Modern insights on gastropod development: Reevaluation of the evolution of a novel body plan

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Synopsis More than a century of speculation about the evolutionary origin of the contorted gastropod body plan has been inspired by adult anatomy and by long-standing developmental observations. The result has been a concept of gastropod torsion that I call the "rotation hypothesis." Under the rotation hypothesis, gastropods originated when all components of the visceropallium (shell, mantle, mantle cavity with contained structures, and viscera) rotated by 180° relative to the head and foot. This evolutionary rotation is echoed during early development of patellogastropods and vetigastropods and occurs to some extent during development of more derived clades. However, comparative developmental data on ontogenetic torsion are minimal and I argue that the rotation hypothesis is a tautological argument. More recent studies on representatives from 3 major clades of gastropods suggest that the highly conserved aspect of gastropod development is not synchronous rotation of all components of the visceropallium relative to the head and foot but rather a state of anatomical organization in which the developing mantle cavity is on the right but the shell coil is posterior (endogastric orientation). This conserved state of developmental anatomy has inspired an alternative hypothesis for the evolutionary origin of the gastropod body plan, the "asymmetry hypothesis." Under the asymmetry hypothesis, the gastropod mantle cavity originated from 1 side only of a bilateral set of mantle cavities. The asymmetry hypothesis does not require a saltation event to explain the origin of gastropods, nor does it require that the ancient molluscan precursor of gastropods carried the shell coil over the head (exogastric orientation).

Introduction

Inherent fascination with the bizarre features of organisms has inspired generations of folklore within the genre of Rudyard Kipling's fanciful "Just So Stories." Nevertheless, interest in novelties of body plan is not merely the stuff of quaint entertainments. A great deal of scientific research has been devoted to questions such as: How did vertebrates get their head? How did tetrapods get their limbs? How did birds get their feathers? Indeed, the need to explain the emergence of morphological novelties has been a major impetus for bringing developmental biology back within the embrace of evolutionary biology, because novelties can be difficult to explain under the gradualism of population genetics (Muller and Wagner 1991; Wagner GP 2000; Rieppel 2001).

Although the tools of developmental genetics have been essential for many contemporary studies of organismal evolution through change in developmental programs, Raff and Love (2004) have emphasized that the overarching questions that drive these studies come from comparative studies of development viewed within a phylogenetic context. We need to know what morphogenetic changes actually occurred during evolution of novel phenotypes before we can ask how changes in gene regulatory cascades produced those changes. In this article, I suggest that developmental data that corroborate a hypothesis about the evolutionary emergence of the gastropod body plan may have been misinterpreted. I also hope to stimulate additional research on comparative patterns of gastropod development as an essential approach to answering the question: How did gastropods get so contorted? This area has received markedly little attention over the past 50 years, possibly because of an impression that all relevant developmental details were uncovered many years ago.

Gastropod torsion: Definition and historical notes

The gastropod fossil record and the inventory of extant species tell us that gastropod mollusks are a stellar example of evolutionary diversification within a clade. Nevertheless, this remarkable evolutionary

success is perhaps no more extraordinary than the prevailing theory for the evolutionary origin of this group of mollusks. The theory is known as gastropod torsion, or what I prefer to call the "rotation hypothesis." A description of the rotation hypothesis and a brief overview of its history follow.

In Lankester's (1883) treatise on mollusks for the ninth edition of the *Encyclopaedia Britannica*, he attempted to reconcile the similarities and differences among members of this huge phylum by formulating a "schematic Mollusc." Lankester warned that "were knowledge sufficient, we should wish to make this schematic Mollusc the representation of the actual Molluscan ancestor from which the various living forms have sprung [but] to definitely claim for our schematic form any such significance ... would be premature" (1883, p 635). Despite this caution, the "schematic Mollusc" did become conceptualized as the ancestral mollusk (Yonge 1947; Morton 1960) and was portrayed as such in generations of invertebrate biology textbooks (Hickman and Lindberg 1985). The hypothetical ancestral mollusk consisted of 2 main body regions. The cephalopodium included the head and foot, and the visceropallium included most of the visceral organs, calcified shell, mantle epithelium that secretes the shell, and an infolding of mantle epithelium that forms the roof of a cavity called the mantle or pallial cavity. The mantle cavity receives the anus and houses a single pair of gills (ctenidia), nephridiopores, and sensory osphradia, which are collectively termed the pallial organs.

