

Terminal addition, the Cambrian radiation and the Phanerozoic evolution of bilaterian form

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SUMMARY We examine terminal addition, the process of addition of serial elements in a posterior subterminal growth zone during animal development, across modern taxa and fossil material. We argue that terminal addition was the basal condition in Bilateria, and that modification of terminal addition was an important component of the rapid Cambrian evolution of novel bilaterian morphology. We categorize the often-convergent modifications of terminal addition from the presumed ancestral condition. Our focus on terminal addition and its modification highlights trends in the history of animal

evolution evident in the fossil record. These trends appear to be the product of departure from the initial terminal addition state, as is evident in evolutionary patterns within-fossil groups such as trilobites, but is also more generally related to shifts in types of morphologic change through the early Phanerozoic. Our argument is contingent on dates of metazoan divergence that are roughly convergent with the first appearance of metazoan fossils in the latest Proterozoic and Cambrian, as well as on an inference of homology of terminal addition across bilaterian Metazoa.

INTRODUCTION

We argue that bilaterian evolution began with, and evolved from, a shared ancestral condition that included terminal addition as a critical component of development. Terminal addition here refers to growth and patterning in a posterior (or in the case of echinoderms, distal) subterminal growth zone. Terminal addition is more obvious morphologically when repeated pattern elements are added in the growth zone and has been most extensively discussed in segmented taxa. Our more general definition of “growth and patterning” permits an examination of the course of modification of terminal addition across the range of bilaterian morphology. In our view, departure from an initial mode of terminal addition provided a “set of avenues” for body plan modification. Thus, we are singling out one, very critical, component of body-plan evolution for an initial examination.

Inferring terminal addition as a starting condition in bilaterian evolution constrains evolutionary interpretation, yielding the following predictions: (1) departure from the ancestral terminal addition state should be evident in the evolutionary transitions among modern bilaterian groups; (2) early phanerozoic patterns of evolutionary departure from a terminal addition condition should be evident in the morphologic history of lineages inferred from phylogeny recon-

struction and from fossil data; and (3) the fossil record should document broad changes in the classes of morphologic transitions observed in evolution following departure from the initial terminal addition condition near the base of the Cambrian. Here we make a preliminary assessment of the consistency of the data with these predictions.

For this perspective on metazoan evolution to have broad explanatory value, two premises must hold. First, the bilaterian component of metazoan evolution must have been relatively abrupt in terms of morphologic and phyletic evolution, consistent with the sudden appearance of most phyla in the Cambrian record. We presume that rapid cladogenesis in combination with evolution of disparate morphology contributes to this phase of departure from an ancestral bilaterian. Second, the ancestor of all (or nearly all) living Bilateria must have used some form of terminal addition involving subterminal posterior growth and patterning during development. Both these premises are controversial, but when considered together, they provide a new lens through which one can view the morphologic evolution of Metazoa.

Below we examine our premises, that a sudden radiation occurred at the base of the Cambrian, and that a terminal addition mechanism is ancestral in the Bilateria; we also discuss caveats to the argument. We then classify the possible evolutionary modifications of terminal addition and discuss

each of these modification types, providing examples of each type—many of which appear to have evolved in parallel in multiple lineages. Lastly, we relate the process of modification of terminal addition to the fossil record, considering Ediacaran and trilobite lineages where evolutionary changes in the terminal addition process can be observed, as well as considering the broader implications of these changes for the evolution of bilaterian form in the Phanerozoic record.

