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# THE BRACHIOPOD FOLD: A NEGLECTED BODY PLAN HYPOTHESIS

by BERNARD L. COHEN, LARS E. HOLMER *and* CARSTEN LÜTER

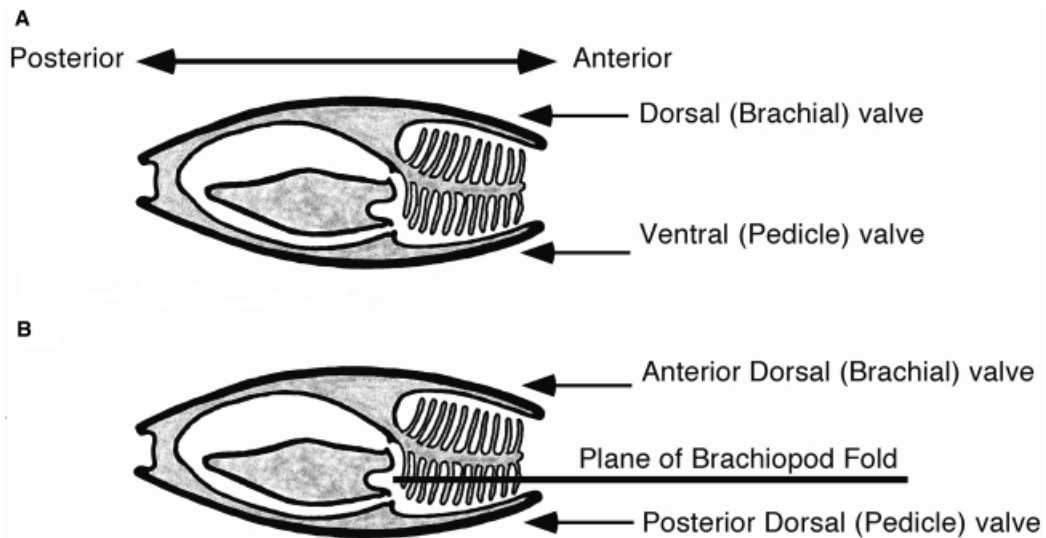
**ABSTRACT.** Attention is drawn to Nielsen's radical body plan concept, here named the 'brachiopod fold hypothesis', under which brachiopods and phoronids are recognized to be transversely folded across the ontogenetic anterior-posterior axis so that, to make useful comparisons with other phyla, these organisms must be conceptually unfolded. Under the hypothesis brachiopod brachial and pedicle shell valves are respectively 'anterior' and 'posterior' rather than 'dorsal' and 'ventral' as traditionally described. The hypothesis makes sense of the symmetry axes of the brachiopod shell, is consistent with various indications from fossil and Recent brachiopods, and gives rise to predicted patterns of axis-determining gene expression that differ from those obtaining under the traditional view of the body plan, whilst the variety of folding movements in different lineages implies that superficially dissimilar morphogenetic folds may be fundamentally homologous. Convergent folding patterns are noted in some other organisms. A previous conjecture that inarticulate linguloid brachiopods were derived from halkieriid-like ancestors is elaborated with proposals that recognize possible functional continuities of coelomic and marginal sclerite functions, and it is noted that an ancestrally facultative fold could have become incorporated by genetic assimilation into the brachiopod developmental program. An experimental approach is outlined to test the possibility that some members of the 'small shelly fauna' may have been members of the halkieriid-like brachiopod stem lineage and it is also suggested that buoyancy modification may have been an important function of mineralization amongst Lower Cambrian floaters and swimmers, since negative buoyancy would facilitate access to the benthic niche.

**KEY WORDS:** body plan, *bauplan*, brachiopod, phoronid, halkieriid, tommotiid, Lower Cambrian.

*'False facts are highly injurious to the progress of science, for they often endure long; but false views, if supported by some evidence, do little harm, for every one takes a salutary pleasure in proving their falseness.'* Charles Darwin, *The Descent of Man*.

