The planispiral or turbospiral shell has therefore a different selective value in those swimming forms. But to conclude from such evidence that the gastropod ancestor was planispiral is nothing more than the reminiscence of NAEF's theory that the gastropod ancestor was free swimming and pelagic.

(7') Gastropod shell form: functional morphology approach

Recently our knowledge of the possible range of gastropod shell form have been extended; the discovery of bivalved gastropods, both Recent and fossil (COX & REES 1960, KEEN 1960, LUDBROOK & STEEL 1961) may be an example. There have been some attempts - first of them RAUP's (1966) and the last one CORTIE's (1989) - to describe the geometry of shells precisely. The importance of orthostrophy versus hyperstrophy and heterostrophy of shells, which may be difficult to determine, has also been pointed out (e.g. LINSLEY & KIER 1984, HADFIELD & STRATHMAN 1990).

There also are numerous papers dealing with the functional morphology of the gastropod shell (e.g. GOULD 1969, VERMEIJ 1971, 1975, LINSLEY 1977, 1978, 1984, McNAIR, KIER, LaCROIX & LINSLEY 1981). The general conclusion is that on the one hand the real range of gastropod shell form differentiation is actually very wide and covers even very peculiar and unusual creatures. On the other hand, only a relatively narrow range of shell form characterizes the actively creeping snails, while the rest of the general range may include only sedentary forms or shell draggers, both representing rather narrow ecological specializations. Therefore, the majority of gastropod species are characterized by the rather restricted morphospace for their shells.

Last but not least, the shell is the only molluscan structure in the fossil record, so some palaeontologists tend to overestimate the stability and importance of its form; the same can be said on some theories of torsion, according to which it is caused by the coiling of the shell. In fact, the shell is made by the mollusc and therefore its form is due to the animal. As we clearly know in the Recent molluscs, its form is hardly stable, easy to be modified. Therefore arguments like the ones

of STANLEY (1982), based on LOWENSTAM's (1978) observations of the Recent *Vema* behaviour and considering that the Cambrian monoplacophorans were exposed to predation because of their small shell, are not convincing. The small shell of *Vema* may be due to secondary reduction, since a bigger shell is unnecessary in the biotope the mollusc inhabits.

(8) *Coiled or limpet-like torting ancestor?*

The question has for a long time been under debate. Theoretically, the uncoiled, limpet-like shell seems more primitive, and such a symmetrical form, uncoiled, or only its protoconch a little coiled symmetrically, was widely accepted as a hypothetical pre-gastropod (e.g. FRETTER & GRAHAM 1962). On the other hand, there are numerous examples of secondary limpets: nearly all the known limpets, belonging to various and not necessarily closely related gastropod groups, have an asymmetrical, conchispiral (dextrose or sinistrorse) protoconch, which is clear evidence of their origin from an asymmetrically coiled ancestor. Therefore a trochospirally coiled, pleuromarioidean-like gastropod archetype is widely accepted (e.g. SALVINI-PLAWEN 1980, GRAHAM 1985).

There are, however, some gastropods having the shell plain symmetrical, with no trace of juvenile helicoid coiling. Such forms have been known for a long time (e.g. MORSE 1910, THOMPSON 1910, THORSON 1946, ANDERSON 1965, BANDEL 1982). Those are some representatives (*Acmaea*) of the *Docoglossa*. Recently, two more groups of symmetrical limpets have been found: the *Cocculiniformia* and "hot-vent-limpets group C" (McLEAN 1985, MOSKALEV 1978, BANDEL 1982, MARSHALL 1986, McLEAN & HASZPRUNAR 1987, HASZPRUNAR 1988a, c, d, e). As discussed by HASZPRUNAR (1988a), the existence of primary limpets, having no coiled, trochospiral ancestor, has to be accepted. It must be pointed out that apart from docoglossans, bulbous protoconchs are known in the *Tryblidiida* and *Scaphopoda*.

The *Docoglossa* show numerous primitive characters (e.g. HASZPRUNAR 1988a); the form and function of their radula, for example, resemble the ones of the Recent *Tryblidiida* and *Polyplacophora* (e.g. McLEAN 1979, WINGSTRAND 1985, LINDBERG 1988). Therefore, the docoglossan-like archetype of the *Gastropoda*, recently suggested by HASZPRUNAR (e.g. 1988a) to have a limpet-like shell, seems convincing.