JUSTIFICATION OF PREMISES

The Cambrian radiation was rapid

Darwin (1859) suggested that the absence of Precambrian animal fossils was an artifact of the fossil record. However, extensive subsequent investigation of the rock record provides no strong evidence of any animal life prior to the Maranoan glaciation 600 Myr, less than 60 Myr before the fossil record of the Cambrian radiation (e.g., Knoll 2000). Despite this lack of fossil evidence, a recently developed neo-gradualist school maintains that animals including taxa within the Bilateria began diversifying a billion years or more before the first fossil evidence of Metazoa (e.g., Wray et al. 1996; Gu 1998; Wang et al. 1999). This interpretation involves a protein “clock” based on aligned amino-acid sequences from many genes combined in a single analysis. This type of approach allows for gene-specific differences in evolutionary rate, but necessarily presumes that lineage-specific differences in rate that influence the evolution of the whole genome are insignificant. If such an assumption were to hold, precise dates of divergence would be calculable, given the accumulation of protein data from genome sequencing and several well-dated fossil divergences for calibration. However, as discussed below, a priori biological evidence and reasoning suggest that the purifying selection that most proteins experience should yield significantly different rates of change across genomes in different lineages, violating the assumptions of the analysis.

Multi-gene calculation of metazoan divergence dates has come under attack from a number of authors for reasons related to those discussed here (e.g., Ayala 1999; Jacobs 2002; Smith and Peterson 2002), as well as from concerns regarding data alignment and concatenation (e.g., Nei et al. 2001), unwarranted claims of precision (e.g., Graur and Martin 2004), and insufficient fossil calibration (e.g., Peterson et al. 2004). Here we present a brief analysis showing that the first sequenced genomes from the fly and nematode model systems are pervasively biased toward high rates of evolution. Studies that use these and other “high-rate” taxa in multi-gene/protein approaches to calculating divergence times (Table 1) are expected to yield early dates as a product of this bias. Consequently, they do not provide evidence of early metazoan divergence as discussed below.

Table 1. Results of a Blast/Z statistic analysis of sponge genes. If there is no lineage-specific bias in rate of evolution, then individual genes should show higher similarity as a consequence of random gene-specific processes. Thus considering homologous genes sampled from sponges, Human and Nematode the null expectation is that in half the genes the sponge example should be more similar in sequence to Human (Hs) half to Nematode (Ce). Similarly, in the comparison of sponge to human and fly (Dm) half the sponge genes are expected to be similar to Human and half to Fly (comparisons that are equally similar are tabulated under 0 and are dropped from the analysis). Length of aligned amino acid sequence as well as number and percent identity of amino acid residues in the alignment are used in comparisons. As can be seen there is a broad bias in the data and the null of equal rates between lineages can be rejected. Thus the nematode and fly lineages are substantially and pervasively higher in rate than the human lineage as is discussed further in the text.

Comparison of sponge/nematode and sponge/human

Aligned AA Hs 0 Ce	Identical AA Hs 0 Ce	%Identity Hs 0 Ce
80 8 53	106 2 33	98 0 43
Z = 2.3	Z = 6.2	Z = 4.6
Significant	Off table	V. H. Significant

Comparison of sponge/fly and sponge/human

Aligned AA Hs 0 Dm	Identical AA Hs 0 Dm	%Identity Hs 0 Dm
70 14 59	97 4 48	89 3 57
Z = 0.97	Z = 4.1	Z = 2.6
Suggestive	V. H. Significant	Highly Significant

Fly and nematode models are of special concern as they have been the focus of several early analyses because of availability of genome sequence (e.g., Wray et al. 1996; Wang et al. 1999). However, these taxa were originally selected for short generation time, an attribute associated with smaller genome size and high rate of deletion (Petrov et al. 2000). There appears to be a deletion mechanism that maintains the small size of genomes in high generation rate taxa, thus contributing to a higher mutation rate. This is corroborated by the extreme genome evolution of *Oikopleura* (Seo et al. 2001), a larvacean urochordate with a 5-day generation time and the smallest genome known to date for animals (72 Mb).

