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TYPES OF OPISTHOBRANCH VELIGERS: THEIR NOTUM FORMATION AND TORSION

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ABSTRACT

Two types of development, which are independent of the amount of yolk provisioned by the parent within the egg, can be observed amongst opisthobranch molluscs: I propose to term these 'Type 1' and 'Type 2' veliger development, according to the Type 1 and Type 2 larval protoconch distinguished by Thompson (1961). In all the studied examples, the notum of the adult originates from the epithelium of the veliger mantle cavity: it never arises from the epipodium. In the case of Type 1 veliger development, the quantity of stored yolk in the embryo may modify the chronology and details of some ontogenetic events. All opisthobranch veligers show 180° torsion at the apex of the visceral mass and a gradient of torsion between the cephalopodium and the apex: torsion of the digestive tract organization remains complete in all adult opisthobranch molluscs.

INTRODUCTION

The three forms of larval protoconch (Types A, B and C), recognized by Vestergaard & Thorson (1938) and Thorson (1946), were re-evaluated and re-categorized by Thompson (1961) into Types 1 and 2 only. In this regard Thompson was correct, because: 1) there is good reason to believe (Thompson, 1961; Tardy, 1970a; but see Boucher, 1986 below) that the so-called Type A veliger shell is an aberrant or incomplete protoconch, and 2) this distinction primarily corresponds to two fundamental veliger types, also termed Types 1 and 2 according to their protoconch. These two larval types differ fundamentally in their anatomy and development and in respects independent of the amount of yolk provisioned within the egg,

JUSTIFICATION OF THE DISTINCTION OF TYPE 1 AND TYPE 2 VELIGER DEVELOPMENT

Type 1 veligers

The Type 1 veliger is the most common form amongst opisthobranchs. Not only do these larvae display a coiled shell, but also they exhibit the following characteristics:

1. The pelagic period of planktotrophic Type 1 larvae is relatively long—15 days or more in temperate latitudes (see Todd & Doyle, 1981; Hadfield & Miller, 1987);
2. There is significant protoconch growth, due to the secretions of the mantle fold which remains functional throughout the larval period. In consequence, it is possible to distinguish the wrinkled surface of the growing protoconch II from the smooth (hatching) protoconch I. At metamorphosis the shape of the completed Type 1 veliger shell is reminiscent of the Type 2 shell by virtue of the columellar appearance. However, a spiral crease line is conspicuous on the left side of the shell. Such growth and development of larval shells has been reported for numerous species of Ascoglossa (e.g. Thorson, 1946), Aplysiomorpha (e.g. Switzer-Dunlap & Hadfield, 1977), and Nudibranchia (e.g. Perron & Turner, 1977; Chia & Koss, 1988, 1989; Tardy, 1970b; Bickell & Kempf, 1983). These growth patterns appear to be a general process, with only exceptional variations (e.g. *Goniodoris sugashimae* Baba, 1960 in Hamatani, 1961; *Aegires punctilucens* (d'Orbigny, 1837) in Thiriot-Quievreux, 1977; *Hypselodoris infucata* (Rüppell & Leuckart, 1831) in Hubbard, 1988);
3. The pallial cavity, which is not very large, is filled mainly by a cellular proliferation of its roof and floor when the veliger approaches metamorphosis; the pallial margin is never implicated in this process and it disappears completely at metamorphosis. Moreover, the mantle proliferation grows upwards and everts under the