There is near-universal agreement that the mantle cavity of the hypothetical ancestral mollusk was confined to the posterior end. Yochelson (1978) is virtually alone in questioning this assumption, although Solem (1974) reconstructed a gastropod forerunner with lateral mantle clefts extending along each side of the foot but with a single pair of pallial organs clustered at the posterior end. Yonge (1947) was sufficiently confident about the existence of a shallow mantle cavity at the posterior end of his "hypothetical primitive mollusk" that he dismissed Naef's (1913) suggestion of 2 pairs of gills in the gastropod precursor because more than 1 pair would not fit into a restricted posterior cavity.

From a starting condition represented by the hypothetical ancestral mollusk, gastropod torsion is defined as a rotation by 180° of all components of the visceropallium relative to the cephalopodium (Naef 1913; Yonge 1947; Raven 1958; Lever 1979; Signor 1985; Ponder and Lindberg 1997). Illustrations of this hypothesized process were sketched by Spengel (1881) and others have appeared many times since then (Fig. 1A and B). The rotation brought the posterior mantle
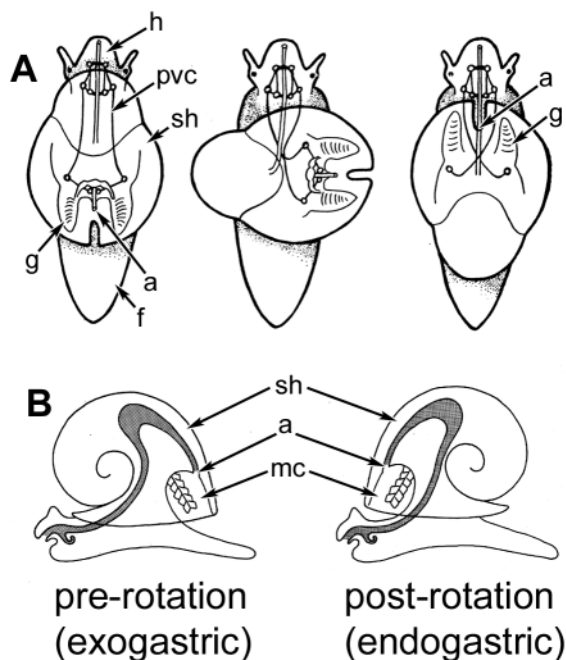

Fig. 1 The rotation hypothesis sketched in dorsal (A) and lateral (B) view. Rotation of the entire visceropallium relative to the head and foot moves the mantle cavity to an anterior position, crosses the pleurovisceral nerve connectives, and changes shell orientation from exogastric to endogastric. a, anus; f, foot; g, gill; h, head; mc, mantle cavity; pvc, pleurovisceral connective; sh, shell. (A) from Naef (1913).

cavity containing the anus and single pair of gills, osphradia, and nephridiopores to an anterior position over the back of the head and simultaneously rotated the coiled shell from an exogastric orientation (shell coil over the head) to an endogastric orientation (shell coil over the posterior end of the foot) (Fig. 1B). In addition to explaining the anterior mantle cavity in gastropods, this hypothesized rotation also accounted for the crossing of the pleurovisceral nerve connectives ("streptoneury"), which is present in all but the most derived gastropod clades.

Although the rotation scenario was first proposed by comparative anatomists studying adult gastropods, it became truly entrenched when embryologists in the late 1800s and early 1900s observed that young larvae of what are now known as patellogastropods and vetigastropods actually undergo this bodily torque as a morphogenetic movement during development (Boutan 1886, 1899; Robert 1902; Smith 1935). This process is known as "ontogenetic torsion." Garstang (1929) read considerable evolutionary significance into the dramatic process of ontogenetic torsion. He proposed that the contorted body plan of gastropods originated during evolution as a developmental aberration first expressed in the larval stage of an ancient

pregastropod with an adult anatomy similar to that of Lankester's schematic mollusk. He further proposed that this mutation has been preserved in gastropod developmental programs and can be witnessed among extant gastropods as ontogenetic torsion. According to Garstang (1929), the emergence of the Gastropoda was a case of evolutionary saltation, a term he actually used.

Torsion as a "grand controversy"

As outlined above, the rotation hypothesis appears to be well supported by both developmental and adult anatomical data. Nevertheless, in a review of gastropod phylogeny and systematics, Beiler (1992) noted that gastropod torsion remains among the "grand traditional controversies" of malacologists. Four controversial issues associated with the concept of gastropod torsion can be described:

(1) A macromutation of the magnitude proposed by Garstang (1929) is difficult to accept (Ghiselin 1966; Salvini-Plawen 1980). However, it is also difficult to imagine functional intermediate forms if the process of rotation occurred gradually, particularly if the shell participated in this rotation (Solem 1974; Yochelson 1979).