Our simple analyses of the fly and the nematode data show that they have pervasively higher rates of evolution than the human lineage (Fig. 1; Table 1). Our analyses use comparisons of sequence data from Porifera (sponges), a universally

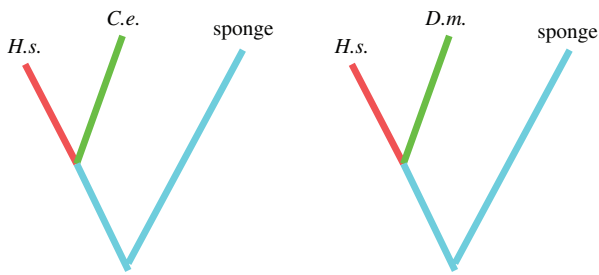


Fig. 1. Branching relationship between sponge, nematode, and human and sponge, fly, and human. Assuming the rates of evolution are the same in the red and green lineages in both examples, then half the genes that have evolved in each lineage should be closer to the sponge. This null can easily be rejected (Table 1) documenting that the green lineages to nematode and fly experience higher rates of sequence evolution across the genome than the red lineage leading to humans.

accepted out-group to Bilateria, first with fly and human sequence data sets, and second with nematode and human data sets. The null prediction is that if rates on the human and fly branches (or the human and nematode branches) are equal, as they must be if lineages have equal rates of evolution as a consequence of random variation and randomly distributed gene-specific processes, then, half the genes should be closer between fly and sponge and half between human and sponge. Thus, 50% of sponge genes are expected to be more similar to a human gene than a fly gene, and 50% will be more similar to a fly gene than a human gene. Significant departure from this null indicates that one of the branches accumulated more changes than the other branch since the time of divergence of these organisms; that is, it has a faster rate of change, therefore creating a broad lineage-related bias in the data. In addition, departure from this null is susceptible to test using the z -statistic, a simple well-established distribution.

The set of sponge genes was selected by retrieving all sponge genes from the NCBI nonredundant protein database (<http://www.ncbi.nlm.nih.gov>), followed by removing redundant gene sequences from the data set that resulted from the multiple sponge species considered, yielding a set of protein sequences. BLAST (Altschul et al. 1990) was used to compare each of these genes to the predicted protein sets from the human, fly, and nematode genomes. Three measures of change from the BLAST output were used: length of aligned sequence, number of amino acids that are identical, and percent identity of amino acids. For the nematode/human analyses, all three comparisons depart in a highly significant manner in the direction of a greater rate of evolution between sponge and nematode than between sponge and human. The results are similar for the fly/human analyses with the exception that the aligned sequence length difference is not significant. This greater difficulty in aligning nematode sequence is consistent with the previous reports (e.g., Jacobs et al. 1998;

Schubert et al. 2000). In summary, where genes can be aligned, human genes are, as an ensemble, more similar to sponge genes than are the genes of nematode or fly. This pervasive lineage bias presumably results from high evolutionary rate in the fly and nematode lineages.

Our approach provides a simple test of the adequacy of the data for use in divergence time extrapolations. In contrast the multi-gene divergence date calculations themselves are complex (e.g., Gu 1998; Wang et al. 1999; Cutler 2000). They generally involve data set-specific γ distributions to account for the variably over-dispersed nature of the data, and are subject to large differences in results as a consequence of simple procedural differences. For example, divergence estimates differ by a factor of two when the proteins are concatenated and analyzed as a single distribution versus the average divergence time when the individual proteins are each analyzed separately (Nei et al. 2001).

The simple test provided here is also far more powerful than the single gene comparisons, such as the relative rate tests, that have often been used on a “gene-by-gene” basis to eliminate “high-rate” genes from multi-gene analyses. Relative rate, and comparable single gene tests have much less statistical power than combined-gene analyses. It is this discrepancy in statistical power between the low-power relative rate analysis used to vet data and the high-power multi-gene analysis that allowed pervasive differences in rate to go unrecognized in previous studies that incorporated nematode and fly data.