As pointed out by LINSLEY (1978), the spiral coiling of the shell offers a higher degree of shell stability, a more compact and mechanically resistant shell form, more freedom of shell form (so much more possibility of radiation), and a greater mobility of the animal. Therefore it is understandable that spiral-coiled shells are numerous within non-gastropod conchiferans. There are numerous, asymmetrically coiled Palaeozoic forms (RUNNEGAR & POJETA 1985) included by LINSLEY & KIER (1984) into the separate class *Paragastropoda*, most probably a polyphyletic taxon.

Anyway, all those "paragastropods" show the general conchiferan tendency to evolve coiled shells. Also the protoconch of the Recent *Neopilina* is dextrally coiled (WINGSTRAND 1985). WARÉN (1988), however, has questioned the presence of coiled protoconchs in all the *Tryblidacea*: in his observations on the apex of *Neopilina goesi*, he has found no traces of rejection of the larval shell, which is contrary to the pattern observed in some *Docoglossa* and to WINGSTRAND's (1985) hypothesis on tryblidiids. On the other hand, the larval shell rejection cannot be excluded in *Micropilina minuta* (WARÉN 1989).

On the other hand, as discussed above, the existence of a coiled, multi-whorl-shelled but still untorted benthic creeping animal is hardly imaginable. Perhaps the larval problems with balance and swimming, which were due to the anopodal flexure, caused some coiling of the larval shell, but the adult must still have been a limpet/limpet-like form. The shell coiling of the adult shell might therefore have been a paedomorphic character, but it appeared not earlier than after torsion.

(8') *Bellerophon* question: gastropod or not yet gastropod?

Those conchiferans lived from the Cambrian to the Triassic. Their fossil shells (Fig. 10) are planispiral, with a most prominent body whorl and a pleurotomariid-like shell slit; no trace of operculum has been found in the fossil record. The question that have given rise to much controversy (e.g. KONINCK 1843, MEEK 1866, WENZ 1940, YONGE 1947, KNIGHT 1952, COX 1960, COX & KNIGHT 1960, KNIGHT, COX, KEEN, BATTEN, YOCHELSON & ROBERTSON 1960, TAYLOR & SOHL 1962, HORNY 1963, 1965a, b, MORTON & YONGE 1964,

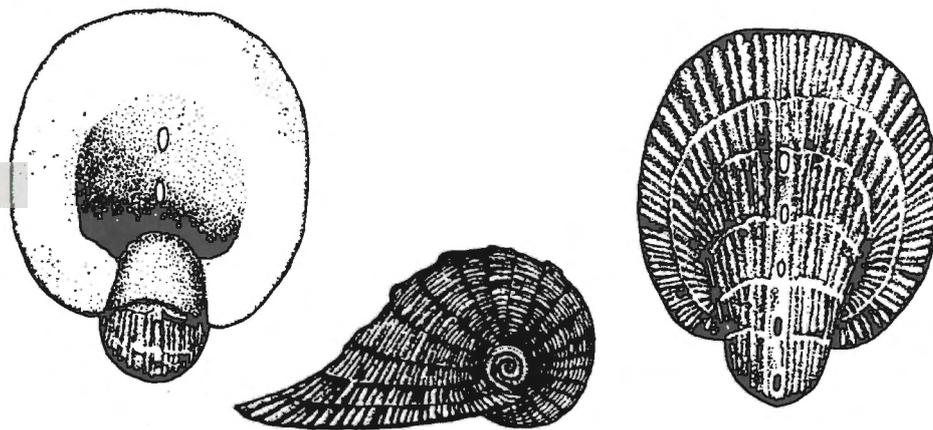


Fig. 10. *Tremantotus alpheus* HALL, a Middle Silurian representative of the *Bellerophon* phontacea, maximum dimension 77 mm; slit in a vestigial form of open tremata (like in Recent *Haliotis*); after McLEAN (1984)