THE phylum Brachiopoda, as traditionally defined, contains a number of morphologically characterised fossil and extant groups with bivalved shells. The two main extant brachiopod lineages, currently treated as subphyla (Williams *et al.* 1996), comprise one numerically dominant group with a highly mineralised, hinged shell (articulate brachiopods), and one group with valves connected only by soft tissues (inarticulate brachiopods, comprising three lineages: craniids, discinids and lingulids). Recent molecular evidence has confirmed the monophyly of brachiopods, but with the qualification that the phylum also includes, as an additional subphylum, the shell-less, tubicolous, former phylum Phoronida (Cohen and Gawthrop 1996, 1997; Cavalier-Smith 1998; Cohen *et al.* 1998; Zrzavy *et al.* 1998; Cohen 2000), though this has been questioned (Peterson and Eernisse 2001). For present purposes, except where stated otherwise, 'brachiopod' includes phoronid. It is clear from multiple, independent lines of molecular evidence that brachiopods are allied to protostomes, not deuterostomes (Cohen 2000 and references therein).

The traditional view of the brachiopod body plan (phoronids excluded) is shown in Text-figure 1A. The sagittal plane of bilateral symmetry passes through both valves from the so-called dorsal to the so-called ventral sides. This dorso-ventral (D-V) plane runs from the traditionally anterior, median margin of the shell commissure to the traditionally posterior, mid-region of the interarea, hinge or pedicle. The dorsal shell valve is closely associated with, and often supports, a feeding organ, the lophophore. Because mineralized lophophore supports are called brachidia, the so-called dorsal valve is also termed 'brachial'. The so-called ventral valve, which in some groups surrounds the fleshy stalk or pedicle, is also described as the 'pedicle' valve.



TEXT-FIG. 1. The brachiopod body plan. Diagrammatic sagittal sections of a generalised brachiopod showing paired valves, the brachial valve supporting the lophophore, and a U-shaped gut with the mouth adjacent to the lophophore base. A, the traditional body plan. The sagittal section, corresponding to the plane of bilateral symmetry, passes medially through the anterior-posterior axis; the dorso-ventral axis is in the paper plane. B, the brachiopod fold hypothesis body plan. The sagittal section passes medially through the anterior-posterior axis but the dorso-ventral axis is transversely folded around the plane shown (perpendicular to the paper). Both exterior surfaces are aboral and correspond to anterior and posterior segments of the traditional dorsal side. Note that the lophophore is bilaterally paired, not medial as the diagram suggests.

This traditional view of the brachiopod body plan appears to be based upon no explicit hypothesis of evolution or ontogeny, nor of relationship to the body plans of other phyla. If the traditional D-V axis layout is correct with respect to developmental origins, then the two shells bear to one another the same sort of relationship as do, for example, the dorsal tergites and ventral sternites of arthropods. But they do not have similar developmental origins.

#### OBSERVATIONS, HYPOTHESIS AND DISCUSSION

A radically different view of the brachiopod body plan (Text-fig. 1B) was originally suggested by Nielsen in his account of the embryology of a craniid (Nielsen 1991), in which he observed that before shell secretion commences, muscular contraction folds the embryo's posterior end ventrally, so that the two shells arise respectively on anterior and posterior portions of the surface opposite where the mouth will later form, i.e. on the aboral, dorsal surface. Thus before folding, the distal, commissure-fated ends of the two shell valves face towards opposite (traditional anterior and posterior) ends of the creature but, after folding, both commissure-fated ends face the (traditional) anterior end. That is to say, the animal folds transversely across its A-P axis, leaving the traditional dorsal side outermost. Nielsen adopted this body-plan interpretation in diagrams representing all extant brachiopod lineages and (with ventral side outermost) phoronids (Nielsen 1991, 1995, 2001), but did not name it or discuss its implications for brachiopod biology.