Recent work based on a wider distribution of nonmodel-system invertebrate taxa that incorporates more tie points in the fossil record (Peterson et al. 2004), and on Bayesian non-stationary rate approaches (Aris-Brosou and Yang 2003), both yield protostome/deuterostome dates identical to, or far closer to the fossil record of metazoan divergence near the base of the Cambrian. Considering our analysis and these recent results we conclude that the available data, both fossil and molecular, are consistent with a metazoan radiation that began after the last Neoproterozoic glaciation now dated at 580 Myr (e.g., Knoll et al. 2004), and a rapid radiation of bilaterian taxa that was initiated a few million years before the Ediacaran/Cambrian boundary dated about 543 Myr. This supports our use of the radiation concept as a premise for our more general analyses of a departure from a bilaterian ancestral condition that included terminal addition as part of its mode of development.

Terminal addition was ancestral

A variety of molecules active in development appear to play similar roles in the terminal addition process of short germ-band insects, crustaceans, and chelicerates, thus supporting homology of the terminal addition process across the arthropods (e.g., Davis and Patel 2002; Chipman et al. 2004;

Simonnet et al. 2004). Many of these same genes appear to play a similar role in the anterior/posterior succession of somite formation, the terminal addition process evident in vertebrate development. Here we infer, as have others (e.g., Damen et al. 2000), that the common aspect of activity of these gene products in early development represents derivation from a common deuterostome/protostome ancestor.

In *Drosophila*, the parahox gene *caudal* is involved in posterior organization of the anterior/posterior (A/P) axis and is required for telson specification (Moreno and Morata 1999) and hind-gut development (Wu and Lengyel 1998). In short germ-band insects such as the beetle *Tribolium* and grasshoppers, *caudal* is expressed in the growth zone where segments are forming (Schulz et al. 1998; Dearden and Akam 2001). Similarly, *caudal* is involved in chordate tail elongation. Experimental manipulation of its expression disrupts posterior elongation in ascidians (Katsuyama et al. 1999) and vertebrates (Joly et al. 1992).

even-skipped (*eve*), a pair-rule gene in *Drosophila*, functions in the growth zone of short germ-band insects, crustaceans, myriapods, chelicerates and leeches (e.g., Sommer and Tautz 1993; Patel et al. 1994; Davis and Patel 2002; Hughes and Kaufman 2002a; Song et al. 2002). Amphioxus and vertebrate *eve* expression occurs in the elongating tail bud (Barro et al. 1995; Ferrier et al. 2001), and is thus similar in expression to protostome posterior addition. Homologues of the gene *hairy*, one of the upstream regulators in the pair-rule phase of the *Drosophila* segmentation process, play a role in vertebrate somitogenesis through a mechanism that involves periodic expression (e.g., Muller et al. 1996; Palmeirim et al. 1997). Subsequently, similar expression was observed in the long germ-band development of spiders (Damen et al. 2000; see also this volume for other pair-rule gene data). Notch signaling was then found to be involved in vertebrate somitogenesis in what was recognized as a periodic “clock-like” feedback mechanism of somite formation referred to as a “segmentation clock” (e.g., Dale et al. 2003; Pourquié 2003). Recognition of a notch-signaling-based iterative component in segment addition was then observed and determined to be functionally required for the segmentation of spiders (Stollwerk et al. 2003; Schoppmeier and Damen 2005). This segmentation clock is thought by most workers to be the most compelling argument for shared ancestry of vertebrate and invertebrate posterior growth zones and the terminal addition process. Furthermore, expression of *eve*, *hairy*, and *notch* homologues is evident in the segmentation process of leech (Song et al. 2002, 2004; Rivera et al. 2005), although these authors do not rule out co-option as the source for these similarities.