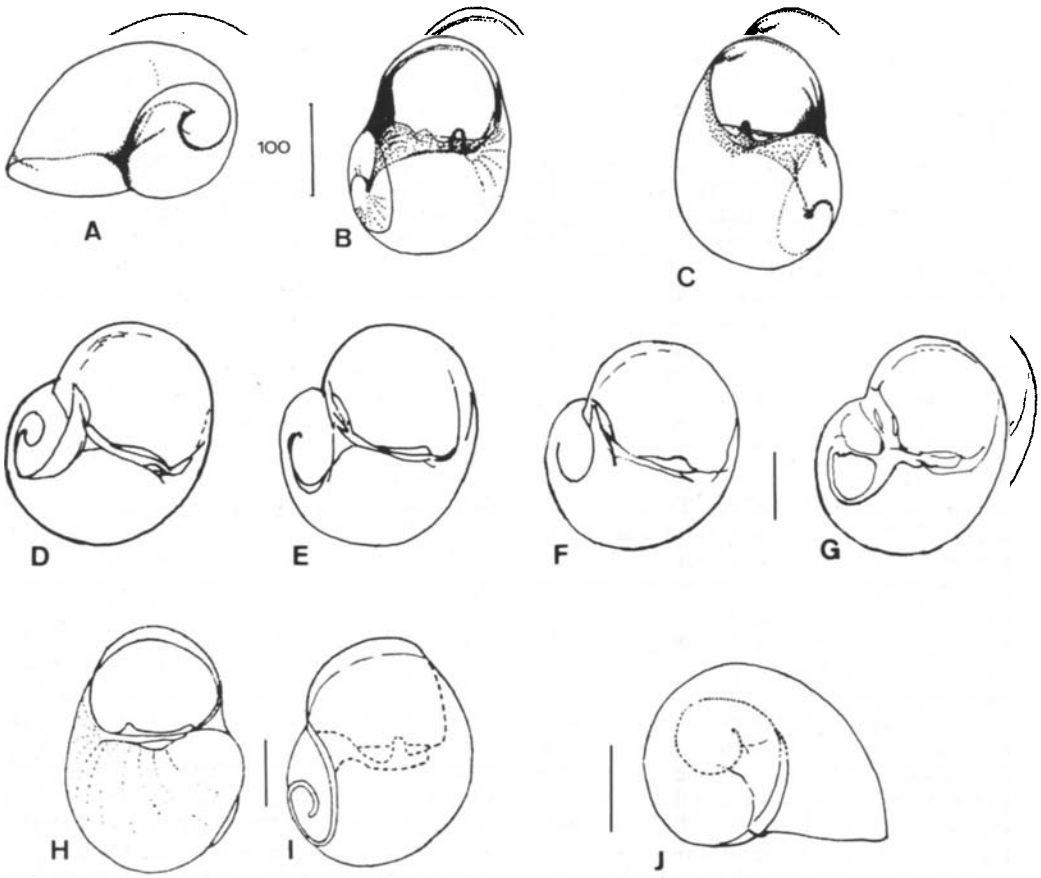

Figure 1. Type 1 larval shells cast off by larvae during metamorphosis. **A-C.** Right side, dorsal views of *Facelina coronata* (Tardy, 1970b); **D-G.** Dorsal view of *Stylocheilus longicaudus, Aplysia dactylomela, Aplysia juliana* and *Dolabdella auricularia*, respectively (after Switzer-Dunlap & Hadfield, 1977); **H,I.** Dorsal and ventral view of *Elysia viridis* (after Thorson, 1946); **J.** Lateral left view of *Onchidoris bilamellata* (after Chia & Koss, 1988). Scale bar = 100 μm.

protoconch, which is then cast off. It is this everted tissue that gives rise to the definitive mantle or notum of the juvenile mollusc (see Fig. 3B);
4. At metamorphosis all the ganglia of the visceral loop are visible: they are well differentiated and localized in the cephalic area, as has been shown by Tardy (1970a, 1974).

Type 2 veligers

These are quite distinct from type 1 veligers in terms of their ontogenetic and anatomical characteristics:
1. Type 2 veligers possess a simple 'egg-shaped' (Thorson, 1946), or cup-shaped, inflated protoconch shell;
2. The length of the pelagic period is apparently relatively short, and perhaps of only seven days or less in duration in temperate waters (Todd & Doyle, 1981);
3. No growth of the protoconch occurs during the pelagic larval phase (see, for example, Tardy, 1964, 1970a; Harris, 1975). It is the breakdown of the pallium, which commences a short time after protoconch development is complete, that is responsible for the lack of further shell growth of Type 2 veligers. Specific observations of this include *Tergipes despectus* (Johnston, 1835) (in Tardy, 1964), *Eubranchus doriae* (Trinchese, 1874) and *Tenellia ventilabrum* (Dalyell, 1853) (in Tardy, 1970a), and *Eubranchus farrani* (Alder & Hancock, 1844), *E. cingulatus* (Alder & Hancock, 1847) and *E. exiguus* (Alder & Hancock, 1848), pers. obs.;
4. As previously specified (Tardy, 1970a)—

albeit perhaps with insufficient detail—the notum of, for example, *Tenellia ventilabrum* and *Eubranchus doriae* originate from an epithelial proliferation of the floor of the pallial cavity, and not the roof of the pallial cavity as in Type 1 veligers. This was determined from comprehensive histological studies, with veligers fixed daily prior to settlement, and every two hours during metamorphosis itself. Several specimens were examined at each stage, and in sagittal, transverse and frontal series sections. The origin of the definitive mantle in these two species was undoubtedly not epipodial, as had been suggested by Bonar (1976) for *Phestilla sibogae*, Bergh, 1905. Initially, there is no continuity between the proliferative tissue which will give rise to the notum and the pedal or nuccal epithelium (Figs 2C,D). The cells of this proliferative tissue are not yet differentiated; they present a high nucleo-plasmatic ratio and some mitosis can be seen. The junction with the cephalopodium epithelium on each side of, and behind, the head is effective only at a later stage, when the functional differentiation of the future notal cells has occurred.