(2) The rotation hypothesis has generated much controversy concerning the interpretation of Paleozoic molluscan fossils with a coiled shell. Debates focus on whether various extinct groups carried their coiled shell in an exogastric or endogastric orientation (Fig. 1; reviewed in Wagner PJ 2001).

(3) Most literature on the evolution of gastropod torsion has not questioned whether the rotation actually occurred; rather it has debated the original adaptive value of the rotation (reviewed in Ghiselin 1966; Lever 1979; Signor 1985; Falniowski 1993). The single attempt to test experimentally any of these hypotheses found little support for Garstang's (1929) suggestion that ontogenetic torsion improves larval survival in the presence of planktivorous predators (Pennington and Chia 1985).

(4) The torsion hypothesis in its traditional form is a circular argument. An anterior mantle cavity containing a pair of pallial organs ("diotocardian condition") is taken as evidence of 180° rotation, based on the premise that the precursor condition was a posterior mantle cavity with a single pair of pallial organs. Yet evidence for a posterior mantle cavity in a gastropod precursor seems to be that a reversal of 180° rotation would place the anterior mantle cavity of diotocardians in a posterior

position. In short, the rotation hypothesis requires a gastropod precursor with a posterior mantle cavity to be valid. The rotation hypothesis became entrenched during a time when there were no data that might contradict the assumption of a posterior mantle cavity within a gastropod progenitor, but neither was there strong independent evidence to support this assumption (no unambiguous fossil evidence, no plausible molluscan sister group with a mantle cavity confined to the posterior aspect). Subsequently, living tryblidiid monoplacophorans were discovered (Lemche 1957) and were placed as the most basal lineage of conchiferan mollusks with extant descendants, although Peel (1991) has suggested that monoplacophorans are a polyphyletic assemblage. The mantle cavity of tryblidiids is in the form of elongate lateral clefts running down each side of the foot and uniting at the posterior end. Furthermore, contemporary phylogenetic hypotheses do not place diotocardians (gastropods with 2 sets of pallial organs) as the most basal group of gastropods (Ponder and Lindberg 1997; see commentary in Hedegaard 1997). Without independent evidence for a posterior mantle cavity in an ancient gastropod precursor, gastropod torsion is not only a "grand controversy" but also a grand tautology.

Goal: An alternative to the rotation hypothesis

Although the concept of gastropod torsion as a 180° rotation between body regions has generated a great deal of controversy, it has persisted since the late 1800s for 2 main reasons: (1) it successfully explains a number of empirical observations concerning gastropod development and adult anatomy, and (2) an alternative hypothesis for the evolutionary origin of the gastropod body plan that is consistent with developmental, anatomical, and phylogenetic data has been elusive. However, new data have emerged concerning gastropod phylogenetic relationships and gastropod developmental patterns. The rotation hypothesis should be reassessed in light of these new data.

In the following section, I will review some comparative observations on gastropod development that suggest that the highly conserved aspect of gastropod development may not be a conserved *process* of rotation by 180°, but rather a conserved *state* of anatomical organization in which the mantle cavity is on the right but the developing shell is fully endogastric. Currently, these observations on development are restricted to only a very few species. Nevertheless, uncovering discordance between these data and widely

held assumptions about gastropod development is a first step toward motivating more critical observations on the process of ontogenetic torsion among a wider sampling of gastropods. To further this goal, I will propose an alternative view of the evolutionary origin of gastropods, inspired by the conserved developmental stage described herein. Hypothesis testing by exploring alternative explanations is an essential part of any critical analysis, but to date the rotation hypothesis as the prevailing explanation for the evolutionary origin of gastropods has had no serious competition.

Comparative observations on gastropod development

Vetigastropoda

Reanalysis of ontogenetic torsion is appropriately begun with a member of the genus *Haliotis*, because the seminal and highly influential work on gastropod ontogenetic torsion was carried out on *Haliotis tuberculata* L., 1758, by Crofts (1937, 1955). As noted by Haszprunar (1988), a great deal of speculation about gastropod evolution has drawn from Crofts's observations.

Crofts (1937, 1955) reported that ontogenetic torsion in *H. tuberculata* occurred in 2 stages (Fig. 2A). Beginning from a stage in which a small mantle cavity was behind the developing foot and the larval shell (protoconch) had an exogastric orientation, the visceropallium then rotated rapidly by 90° so that the mantle cavity moved to the right of the head and foot and the protoconch was "half endogastric." A further 90° of visceropallial rotation occurred

during a much longer second stage requiring 8–10 days. Crofts (1937) stated that she was able to resolve these 2 stages because she prepared histological sections of developing larvae.