Nielsen's interpretation of the brachiopod body plan is supported by observations of a relevant folding event in at least one representative of each principal extant lineage except discinids, whose embryology is not yet fully described. In the lingulid *Lingula*, the shell is secreted by the mantle on the aboral side of the

embryo and folds across its middle to form the two valves (Yatsu 1902). In another lingulid, *Glottidia*, the shell begins to form considerably earlier, before gastrulation is completed, and it is not clear whether any fold-like movement occurs (Freeman 1995), but the overall body plan is similar to that of *Lingula*, with a U-shaped gut and bivalve shell. In the discinid, *Discinisca*, the two shells grow holoperipherally from separate *anlagen* to enclose the body and no equivalent folding movement has been clearly observed (Chuang 1977; Freeman 1999). However, as in *Glottidia*, the overall form of discinids makes it reasonable to infer that an obvious fold has either been lost or has so far escaped notice. In articulate brachiopods the situation is complicated by the existence in larvae of a third, pedicle lobe, basal to the shell-forming mantle lobe. In this lineage a skirt-like fold of mantle first extends posteriorly from the mantle lobe and this mantle skirt later reverses so that it comes to extend apically, causing the developing shell valves to enclose the lophophore and main body mass, and enabling the pedicle to take its final position in the interarea between the valves (Williams *et al.* 1997, fig. 160). Thus, in articulate brachiopods mantle reversal represents the relevant folding event. Phoronids (except *Phoronis ovalis*) are notorious for the morphogenetic revolution by which the anterior-posterior (A-P) axis of the actinotroch larva is transformed, by evagination of the metasomal sac at right angles, into the folded axis of the adult, although compared with brachiopods this fold has a different orientation relative to the dorso-ventral (D-V) plane (Emig 1977). Thus, as Nielsen suggested (Nielsen 1991), some sort of transverse fold across the A-P axis has been observed (or may be inferred) in all major lineages of extant brachiopods and in phoronids. We propose to call Nielsen's body plan concept the 'brachiopod fold' (BF) hypothesis.

One point immediately in favour of the BF hypothesis is that, compared with the traditional view, it makes better sense of the symmetry axes of the brachiopod shell. The traditional symmetry axes (Text-fig. 1A) are superficially unlike those of any other phylum and defy any simple ontogenetic interpretation. By contrast, on the BF hypothesis the brachial valve is indeed 'dorsal' (i.e. on the aboral side of the ontogenetic A-P axis) but the pedicle valve is not 'ventral' except in the trivial sense of ending up opposite the dorsal valve; instead, it is posterior dorsal (Text-fig. 1B). Moreover, the axis of bilateral symmetry no longer appears to be perpendicular to that of other organisms, most conspicuously of bivalve molluscs. Instead, it corresponds, as usual, to the mid-dorso-ventral (sagittal) plane along the ontogenetic A-P axis.

Other points consistent with or supporting the BF hypothesis include: (1) it provides a potential ontogenetic pathway of continuity between embryonic or larval longitudinal muscles and adult shell valve adductors; (2) if, as seems likely, the plesiomorphic mantle was a continuous A-P structure, then in terms of brachiopod anatomy, fused posterior mantle lobes would have been present, as they are in *Lingula* embryos today. Fused mantle lobes have also been inferred to be present in the earliest known fossil brachiopods (Class Paterinata, lower Tommotian) and were probably also present in the problematic (Early Cambrian–Permian) chileate rhynchonelliformeans (Popov *et al.* 1996; Williams *et al.* 1998b). In this respect a possible inconsistency arises in *Nisusia*, which has been said to have a posterior anus (Rowell and Caruso 1985). However, the putative fossil faecal material on which this was based is now thought to be a misidentified pedicle (Popov and Holmer, unpublished) or a faecal extrusion from a *Crania*-like secondary anus (Nielsen 1991). This minor and uncertain exception aside, we know of no definite evidence from fossil or living brachiopods that is inconsistent with the BF hypothesis. Therefore, extant and fossil adult brachiopods, and extant phoronids, may best be understood as folded across the primary A-P axis; they must be conceptually unfolded in order to make useful comparisons with other phyla. To give consistent expression to this view, the brachial valve should henceforth be described as 'anterior' rather than 'dorsal', and the pedicle valve correspondingly should be 'posterior' rather than 'ventral'.