What led Bonar to his assertion of the origin of the notum? With regards to *Phestilla sibogae*, he stated (p. 577) that '... The two possible origins of adult epidermis are 1) the transformation of existing pallial tissues, or 2) the enclosure of the visceral mass of epipodial tissue migration over the lateral and dorsal sides of the body'. Thereafter, he deduced that '... the morphological similarities of the epidermis of the entire postlarval body to that of the larval foot make it clear that the latter mode is the most likely one', and '... since the definitive epidermal cell type is already present in the larval foot, it is reasonable to conclude that these cells migrate to enclose the entire body'. Both Thompson (1958, 1961, 1962, 1967), for *Adalaria proxima* (Alder & Hancock, 1854),*Tritonia hombergi* Cuvier, 1803 and *Cadlina laevis* Cuvier, 1804, and Tardy (1970a), for *Aeolidiella alderi* Cocks, 1852, had, however, clearly shown that this is not the case.

Bonar (1976) assessed the possible rôle of cell division in epidermal migration by stimulating larvae of *Phestilla sibogae* to metamorphose in the presence of colchicine, a mitotic inhibitor. Such treatment led him to conclude that '... larvae were able to metamorphose and undergo epidermal migration ... although further post-metamorphic development was arrested.' Bonar was almost certainly correct in concluding that colchicine blocked mitotic divisions related to foot elongation because such mitotic activity is important throughout juvenile life. Moreover, he also noted that '...no mitotic figures were ever detected (in the notum) in metamorphosing larvae' of *P. sibogae*. However, during the period chosen for this blocking experiment, it is highly likely that the mantle proliferation was already complete, as it is for *Eubranchus doriae* and *Tenellia ventilabrum* metamorphs (Fig. 2), and there is, therefore, no reason why normal metamorphosis should not proceed. Indeed, the same explanation would extend to his deduction (from experiments with cytochalasin B) that no intracellular contractile system is involved in the metamorphic process.

In fact, all the main benthic juvenile structures, including the buccal bulb, radula and initial notum cells, are present or almost complete at the onset of the larval competent period. Although the notal cells are not yet differentiated at competence, it is likely that the cell proliferation in *Phestilla sibogae* is extremely rapid.

For the above reasons it therefore appears that an epipodial origin for the notum of Type 2 nudibranch veligers seems unlikely. Furthermore, the well known details of this phenomenon, observed during the metamorphosis of *Berthella plumula* (Montagu, 1803) (Tardy, 1970a), *Pleurobranchaea japonica* Thiele, 1925 (see Tsubokawa & Okutani, 1991), and Type 1 and Type 2 nudibranch veligers (above), perhaps are indicative of the evolutionary and phylogenetic trends in the formation of the definitive mantle (Fig. 3). First, in the Pleurobranchidae (putative ancestors of the Doridoidea), the entire pallial roof undergoes cell proliferation beyond the aperture of the shell to result in its internalization. The second process can be seen in Type 1 nudibranch veliger larvae, in which mantle proliferation occurs at the roof and floor of the pallial cavity but does not include the mantle fold. The third process characterizes Type 2 nudibranch veliger larvae: here, the proliferation occurs only amongst the cells of the floor of the pallial cavity. With subsequent cytodifferentiation the inflated cells of the pallial floor join the lateral epipodial and nuccal epithelium and overlay the visceral mass, which itself subsides into the enlarged cavity formed by the elongation of the cephalopodium.

5. The visceral loop of Type 2 veligers is more compact and cephalized than is that of Type 1 veligers. However, as Tardy (1974) has shown, it is impossible to distinguish all the different typical ganglionic masses of this part of the nervous system (Tardy, 1974).