Clearly arthropod, annelid, and vertebrate clades have common aspects of molecules and morphology in the segmentation process. We accept the inference that a terminal addition process involving notch signaling and perhaps other

regulators such as *caudal* and *even-skipped* was present in the protostome–deuterostome ancestor at or near the base of the bilaterian tree. In response to those that argue for independent co-option of notch signaling for similar processes, we note that a range of other molecules, as discussed above, appear to function in similar ways in chordates and in the terminal growth zones that have been examined in protostomes. In addition, Hox gene evidence leaves little doubt that the A/P axis of all bilaterians is homologous. Consequently, there also must have been some mode of development of this ancestral axis. One can easily point to the range of variation of axial development and body-plan formation across modern Bilateria and advocate against any particular argument of homology of development. On the other hand, if the axis of protostomes and deuterostomes are homologous, then they must descend from a single species that formed its axis using some particular developmental mechanism. The commonality of developmental process associated with terminal addition suggests that this is the ancestral mechanism. There are, in essence, two ways to look at the distribution of data regarding bilaterian terminal addition: either there has been significant convergence toward a terminal addition mode involving similarities in molecules and morphology, or there has been significant loss or modification of the terminal addition mechanism. We argue from two directions that that loss rather than gain of terminal addition is the likely scenario. First, if some other mechanism of development other than terminal addition were the ancestral condition in the protostome/deuterostome ancestor, then it would have to be lost and terminal addition regained in just a very short period of time in a process largely hidden from view in the latest Precambrian and Cambrian. Thus, it seems simpler to invoke ancestral terminal addition rather than loss of some other, as yet undefined, mechanism of axis development. Second, evolutionary loss of terminal addition is documented in several lineages, suggesting that loss of these features can take place relatively easily. The greater likelihood of modification via loss in developmental systems has been discussed in regard to other aspects of the genetic regulation of development (e.g., Jacobs and Gates 2003). For the purposes of our discussion, we emphasize the view that loss and modification are preferred explanations in the context of the evolution of terminal addition.

Caveats

In addition to the premises discussed above that the Cambrian radiation was rapid and that terminal addition is ancestral in Bilateria, ambiguities involving the topology at the base of the bilaterian tree, the distribution of certain morphological and developmental-genetic features early in metazoan evolution, and whether shared ancestry of terminal addition necessarily implies shared ancestry of segmentation across the Bilateria, must be considered.