Crofts's (1937, 1955) observations stood for many years until Voltzow (1987) videotaped the process of ontogenetic torsion in developing larvae of *Haliotis kamtschatkana* Jonas, 1845, and found that the second half of rotation required only 18 h at 12°C, an observation later confirmed by Page (1997) (Fig. 3A and B).

Further analysis of the process of ontogenetic torsion in *H. kamtschatkana* using histological sections of sequential developmental stages indicated that mantle epithelium lining the initial mantle cavity of prerotational larvae does not rotate in close synchrony with other components of the visceropallium during ontogenetic torsion (Page 1997). As a result, there is a transient stage in the development of *H. kamtschatkana* during which the protoconch is fully endogastric, indicating full 180° rotation of the larval shell relative to the head and foot, but the developing mantle cavity lies to the right of the cephalopodium, indicating only 90° rotation of mantle fold epithelium relative to the head and foot (Figs. 2B, 3C and D). However, during the 9–12 days between the end of protoconch rotation and the onset of metamorphic competence, the mantle cavity gradually expands over the entire dorsal surface of the head (Page 1997).

Crofts (1937) appears to have observed a transient stage in *H. tuberculata* in which the mantle cavity was on the right (indicating 90° rotation of the mantle cavity) but the larval shell appeared fully endogastric (indicating 180° rotation of the shell). Nevertheless,
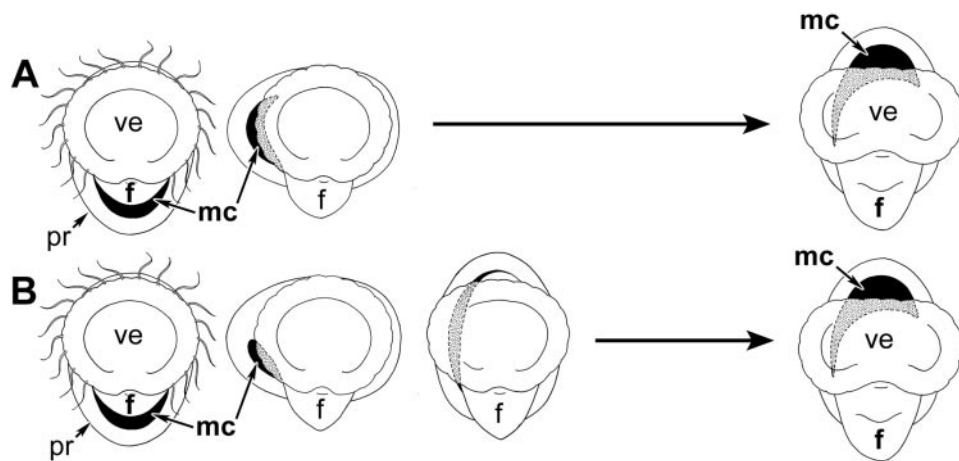

Fig. 2 Two interpretations of ontogenetic torsion in abalone. (A) Crofts (1937) described a rapid initial rotation by 90° and a subsequent, much slower rotation by a further 90°. (B) Page (1997) observed 180° rotation of the shell and visceral lobe relative to the foot within approximately 24 h (12°C), but at the end of this process the mantle cavity was on the right despite a fully endogastric shell. During the following days the mantle cavity enlarged and spread over the back of the head. f, foot; mc, mantle cavity; pr, protoconch; ve, velum (velar cilia shown for the prerotational stage only).
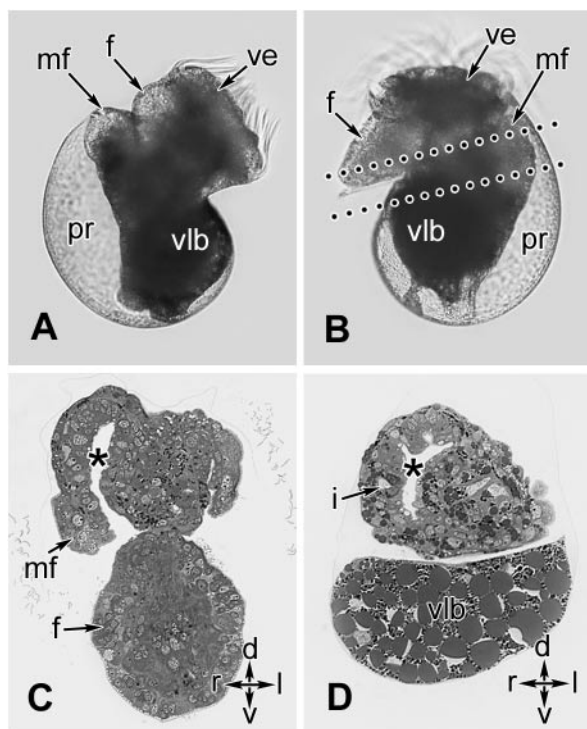
Fig. 3 Ontogenetic torsion by the vetigastropod *Haliotis kamtschatkana*. (A) Light micrograph of live larva prior to ontogenetic torsion. (B) Light micrograph of live larva 24 h after 180° rotation of the protoconch (larval shell) relative to the head and foot; dotted lines indicate levels of transverse sections in (C) and (D). (C) Transverse section through level of the foot at 24 h after rotation showing mantle cavity (asterisk) on the right side. (D) Transverse section at deeper level of the mantle cavity (asterisk) at 24 h after rotation showing terminal end of the intestine. f, foot; i, intestine; mf, mantle fold; pr, protoconch; ve, velum; vlb, visceral lobe. Orientation arrows: d, dorsal; l, left; r, right; v, ventral.