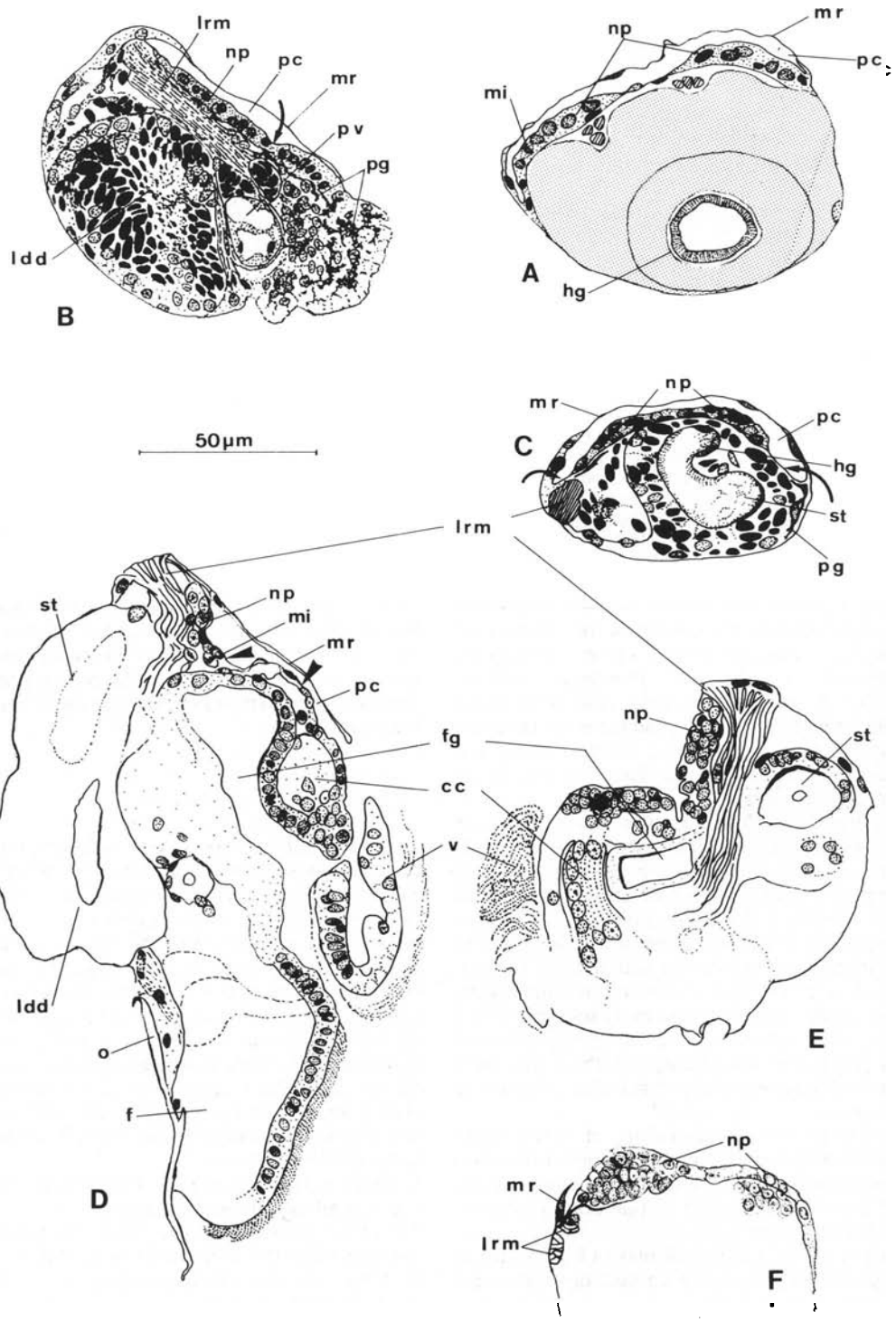

Figure 2. Drawings of histological sections of veligers of *Embletonia pallida* (**A-C**) and *Eubranchus doriae* (**D-F**). **A.** Transverse section through the visceral mass of a veliger at hatching: here, the cells of the notum primordium lie on each side of the roof of the pallial cavity and approximately 11% of these cells show mitosis. **B.** Parasagittal section, of a searching phase veliger, at the level of the larval retractor muscle, showing the notum primordium joining the neck epithelium (arrow). No mitosis has been seen in the cells of the notum primordium. **C.** Same veliger stage as **B**: transverse section through the upper part of the mantle cavity. There is no mitosis seen in the notum primordium. Note the complete separation of the notum from the lateral edges of the pallial cavity (arrowed). **D.** Parasagittal section of *E. doriae* at hatching; the notum rudiment comprises a few cells in which some mitosis can be seen. A thin embryological epithelium clearly separates this rudiment from the neck epithelium (arrow heads). **E.** Oblique section of a 6 h 'diapause' veliger: the notum is thicker, but there is no mitosis seen. **F.** Transverse section of a 12 h 'diapause' veliger. There is no mitosis seen, but the characteristic functional differentiation of the definitive mantle has appeared. Abbreviations: cc, cerebral commissure; f, foot; fg, foregut; hg, hidgut; ldd, left digestive diverticulum; lrm, larval retractor muscle; mi, mitosis; mr, mantle remains; np, notum primordium; o, operculum; pc, pallial cavity; pg, pigment; pv, pulsatile vesicula; st, stomach; v, velum.

6. Type 2 veligers are recorded for some species of the Dendronotoidea (e.g. *Lomanotus staueberi, Dendronotus frondosus* (Müller, 1776), *D. iris* Cooper, 1863, *Hancockia burni, Thetys fimbria* L., 1767) and for many genera of Aeolidoidea (e.g. *Calma, Catriona, Cuthona, Eubranchus, Fiona, Phestilla, Tergipes, Tenellia* and *Trinchesia*).

Type 2 veligers occur only amongst the most highly-evolved opisthobranchs (i.e. the Nudibranchia), and amongst these they are represented only by the most advanced genera, such as *Thetys, Fiona* and *Calma*. It therefore appears that the structure and developmental details of opisthobranchs with a Type 1 veliger might conform to the ancestral, or more primitive, forms amongst these molluscs. The derivative, Type 2, veliger has retained many features of Type 1 development, but there are three main developmental features which distinguish the two:

a) The protoconch shell shape of Type veligers at hatching is similar to that of Type 1 following completion of larval growth at metamorphosis;
b) Development of the notum occurs at its definitive position;
c) The nervous system displays a high degree of cephalization from the earliest developmental stages.