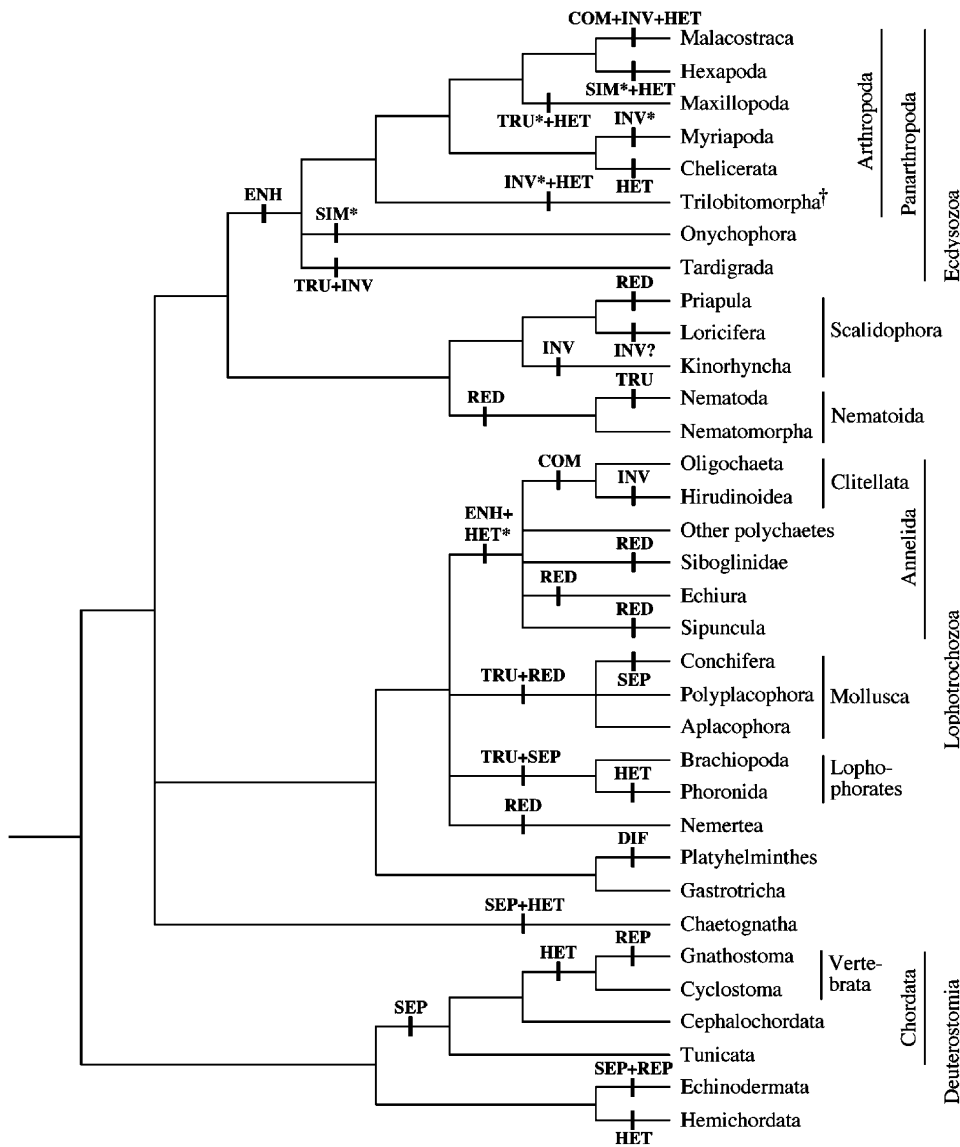


Fig. 2. Bilaterian phylogeny showing the distribution of the 10 proposed modes of terminal addition. This tree is based on the recent molecular-phylogenetic findings of Jennings and Halanych (2005) and Telford et al. (2005), the review of Halanych (2004), and the morphologic analysis of Dong et al. (2004), which joined nematoids and scalidophorans as sister taxa. For simplicity, many taxa have been excluded, and some groups (e.g., most polychaetes) are shown as monophyletic, despite strong evidence for their paraphyly. Each mode is abbreviated with a three-letter designation: COM, terminal addition becomes more comprehensive (occurring in all tissue layers); HET, heteronomy, the evolution of distinct trunk regions; ENH, enhancement of serial features; DIF, terminal addition becomes more diffuse (less localized to a posterior growth zone); INV, invariant serial element/segment number; RED, reduction of metamerism; REP, replication of axes; SEP, separation of anus and terminus of body axis; SIM, simultaneous formation of segments; and TRU, truncation of terminal addition. Abbreviations followed by an asterisk indicate that only a portion of the labeled taxon exhibits that mode (see text for details). The dagger indicates an extinct taxon.

The following phylogenetic concepts have recently reached a fair degree of support (see Fig. 2): (1) the superphyletic clades Lophotrochozoa and Ecdysozoa within the protostomes; (2) a phoronid+brachiopod lophophorate group within Lophotrochozoa; (3) the placement of Echiura, Pogonaphora+Vestimentifera (Siboglinidae), and Sipuncula within an annelid clade within the Lophotrochozoa; (4) the grouping of loriciferans, priapulids and kinorhynchs into Scalidophora, which is sister to the Nematoida (nematodes+nematomorphs); and (5) the combined group of Scalidophora+Nematoida sister to Panarthropoda (tardigrades+onychophorans+arthropods). Thus, the resolution of superphyletic bilaterian taxa has improved over the last 20 years (see Halanych 2004 for review), although questions still remain; for example, placement of chaetognaths. The exact relationship of bilaterians with more basal metazoan groups

has also improved (e.g., Medina et al. 2001; Wallberg et al. 2004). Some uncertainty remains in the placement of acol flatworms (although support seems to be firming for a basal placement as sister to the rest of the Bilateria (e.g., Ruiz-Trillo et al. 2004), the position of cnidarians and ctenophores relative to the Bilateria, and the class level relationships within the sponges.