she discounted this as an illusion created by a presumed asymmetric deposition of shell material around the rim of the shell aperture at this stage of development (see Crofts (1937), p 242–3 and Fig. 47). However, the protoconch of haliotids is somewhat laterally flattened. It is therefore difficult to accept that asymmetric shell growth could drastically disguise the orientation of this laterally flattened protoconch. I suggest that Crofts's (1937, 1955) observations were not an illusion. There really is a stage during haliotid development when the mantle cavity is on the right despite a fully endogastric protoconch. If this is the case, then haliotid development does not exactly recapitulate an ancient evolutionary event hypothesized under the rotation hypothesis.

Recent work has demonstrated directly that displacement of mantle fold epithelium in developing larvae of *H. kamtschatkana* is not rigidly coupled to rotation of the larval shell and visceral lobe. Antibodies

against serotonin (5-hydroxytryptamine) intensely label a cell embedded in the mid-sagittal plane of mantle fold epithelium beginning well before the onset of ontogenetic torsion. After full rotation of the larval shell and visceral lobe relative to the head and foot, this cell is located on the right side of the larva, rather than directly behind the larval head (L.R.P., unpublished observations).

In conclusion, developing larvae of the abalone *H. kamtschatkana* pass through a stage during development in which the larval shell is fully endogastric with respect to the head and foot but the mantle cavity including the anus is on the right side. This transient stage has also been observed in developing larvae of the vetigastropod *Diodora aspera* (Page 2003).

Caenogastropoda

Fertilized eggs of the caenogastropod *Trichotropis cancellata* Hinds, 1843 (Capulidae), are deposited within benthic capsules and develop into planktotrophic larvae (Parries and Page 2003). As described by Page (2003) and summarized below, morphogenetic movements that generate asymmetries associated with torsion occur during encapsulated embryonic development.

The images in Figure 4A–D show scanning electron micrographs of *T. cancellata* embryos at sequential stages during the process of ontogenetic torsion. At the stage shown in Figure 4A, embryos exhibit little external evidence of asymmetry and the shell is merely a shallow bowl (shell not visible in this image). The mantle cavity first appears as a shallow cleft on the right side (Fig. 4B) and it subsequently enlarges to occupy the entire right side of the embryo (Fig. 4C). During later development prior to hatching, the mantle cavity spreads over the entire dorsal surface of the embryo behind the velar lobes of the head.