The planktotrophic larvae of two species of Doridoidea, *Gymnodoris striata* Eliot, 1905 and *Gymnodoris* sp. (Boucher, 1986), appear to display a vestigial protoconch shape reminiscent of Vestergaard & Thorson's (1938) shell Type A. However, because all other Doridoidea display Type 1 veliger shells, it is likely that this development is only a modification of the typical Type 1 shell, as is similarly shown by *Cadlina laevis* (Thompson, 1967) but which undergoes non-pelagic lecithotrophic development. The same probably extends to the ascoglossan *Coenia cocksi* (Pelseneer, 1911), in which only a shell gland is differentiated, despite all other representatives of the family displaying exclusively the Type 1 veliger shell.

Although shell shape is not invariate amongst Type 1 species, the developmental pattern amongst these veligers does appear to be consistent. The Type 2 veliger shell does not, by contrast, show any variation or deviation from the theme, and this remains the case even for those species with larger eggs and higher yolk content and which show prolonged intra-capsular development. Amongst nudibranchs the larval strategies of planktotrophy, pelagic lecithotrophy and non-pelagic lecithotrophy clearly correlate with egg size, and thereby yolk content (see Todd & Doyle, 1981), but are not associated with either veliger type. There is, therefore, no phylogenetic basis to the occurrence of the above larval strategies amongst the opisthobranchs.

TORSION

Aspects of the process of torsion among nudibranch molluscs are still controversial. With regard to the adaptive significance of torsion, Garstang's (1928, 1929) hypothesis is still pre-eminent, but remains to be validated. Garstang maintained that the advantage of torsion lay in its conferring upon the larva the ability to withdraw first the (vulnerable and important) head and velum in response to putative predator attack: the foot is the last structure to be retracted into the shell aperture. Both Ghiselin (1966) and Thompson (1967) have addressed this perplexing problem and here, I address three specific questions:

1) Does a 180° twisting of the visceral mass occur in all opisthobranch veligers?
2) Are the movements of the anal cells a useful criterion indicative of the real extent of torsion?
3) What are the processes involved in this phenomenon?

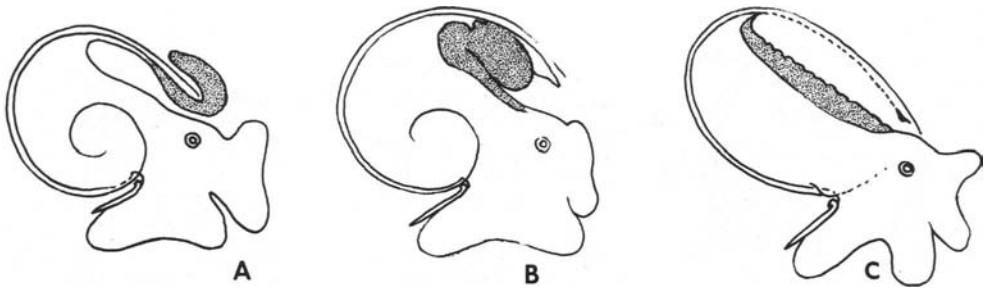

Figure 3. Schematic drawings of veligers just prior to metamorphosis. The proliferative tissue which will give rise to the notum is stippled. **A.** *Berthella plumula* (note that the proliferation covers the shell). **B.** *Aeolidiella alderi* (note that the mantle fold is not involved in the formation of the notum). **C.** Type 2 veliger (e.g. *Tenellia ventilabrum, Eubranchus doriae*); proliferation of the notum occurs in its definitive position.

Pelseneer (1911) noted that a clear and full 180° twisting occurred in the veligers of *Cuthona concinna* (Alder & Hancock, 1843) and *C. foliata* (Forbes & Goodsir, 1839) and Hamatani (1960) observed the same for *Catriona ornata* (Baba, 1937) and *C. pinnifera* (Baba, 1949). Conversely, Thompson (1958) suggested that '. . . torsion, as it affects the visceral organs in the opisthobranch embryo, never approaches the full 180° twisting in living Diotocardia.' Subsequently, in discussing the displacement of the anal cells, Thompson (1962) claimed that '. . . this movement is the sole vestige in *Tritonia hombergi* of the ontogenetic mechanical processes of gastropod torsion and ventral flexure.' He later (Thompson, 1976) maintained this opinion, despite Tardy (1970a) having demonstrated a full 180° torsional twisting which persists throughout the adult life of *Aeolidiella alderi*, and which was proposed to be characteristic of all opisthobranchs.

It seems likely that the major problems in interpreting torsion lie in the fact that the process is generally complete within a few hours, and that it is thus difficult to study in detail. More importantly, however, torsion usually has been studied in species with lecithotrophic development, in which species the large amounts of embryonic yolk may occlude the process of interest. Furthermore, torsion occurs earlier amongst lecithotrophic, than among planktotrophic, veligers and this further exacerbates comparative analyses. In the specific instance of opisthobranchs there is also the related complication of the process of 'detorsion'.