YOCHELSON 1967, 1978, 1979, TERMIER & TERMIER 1968, ROLLINS 1969, STAROBOGATOV 1970, PEEL 1972, 1974, 1976, 1980, RUNNEGAR & POJETA 1974, 1985, STASEK 1972, GOLIKOV & STAROBOGATOV 1975, POJETA & RUNNEGAR 1976, RUNNEGAR & JELL 1976, BERG-MADSEN & PEEL 1978, LINSLEY 1978, SALVINI-PLAWEN 1980, DZIK 1981, RUNNEGAR 1981, HARPER & ROLLINS 1982, STANLEY 1982, McLEAN 1984, HASZPRUNAR 1988a) is: were they torted or not? Considering the facts discussed above, from the functional point of view, the existence of such untorted benthic conchiferans seems hardly believable. Within the *Bellerophontida*, besides the thin-walled shells of possibly pelagic animals, numerous thick-walled shells of evidently benthic animals are known.

The first authors, who were struck by the similarity between the bellerophontid slit and the one of pleurotomariid gastropods, were perhaps KONINCK (1843) and MEEK (1866). In fact, the function of the slit is easily understandable in torted animals, but there is no convincing theory to explain its function in an untorted mollusc. However, it might have served as an outlet of the posteriorly situated mantle cavity of the untorted animal, which would have been less important than in a gastropod but still useful, like the snorkel in *Yochelcionella* (Fig. 6A). On the other hand, its presence can hardly indicate any closer relationship between the bellerophontids and pleurotomariaceans.

WINGSTRAND (1985) has pointed out one important character, easy to discern also in fossil material, discriminating *Tryblidiida* from *Gastropoda*. In tryblidiids, like in polyplacophorans, there is a *musculus radulae longus* connecting the radula with the shell (the first plate in *Polyplacophora*), which is absent in all the *Gastropoda*. Its scars are well marked on the shell, and characteristic, which enables one to recognise tryblidiids/gastropods in fossils. On the other hand, the reduction of this muscle seems to have been connected not only with torsion as such, but also with the head development: probably the muscle would not be able to occur and function in a form with a big and well marked head. Therefore, both torsion and the reduction of the *musculus radulae longus* had the same background, and there were probably some yet untorted forms (although being not far from the torsion necessity) having no *musculus radulae longus*. Therefore, the absence of this muscle in bellerophontids is not necessarily an evidence of their torted, gastropod morphology.

The *Bellerophontida* seem therefore torted animals - a very early offshot of the *Gastropoda* trunk, but the question: torted or not? remains still open. For example, KNIGHT (1952) and KNIGHT & YOCHELSON's (1958, 1960) data suggest rather the torted condition of bellerophontids, while ROLLINS & BATTEN's (1968) concept that the broad shell slit of bellerophontids was filled with the posterior part of the cephalopodium, which enabled the more coiled, bigger exogastric shell to avoid pushing the head with its bulk spire, seems rather convincing.

McLEAN (1984) has collected data to confirm GOLIKOV & STAROBOGATOV's (1975) theory that the Recent *Fissurellidae* are the descendants of the *Bellerophontacea*. In my opinion, the similarity of the shell structure is not convincing: the innermost layer can occur or not even in the same species, and the unetched sections are poor in information (FALNIOWSKI 1989, 1990). On the other hand, the peculiar organization of the pallial organ complex (e.g. FRETTER & GRAHAM 1962, McLEAN 1984) clearly indicates that fissurellids are not closely related with the other gastropods. The other arguments put forward by McLEAN are quite convincing. At the same time, McLEAN develops LINSLEY's (1978) concept assuming the shell of some bellerophontids (Fig. 11) to be internal (covered with the mantle). The latter is important: if the shell had been internal the size of the body would have been much bigger and the soft parts much less restricted as to their form.

On the contrary, RUNNEGAR & POJETA (1985) consider all the *Bellerophontida* untorted monoplacophorans because there is a continuous lineage of intermediate forms between the limpet-like tryblidiids and the bellerophontids, and because the shells bear numerous, paired, nearly symmetrically arranged muscle scars. At the same time, they do not consider bellerophontids the gastropod