In order to identify whether *T. cancellata* exhibits a stage in which the mantle cavity is on the right but the protoconch is fully endogastric, precise information about protoconch orientation during the embryonic interval represented in Figure 4A–D is needed. Scanning electron microscopy is inadequate for this purpose because the axial coordinates of the symmetrical, bowl-shaped shell at the outset of the process cannot be identified. Furthermore, damage to the fragile protoconch during preparation for scanning electron microscopy confounds efforts to ascertain its precise shape and orientation. However, it was possible to monitor change in shell orientation by tracking changes in orientation of shell-anchored muscles using fluorophore-tagged phalloidin (Page 2003). Two sets of muscles are attached to the inner wall of the protoconch via specialized mantle epithelial
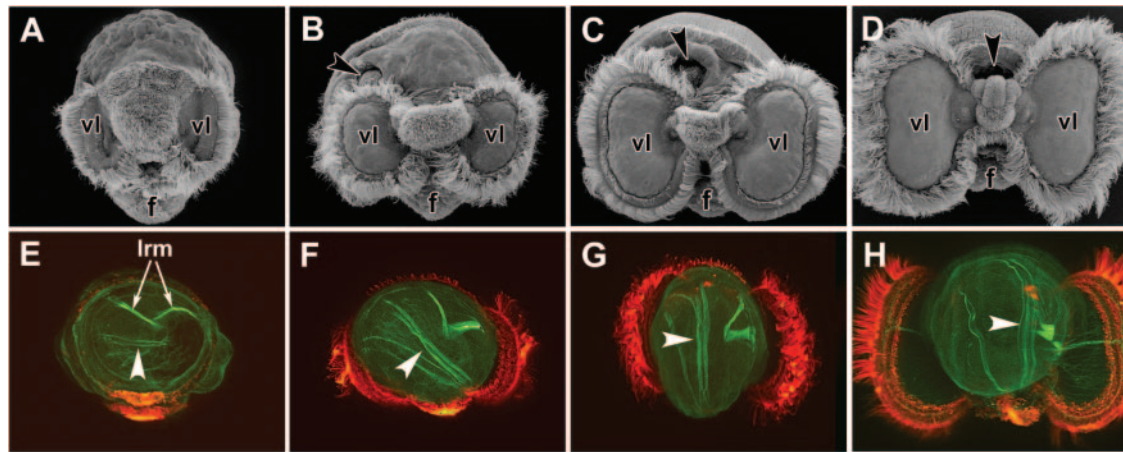
Fig. 4 Ontogenetic torsion by the caenogastopod *Trichotropis cancellata*. (A–D) Scanning electron micrographs of 4 successive developmental stages viewed from the apical pole. (A) Prior to formation of mantle cavity. (B) Mantle cavity (arrowhead) forms as a shallow cleft on the right side. (C) Mantle cavity (arrowhead) has enlarged and spread dorsally. (D) Mantle cavity (arrowhead) has expanded over the entire dorsal surface of the head. (E–H) Fluorescence images of the same embryonic stages shown in (A–D), showing shell-attached muscles labeled with phalloidin-Alexa 488 (green) and cilia labeled with an antibody against acetylated α-tubulin (red). (E) Arrowhead indicates a fan of mantle muscles underlying the bottom of the shell; also note the larval retractor muscle (lrm). (F) Mantle muscles (arrowhead) have rotated 45°. (G) Mantle muscles (arrowhead) have rotated another 45°. (H) Mantle muscles (arrowhead) show no additional rotation. f, foot; vl, velar lobe. Phalloidin-labeled embryos were imaged from the posterior end but the images were flipped so that the position and orientation of muscles corresponds with the apical views shown in the scanning electron micrographs. Adapted from Page (2003).

cells: the larval retractor muscle with distal fibers extending into the head and base of the foot and a spray of mantle muscles that underlie the protoconch.

Fluorescence micrographs in Figure 4E–H show orientation of the mantle muscles in stages corresponding to those shown in the scanning electron micrographs. They suggest that shell rotation stops at the last stage when the mantle cavity is still confined to the right side of the embryo; at this stage the protoconch must be fully endogastric (Fig. 4G). Thus, similar to *H. kamtaschatkana*, embryos of *T. cancellata* have a stage of development in which the mantle cavity is confined to the right of the mid-sagittal plane but the protoconch is fully endogastric.

Heterobranchia

The Heterobranchia is a gastropod clade that includes opisthobranchs, pulmonates, and several additional groups (Haszprunar 1988; Ponder and Lindberg 1997). Figure 5 shows an apical view of the planktotrophic larva of the notaspidean *Pleurobranchaea californica* Macfarland, 1966. The mantle cavity is located to the right of a mid-dorsal ridge of ciliated mantle fold epithelium. In this species and in the pulmonate *Amphibola crenata* (Little and others 1985), the posterior part of the mantle cavity expands over to the left side during later larval development. According to Thompson (1976) organs and tissues of the opisthobranch visceropallium either differentiate in
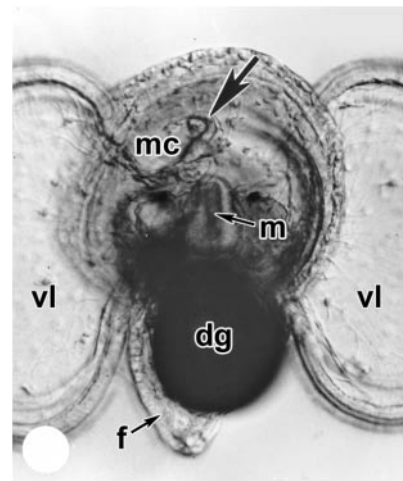

Fig. 5 Light micrograph of a larva of the notaspidean opisthobranch *Pleurobranchaea californica*, observed from the apical pole. The arrow indicates a ciliated ridge that borders the entrance to the mantle cavity on the right side. dg, digestive gland; f, foot; m, mouth; mc, mantle cavity; vl, velar lobe.

positions of partial rotation or undergo only modest displacements during embryogenesis.