Necessarily, because of the anatomical connexions between the visceral mass and the cephalopodium, it is obvious that a full twisting is not possible at the immediate junction of these two morphological components of the body. At the apex of the visceral mass, however, a full twisting occurs within approximately 12 h in *Aeolidiella alderi* (Tardy, 1970a), despite the presence of large quantities of embryonic yolk. For example, the stomachal opening of the hindgut—which is initially ventral—becomes dorsal following torsion, and the shell gland undergoes a similar relocation. Meanwhile, however, the anal cells move only by an angular twisting of approximately 35-40° (see Fig. 4).

If the visceral mass is sectioned in a series of parallel plan slices, taken perpendicular to the torsional axis of rotation, Z—Z′ (Fig. 5), and if it is postulated that all the parts of the plan containing 'a' (joining the visceral mass and cephalopodium) remain fixed, we can visualize all parts containing 'b' to undergo an angular relocation of 30° to the right. Similarly all those parts of the plan containing 'c' would move 60° to the right, and so on. All parts of the 'g' section and above undergo a full 180° displacement.

What is the mechanism involved? All muscular activity would appear to be precluded because these are not yet differentiated, and indeed, may not do so during embryogenesis of, for example, *Cadlina laevis* (Thompson, 1967). The most likely mechanism is one of differential cell growth and proliferation. In the case of *Aeolidiella alderi*, torsion occurs in embryos with a substantial connexion between the visceral mass and cephalopodium, and with only a shell gland (before the shell is formed). This latter feature is perhaps especially important in facilitating the mechanical twisting of the embryo and subsequently allowing deposition of the restrictive shell in its definitive position. In the cases of *Adalaria proxima* (Thompson, 1958), *Trionia hombergi* (Thompson, 1962) and *Cadlina laevis* (Thompson, 1967) there are very similar

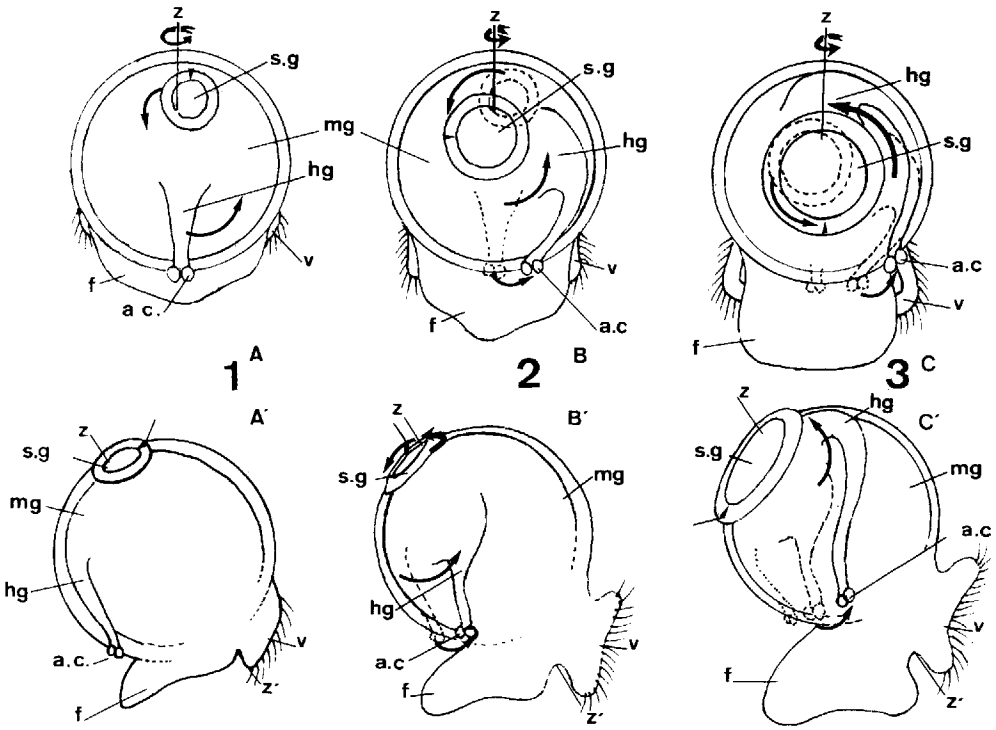

Figure 4. Three schematic stages of torsion in *Aeolidiella alderi*. 1. Pre-torsional larva, (**A**) posterior and (**A'**) right lateral views. 2. Intermediate stage (same angular views). 3. Post-torsional larva (arrows indicate the twisting displacements). Abbreviations: ac, anal cells; f, foot; hg, hindgut; mg, midgut; sg, shell gland; v, velum; Z—Z', axis of torsion.

patterns of development to *A. alderi*: the likelihood is that this scheme applies to all Type 1 lecithotrophic or intracapsular species even if, as in *Coenia cocksi* (Pelseneer, 1911), no shell is developed.

For all other veligers, irrespective of the shell type or quantity of yolk, the torsion gradient zone is a rather narrow and elongate peduncle linking the apex of the visceral mass to the cephalopodium. The protoconch is almost complete at the time that torsion occurs, and in no instance does the shell hinder or constrict torsional movements: torsion here concerns only the twisting of the umbrella-like visceral apex relative to the cephalopodium.