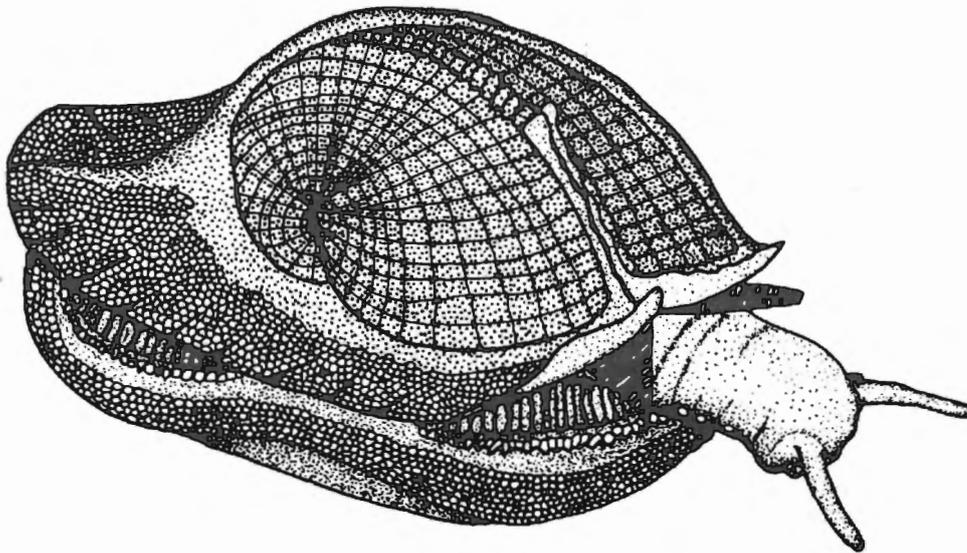


Fig. 11. Reconstruction of the bellerophontacean *Retispira* (after McLEAN 1984) based on assumption that its shell was internal and its soft parts gross morphology resembled the one of fissurellids. Overall length about 2 cm. The ctenidia projected forward outside the mantle cavity, one fold of the mantle covers the shell, other covers the ctenidia and the head if necessary, epipodial tentacles in a row along the side of the foot and neck

ancestors. However, it must be pointed out that the molluscan musculature is very plastic and variable, and in ontogeny torsion can be finished before the development of muscles has started. Therefore, the actual value of all the muscle scars in deriving the phylogeny of the fossil molluscs may be overestimated.

(9) *What must the ancestor have been like?*

The question of gastropod ancestor has been discussed for long. Numerous conditions of torsion were listed. Among them, the gradual reduction of numerous organs (e.g. gills) to one pair finally, was postulated. This must be rejected, since for the *Conchifera*, one pair of these organs seems primitive (HASZPRUNAR 1988a). The pronounced reduction of successive pairs of dorsoventral muscles, postulated e.g. by EDLINGER (1986, 1988a, b), seems to be of overestimated importance, as well as are the numerous considerations in the case of muscle scars on the tryblidiid shells (one/more pair/pairs), especially since BANDEL (1982) showed that phase I of larval torsion goes on by differential growth only. The latter contradicts both CROFT's data (1937, 1955) on the differential development of the muscles and the muscular action during the process. Moreover, there are numerous data on the great plasticity of the molluscan musculature, depending on several factors, some of them environmental. Also the characteristic, horseshoe-shaped muscle (in fact, a pair of muscles joined together) in docoglossans, which have recently been regarded as the most primitive Recent gastropods, hardly confirms "muscular conditions" being the crucial factor enabling torsion.

All the facts presented above reconsidered carefully, the prerequisites of torsion may be as follows:

(a) **cyrtosomatid conditions**

(b) **benthonic and actively creeping adult**

(c) **development with a free-swimming larva**

These were necessary and enough to make the process possible: these, and nothing more, were also enough to render the process unavoidable.

(10) *Second phase of torsion - necessity and profits*

The profits of finished torsion to the adult gastropod have been discussed above (see chapter 3) in detail. They all seem unquestionable. However, although the completely torted (which means: after phase II of torsion) gastropod seems obviously better adapted than the untorted ancestor, at the same time a partly torted animal, which has only finished the first, pelagic phase of torsion, seems completely unable to live on the bottom. The behaviour of the *Haliotis* larva after it just has settled down can serve as an example (e.g. FRETTER & GRAHAM 1962). The second phase of torsion is therefore simply absolutely necessary for

the survival of the gastropod.