Acceptance of the BF hypothesis bears on the general question of the recognition of putatively homologous structures and processes in different phyla; it implies (we believe) that superficially dissimilar morphogenetic folds may be fundamentally homologous. Other examples of superficially different, but apparently homologous, fundamental features of protostome embryology which vary amongst taxa ranging from phylum to species include: (1) the blastopore which generally, but not invariably, forms the mouth; (2) the coelom, which forms in different ways in quite closely related taxa; and (3) the relationship between the first cleavage division plane and the future larval plane of bilateral symmetry (Freeman 1995 and references therein). Thus, there is ample precedent for identification of apparently

divergent phylum-level, body-plan characters as putatively homologous. This morphological variability can be rationalised if, in the present state of knowledge, the crucial question is not whether developmental events take place by cellular or tissue mechanisms of proven homology (for which there is no absolute criterion) but whether they occur in lineages that share a common ancestor and achieve similar end-results by broadly comparable means. Only the fact of descent from a common ancestor guards (however weakly because dealing with discontinuities of *bauplan*) against the similarity being convergent. It remains to be seen whether more stringent homology criteria will become applicable when the roles are known of specific morphogenetic gene complexes in such movements. Current data tend to suggest that gene recruitment is also plastic and convergent, so that stringent comparisons even at the level of gene expression or genomic architecture may provide little more certainty about *bauplan* inter-relations. However, if not obscured by such complications, the BF hypothesis predicts that in brachiopods: (1) the expression of D-V axis-determining genes in both valves will result in a gradient running from the dorsal, exterior, shell-secreting epithelium to the ventral, interior, mantle epithelium: and (2) the expression of A-P axis-determining genes will result in a gradient running from the commissure to the interarea in the brachial valve and from the interarea to the commissure in the pedicle valve (see also Cohen and Gawthrop 1997). These predictions differ from those arising from the traditional view of the body plan.

The ubiquity of convergence in evolution has been stressed (Moore and Willmer 1997) and it is not surprising to find that elements similar to the brachiopod fold appear elsewhere. For example, a facultative transverse axial fold (i.e. rolling up) and similarly shaped but oppositely facing anterior and posterior dorsal shells occur in agnostid trilobites (Upper Cambrian) (Muller and Walossek 1987), although there is no indication that trilobite flexure ever became genetically assimilated. A somewhat U-shaped gut also occurs in lepadomorph cirripedes and in ascidians, where it is a correlate of sessility.

## SPECULATIONS

### *From halkieriid-like stem organism to brachiopod*

Detailed consideration of the structure and possible functional roles of articulated halkieriid shells and sclerites, and the possible relationships of halkieriids to other animals, led Conway Morris and Peel (1995) to argue that these creatures may be regarded as stem-lineage brachiopods. Conway Morris (1998, fig. 86) also outlined a conjectural series of transformations, involving a (possibly facultative) brachiopod fold, for the origin of brachiopods from a halkieriid-like ancestor. We wish to suggest a modification of this conjecture, based upon the conserved Cambrian–Recent infaunal habit of lingulids.