This process is especially readily seen in Type 2 veligers (see Figs 6A, B, before and after torsion). Here also it clearly can be seen that the stomachal opening of the hindgut (ventral pre-torsional, dorsal post-torsional), the shell and the larval retractor muscle undergo a full 180° twisting. Contemporaneously, the anal cells, left and right digestive diverticula and the larval kidney move only slightly, as had previously been noted for the above lecithotrophic species. In no case, therefore, does movement of the anal cells provide an adequate measure of the true amplitude of overall torsion: all opisthobranchs display a torsional gradient culminating in an apical 180° twisting. Moreover, for adult opisthobranchs, the only evidence of 180° torsion is the post-torsional dorsal location of the hindgut opening of the stomach—this persists throughout the adult's life, from the veliger stage onwards, despite the process of detorsion. It is important to note, in this context, that it is only an apparent, superficial detorsion that occurs amongst opisthobranchs. This is clearly illustrated amongst, for example, the Aeolidoidea (see Fig. 7), in which all of the posterior right-side groups of cerata emanate from the left digestive diverticulum.

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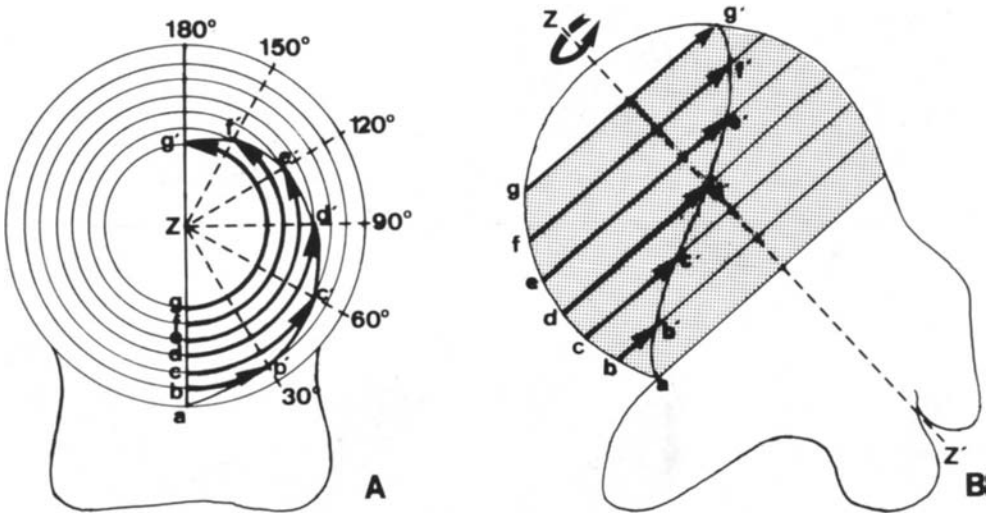

Figure 5. Hypothetical diagrams illustrating how the gradient of torsion might be achieved for a Type 1 veliger with intracapsular metamorphosis. (To clarify the figure, the a, b and c slices of the visceral mass are exaggerated and represented as being larger than all the others. The torsional axis is perpendicular to the drawing at point Z.) **A.** Posterior view. **B.** Lateral right side view, with the gradient torsion zone stippled.