Ruthensteiner (1997) described observations on developing larvae of a patellogastropod, a vetigastropod, and a cerithioid caenogastropod that are consistent with data reviewed here, because a right-sided mantle cavity is a common denominator during the

development of all species examined. Ruthensteiner (1997) argued that the lung of the pulmonates *Ovatella myosotis* (Ellobiidae) and *Onchidium* c.f. *branchiferum* (Onchidiidae) is a true homologue of the gastropod mantle cavity because the lung originates during development from an in-pocketing of inner mantle fold epithelium on the right side.

The foregoing survey of mantle cavity development among gastropods does not include developmental observations on the Patellogastropoda, despite the fact that patellogastropods have been placed as the most basal group of living gastropods (Haszprunar 1988; Ponder and Lindberg 1997). Wanninger and colleagues (2000) have meticulously documented the fact that rotation between the cephalopodium and protoconch of *Patella caerulea* is a rapid, monophasic morphogenetic movement that is not subdivided into slow and rapid phases. However, existing histological data on the morphogenesis of the mantle cavity in patellogastropods are currently inconsistent, possibly reflecting real differences among species. Smith (1935) and Lespinet and colleagues (2002) interpreted deep invaginations of epithelium on either side of the stomodeum, anterior to the foot rudiment, in pretorsional larvae of *Patella vulgata* (Patellidae) as rudiments of the mantle cavity. Alternatively, Wanninger and colleagues (2000) found that the pretorsional mantle cavity in *P. caerulea* was beneath the foot on the ventral side, but the mantle fold became dorsal after ontogenetic torsion. Ruthensteiner (1997) found that the initial mantle cavity of the patellogastropod *Cellana sandwicensis* (Patellidae) was an in-pocketing of mantle epithelium on the right side after ontogenetic torsion. These apparent discrepancies, together with the basal position of the Patellogastropoda, underline the need for a detailed study on mantle cavity morphogenesis within the Patellogastropoda.

Asymmetry hypothesis for the evolution of the gastropod body plan

Gastropod torsion, if defined as a suite of anatomical conditions in adult gastropods that includes an anterior position for the mantle cavity and anus, is unique to this clade of mollusks. Therefore, outgoups are silent about the earliest stages in this body plan transformation and fossils of gastropod-like shells preserve only half of the torsion equation (if torsion was indeed a rotation between 2 body regions). Lindberg and Ponder (2001) used outgroup comparison to conclude that a pair of pallial organs flanking a medial anus, as present in diotocardian mollusks, is ancestral for gastropods because other mollusks have pallial organs on either side of the anus. However, the bilateral pairs of pallial organs in other mollusks develop synchronously on the left and right sides, whereas the 2 gills of haliotids develop asynchronously (Crofts 1937; gill development in other diotocardians has not been described).

For some authors, torsion as a synapomorphy of gastropods is best characterized as a developmental phenomenon (Runnegar 1981; Signor 1985). However, even the few species surveyed here show that developmental events associated with ontogenetic torsion can be highly variable. For example, the mantle cavity of haliotids appears initially behind the foot and the protoconch rotates by a full 180°, the mantle cavity of *T. cancellata* initially appears on the right and the protoconch rotates by only ~90°, and the protoconch of some opisthobranchs is secreted in its post-torsional orientation. A conspicuous absence of detailed, comparative studies on ontogenetic torsion has perhaps led to a perception of greater uniformity in this process than actually exists.

Despite the diversity of developmental processes involved in ontogenetic torsion and despite the ongoing difficulties in resolving the branching sequence along the trunk of the gastropod phylogenetic tree, comparative developmental data may nevertheless hold clues to the early evolution of the gastropod body plan. If a specific organization of developmental morphology is seen to arise in multiple clades of distant relationship, then this organization may have occurred also in the first gastropods and may be highly informative about the nature of the body plan that pioneered the gastropod lineage. In the absence of alternatives, a high degree of conservation can substitute for mapping diverse characteristics onto a highly resolved phylogeny to infer ancestral characteristic state. The conserved developmental stage in which the protoconch is endogastric and the mantle cavity lies to the right of the cephalopodium inspires an alternative proposal for the early evolution of the gastropod body plan. With this proposal, I have abandoned the premise that pregastropods had a mantle cavity restricted to the posterior end and have instead assumed that the ancient conchiferans that eventually gave rise to gastropods had lateral mantle cavities that merged posteriorly, as in extant tryblidiid monoplacophorans.