With a fluid-filled coelom and (if *Halkieria evangelista* is representative) a close covering of epidermally embedded, dorso-lateral sclerites and other embedded rods, the body of a halkieriid-like animal would be relatively resistant to longitudinal compression but not necessarily resistant to flexure. Hence a facultative brachiopod fold could be formed by the almost-isometric contraction of paired longitudinal muscles if these inserted into the anterior and posterior shells. Such a fold would lead to quasi-apposition of the shells. Could such apposed shells have had, or been preadapted to permit the evolution of, another function? It may be peculiarly relevant that the infaunal habit of linguloids has persisted, with minor variations (Savazzi 1986), from the Early Cambrian (Pemberton and Kobluk 1978) to the present day. Observations and experiments on living linguloids (Thayer and Steele-Petrovic 1975; Savazzi 1991) reveal that when they burrow, scissors-like oscillations of the valves cause the overlapping marginal setae to transport mineral grains rearwards. By analogy, if a facultatively folded halkieriid-like animal could also move ('wiggle') its shell-bearing ends relative to one another (perhaps by phased unilateral contractions of longitudinal mantle muscles), its marginal sclerites might well have generated a linguloid type of grain transport, facilitating burrowing or some other form of bioturbation. There is no evidence that known halkieriids were infaunal, but this is not excluded, and at least some are loosely associated with burrows (Conway Morris and Peel 1995; Conway Morris *et al.* 1998). This combination of a facultative brachiopod fold with linguloid-type sediment engineering provides a novel route for a functionally continuous transition from stem-group halkieriid-like ancestor to linguloid-like brachiopod. Another plausible functional continuity would exist if coelom pressure was used to unfold a

facultatively folded halkieriid, as it is to open the linguloid gape (Guttman *et al.* 1978; Trueman and Wong 1987). The suggestion that a facultative fold became a fixed component of the body plan may appear over-speculative, but it is consistent with an experimentally established evolutionary mechanism, 'genetic assimilation', through which an environmentally contingent modification of the phenotype, if favoured by selection, may become developmentally programmed (Waddington 1953, 1957). Thus, the proposal that halkieriid-like organisms should be viewed as members of the stem-group that gave rise to the brachiopods, and had a close affinity to linguloids (Conway Morris and Peel 1995), is morphologically, functionally, genetically and palaeontologically plausible.

Incidentally, we note that development of a mineralized shell (or other body parts) will facilitate the settlement of otherwise pelagic and nektonic organisms. This buoyancy-modifying role of mineralization appears previously to have been overlooked (e.g. Bengtson and Conway Morris 1992), but it may have been a crucial development since it could have provided an energetically favourable (or simply practical) way to enter, occupy and exploit the benthic niche whilst also providing protection against predation. Thus, the appearance of a range of mineralized taxa such as trilobites, tomotiids and halkieriids in the Lower Cambrian may simply reflect the sporadic origin, amongst a wide range of existing unmineralized floaters and swimmers, of negatively buoyant, mineralized lineages. Buoyancy modification may also account for the array of silica tablets recently discovered to decorate the larval periostracum of Palaeozoic–Recent discinid brachiopods (Williams *et al.* 1998a, 2001; Williams 2003).

#### *The brachiopod fold in 'small shelly fauna' fossils?*

Many 'small shelly fauna' fossils (such as tomotiids) may represent disarticulated halkieriid-like organisms or other stem-group brachiopods. The possibility that in some cases these shells were facultatively apposable and quasi-apposed in some life conditions may be open to test if anything approaching a commissure had evolved, since principal components analysis of digitised shell outlines could suggest that a population of shells from a single geological horizon cluster in pairs, ideally corresponding to anterior and posterior shells of individuals. Amongst a large collection of such paired shells growth anomalies such as follow an arthropod claw-nip could provide unambiguous evidence of apposition. In *Halkieria evangelista* minor damage of this type has been reported, but only in a single shell (Conway Morris and Peel 1995, fig. 39c).

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BERNARD L. COHEN

University of Glasgow  
Institute of Biomedical and Life Sciences  
Division of Molecular Genetics  
Pontecorvo Building  
56 Dumbarton Rd.  
Glasgow G11 6NU, UK  
e-mail b.l.cohen@bio.gla.ac.uk

LARS E. HOLMER

Institute of Earth Sciences, Historical Geology  
and Palaeontology  
Norbyvägen 22  
S-75236, Uppsala, Sweden  
lars.holmer@pal.uu.se

CARSTEN LÜTER

Humboldt-Universität zu Berlin  
Museum Für Naturkunde  
Invalidenstrasse 43  
D-10115, Berlin, Germany  
carsten.lueter@rz.hu-berlin.de