Several authors (e.g. GHISELIN 1966, UNDERWOOD 1972) pay attention to the relatively long period of phase II after the settlement of the larva which is then for a relatively long time totally unable to creep. They suggest that these problems with locomotion make phase II unavoidable or are even the cause of the whole process of phylogenetic torsion. However, the observed impossibility of creeping may rather be caused by the foot musculature not enough developed yet, than by the position of the visceral mass.

On the other hand, the necessity of the second phase of torsion, undoubtedly proved by the fact that all the prosobranchs positively passed this phase in their phylogeny, provides some information on the hypothetical gastropod ancestor. If the shell and visceral mass were approximately perpendicular to the axis of the cephalopodium, with the mantle cavity lying on one side, it would be a hardly survivable condition for the benthic gastropod. This however would not be a problem if the Recent gastropods were concerned. They are capable of rotating free (within a wide angle) with their visceral mass covered within the shell (physiologic torsion). But this was not the case of the gastropod ancestor, since it was necessary for it to pass the second phase of torsion. Therefore, the ancestor must rather have been a limpet-like than a coil-shelled animal. Moreover, this contradicts all theories that the pronounced separation of the cephalopodium from the visceral mass, enabling the rotation of the first in relation to the latter, was the background of torsion. This really took place, but after torsion, not before.

3. Conclusions - phylogenetic torsion outlined

Basing on the facts and arguments presented above, a scenario of what happened about 600 million years ago, in the Cambrian, can be drawn. Firstly, an "unusual" mutation as the cause of the torsion process must be rejected. Secondly, all observations of the Recent larval torsion may help to understand the evolutionary processes, but they all have to be exploited very carefully. Thirdly, there is no theory that describes the process of phylogenetic torsion satisfactorily and bases on one ontogenetic phase - larva or adult - solely.

In the Precambrian, within the early *Conchifera*, represented by the class *Tryblidiida*, some progressive line branched into the *Diasoma* and *Cyrtosoma*. The latter, probably due to their active mode of life on the bottom surface, lost the primitive peripodal condition of the mantle cavity. Now, the mantle cavity (as well as the shell) is restricted to the visceral region, leaving the cephalopodium (head and foot) free.

The further development showed still the same general trends. For active creeping a bigger foot was necessary, as well as bigger sense organs (so, a bigger

head) and a higher metabolism level. The latter involved developing larger gills (so, a capacious mantle cavity), a longer alimentary tract (than a bigger visceral hump), and a bigger radula (within the bigger head). All these resulted in the proportional development of both the cephalopodium and shell. At that point, a strong, positive biofeedback must have occurred.

Because of serious functional problems discussed earlier in detail, the above process of progressive development was stopped at a relatively low level. The animal was not able to surpass some rather early stage of the relative development of the visceral mass/shell. The shell had to be limpet-like or nearly limpet-like (with a coiled protoconch, probably).

At that time, a free-swimming, pelagic larva appeared in ontogeny. For the larva, the stage of the proportional development/separation of the cephalopodium/visceral mass was then advanced enough to cause serious problems connected with the ano-pedal flexure. The latter became therefore so prominent as to affect the larval balance and directional swimming. Any higher degree of the flexure was then lethal, while any further growth to decrease the flexure had to affect the mantle cavity and, therefore, numerous physiologic processes in this region.

The problems were solved in the simplest way: by turning the visceral mass so that it would lie at a right angle to the cephalopodium, which probably was due to differential growth. After that, the decreasing of the ano-pedal flexure did not affect the mantle cavity region.

Such a relative position of the visceral mass was hardly functional on the bottom: a further 90° rotation of the visceral mass, by differential growth, completed therefore the torsion process. As a result, the completely torted animal would not only be able again to live on the bottom, but also far more better adapted to the benthic mode of life than its untorted ancestor. Moreover, the progressive evolution began long before the torsion process started, and then stopped by functional reasons. In torted forms it could run again to result in the arising of the Recent gastropods with their high, coiled shells, widely varying in form and size and bearing numerous whorls. The untorted ancestors became then eliminated by competition with the torted gastropods.

4. Acknowledgments

I am deeply grateful to the Stefan Batory Trust, Oxford, Great Britain, and to Prof. T. S. Rowlinson (Physical Chemistry Laboratory and Exeter College, Oxford), for enabling me to make profound library studies to confront my ideas with already known facts.

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