Although fossil evidence for Yonge's (1947) hypothetical gastropod ancestor with a posterior mantle cavity is ambivalent at best, the fossil record strongly suggests that the gastropod shell evolved from the dorsal shield of monoplacophorans by elongating along its dorsoventral axis, which was accompanied by shell coiling and narrowing of the apertural gape of the shell. How did ancient gastropod predecessors reconcile progressive narrowing of the shell aperture

with the need to efficiently aerate gas exchange epithelia within lateral mantle cavities, particularly when viscous forces must have significantly influenced water flow through the increasingly constricted mantle cavities of these small mollusks? The conserved developmental state described here may be reminiscent of the response to this dilemma by the first gastropods: abandon the condition of increasingly constricted lateral mantle cavities on both the left and right sides for a single, unilateral mantle cavity of increased size. Under this hypothesis, an asymmetric mantle cavity (1 side only) is the essential derived condition from which all descendant gastropod clades are derived, as illustrated in Figure 6A. As increasing body size demanded ever more gill surface area, the response may have been to expand the unilateral mantle cavity (the right cavity in dextral snails) over the back of the head (Fig. 6B–D).

The "asymmetry hypothesis" for the evolutionary origin of gastropods has a number of attractive features:

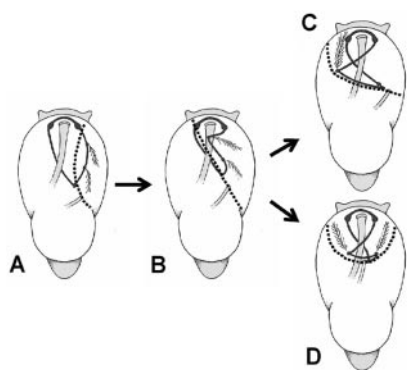(1) The asymmetry hypothesis does not require that a macromutation of the size proposed by Garstang

Fig. 6 Illustration of the "asymmetry hypothesis"; dextral snails shown in this scenario. Ancient conchiferan mollusks that gave rise to gastropods had bilaterally symmetric, lateral mantle cavities, possibly with more than 1 gill in each lateral cavity (not shown). (A) The essential gastropod synapomorphy is loss of the mantle cavity on 1 side; the remaining cavity receives the laterally deflected anus and may also have had 2 gills. (B) Unilateral mantle cavity deepens and spreads over the back of the head, carrying a gill to the left side; this process is not accompanied by shell rotation. (C) Continued leftward expansion of the mantle cavity and loss of the second gill produces the monocardian condition of most extant gastropods. (D) Diotocardian condition seen in many vetigastropods; this condition may represent retention of 2 sets of pallial organs from the right side (as illustrated). Alternatively, only 1 set of pallial organs may have been present in stage A and the second gill has resulted from a duplication event.

(1929) launched the gastropod lineage. The origin and subsequent remodeling of the gastropod body plan is a saga of gradual change in the dimensions and positioning of inner mantle fold epithelium delineating the mantle cavity.

(2) The notion that benthic mollusks crawled about with a heavily calcified shell coil positioned over the head can be discarded under the asymmetry hypothesis, because it does not propose that shell rotation occurred. Although the shell of nautiloid cephalopods is exogastric, there is a clear functional explanation for this shell orientation because it allows the body of a nautiloid to be suspended beneath its gas-filled buoyancy device, rather than balanced precariously on top of its "balloon."

(3) Finally, the asymmetry hypothesis does not require the existence of a maladaptive intermediate stage in order to justify subsequent stages. For example, there are no "sanitation problems" as proposed by Garstang (1929) and Yonge (1942).

The asymmetry hypothesis as introduced here will be analyzed in greater detail in a subsequent publication. Outstanding issues include how the asymmetry hypothesis explains streptoneury in gastropods, how it relates to the seemingly universal trait in larval gastropods of only a single larval retractor muscle extending from the posterior wall of the protoconch in to the foot and head (a second retractor may be present but it never has this trajectory), and how it integrates with the phenomenon of anisotropic shell coiling and the presence of an operculum in gastropods.

In conclusion, I seek to erase the pervasive view that developmental "facts" relevant to gastropod torsion as a developmental, phylogenetic, or evolutionary phenomenon were uncovered long ago. There is virtually nothing known about the ontogeny of anatomical torsion in the Neritopsina and Cocculinoidea, or in any of the recently discovered hot-vent gastropods, and existing accounts of better-studied groups often lack the required morphological detail for accurate comparisons with members of other clades. Efforts to incorporate development into a holistic view of gastropod evolution will require much additional research within an area that has been neglected for many years and has labored under long-standing prejudices that may lack firm foundation.

Acknowledgments

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