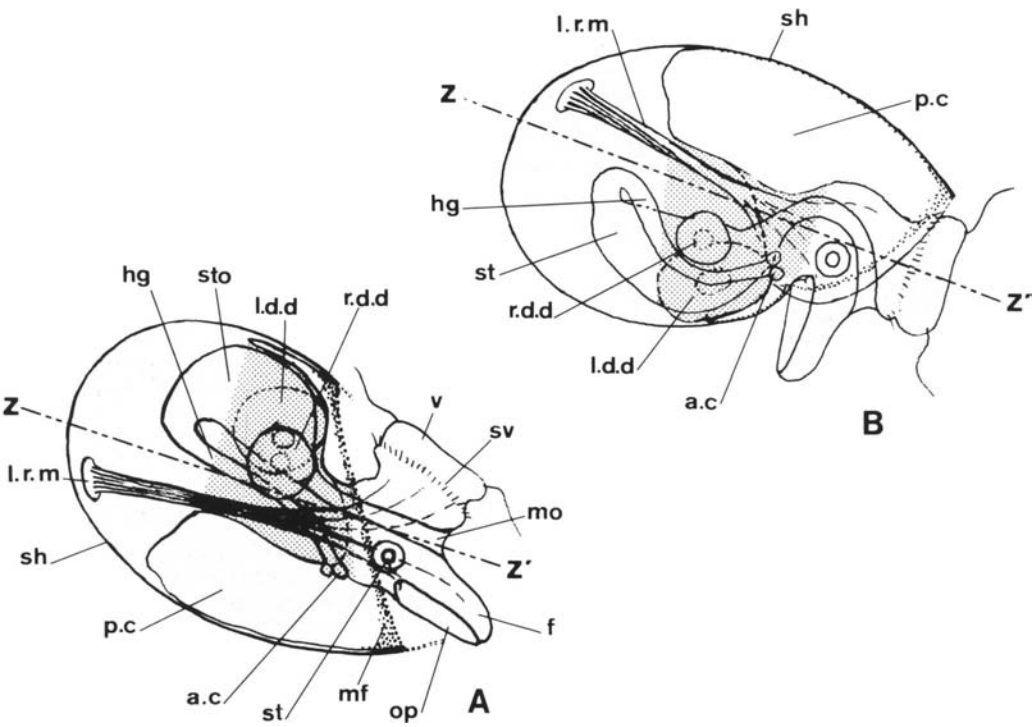

Figure 6. Hypothetical diagrams illustrating how the gradient of torsion might be achieved in a Type 2 veliger. **A.** Pre-torsional larva, lateral right view. **B.** Post-torsional larva, lateral right view. The Z—Z′ axes have been illustrated as parallel, but it is not possible to place the cephalopodium in the same position owing to the differential growth of the shell and of the visceral mass. Abbreviations as for Figs 2 & 4, except mf, mantle fold; mo, mouth; rdd, right digestive diverticulum; sh, shell; st, statocyst; sto, stomach; sv, subvelum. The gradient of torsion is shown stippled.

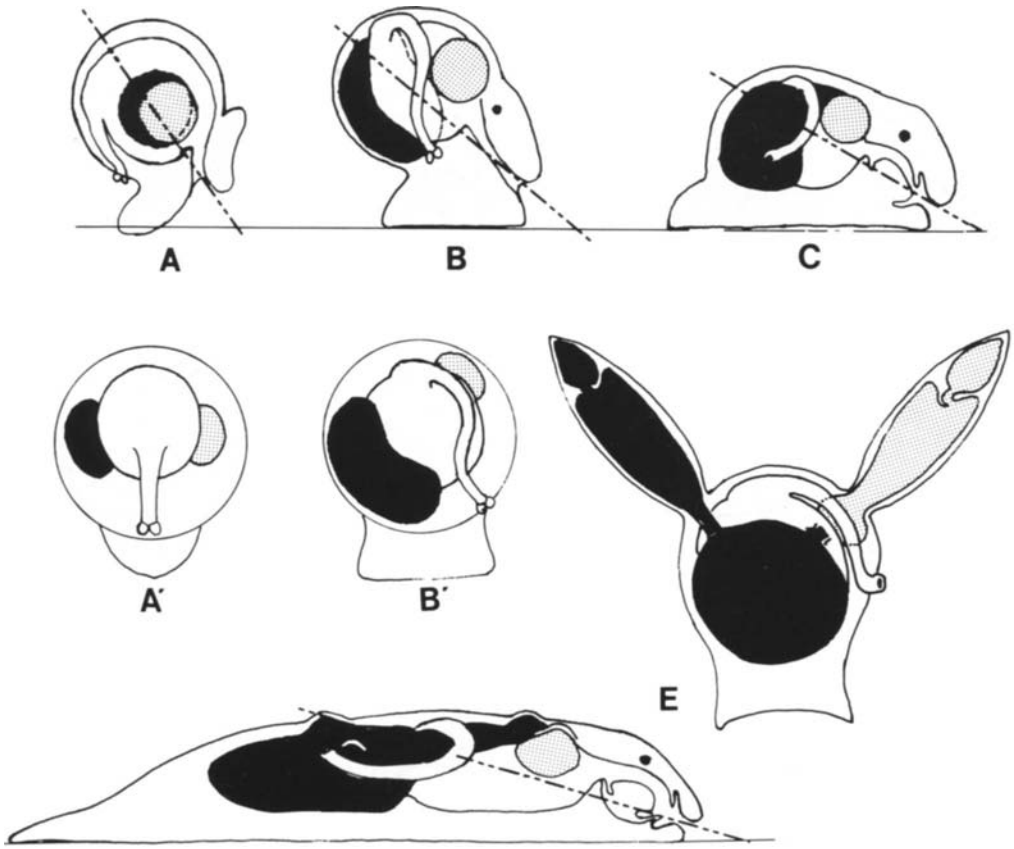

Figure 7. Schematic drawings of *Aeolidiella alderi* (**A-D**) and *Tergipes despectus* (**E**), showing the progressive proximity of the torsional axis (Z—Z') to that of antero-posterior elongation during larval development. **A** and **A'.** Hypothetical pretorsional veliger, lateral right and posterior views. **B** and **B'.** Post-torsional larva, lateral right and posterior views. **C.** Flattening larva. **D.** 'Limapontioid' stage. **E.** Posterior view: for clarity, only the root of the first right ceras (emanating from the left digestive diverticulum) is illustrated. The right and left digestive diverticulum are shown, respectively, stippled and darkly shaded.

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