For our purposes, uncertainty as to where/when bilaterian features (including features associated with terminal addition) first appeared on the metazoan tree, adds another level of ambiguity beyond uncertainty in topology. It has long been argued that the planula larvae of Cnidaria could provide a suitable model for the bilaterian ancestor (see Willmer 1990 for review). More recently it has been argued that adult cnidarians, especially anemones, have aspects of bilaterian morphology and possess a cryptic dorso-ventral axis determined

by the same morphogens that determine this axis across Bilateria (Finnerty et al. 2004). Similar arguments have been made with respect to ctenophore morphology. Acoels and cnidarians lack the full complement of medial/trunk hox genes common to deuterostomes and protostomes (e.g., Bagaña and Riutort 2004), and addition of medial hox genes to differentiate an elongate body plan could correlate with the acquisition of terminal addition near the protostome/deuterostome node.

Turning specifically to genes thought to be involved in the terminal addition process, notch signaling, as well as the *caudal* and *even-skipped* genes are all present in taxa that branch basal to the Bilateria (e.g., Manuel et al. 2004) and lack clear homologues of terminal addition. Either these molecules evolved to perform roles others than those they perform in terminal addition, or terminal addition evolved well before the Bilateria *sensu stricto* and has subsequently been lost, or has yet to be recognized, in basal Metazoa. There are some phenomena, such as strobilation, in the life cycle of medusoid cnidarians that generate terminal repeated structures. However, to date no detailed molecular or morphologic connection has been made between such processes in basally branching metazoans and the terminal addition process found in Bilateria. Thus we infer that these molecules, that function in the terminal addition process of Protostomes and Deuterostomes, initially assumed their roles in terminal addition along the stem of the bilaterian tree. Thus this evolution took place on one or more of the branches leading to the protostome/deuterostome node as ctenophores, cnidarians and presumably acoels, and perhaps a number of now extinct Ediacaran lineages branched off.

Some have argued (e.g., Balavoine and Adoutte 2003; Prud'homme et al. 2003) that segments themselves are homologous in detail. However, the term segment has been used variably—in a permissive sense to refer to any repeated structure along an axis, and in a strict sense to refer to coordination of musculature, organ systems, and even coelomic compartments into repeated units. Thus the number of segmented taxa depends on the strictness of the definition used. Even within “segmented” groups evidence of variation in segments, the segmentation process, and the control of segmentation by different processes, is often evident. For example, anterior segments, such as the naupliar segments of Crustacea, appear to form independent of the terminal addition process (see Minelli and Fusco 2004 for review of these and other complexities that arise in inferring segmental homology across the Bilateria). In this work we focus on terminal addition and on the consequences of *assuming* terminal addition evolved in the stem of the bilaterian clade. Terminal addition is most easily recognized when obvious repeated pattern elements are added and historically it has been associated with segmentation. However, we remain agnostic as to whether terminally added units in the deuterostome/protos-

tome ancestor were canonical segments in the sense of the coordination of multiple systems in repeated units.

In the following section, we categorize modes of modification of terminal addition. These modes constitute morphologically and developmentally defined classes of parallel evolution. However, these modes may not always be governed by identical mechanisms at the molecular level, although they could be referent to common aspects of molecular control of development. This is the case in homeotic changes in Crustacea. Homeotic changes, where they have been explored in detail, are mechanistically different from one another in terms of which aspect of the regulatory architecture has been modified to effect homeotic change (e.g., Deutsch and Mouchel-Vielh 2003). On the other hand, these changes are referent to the same Hox gene regulatory architecture. In this attempt at categorizing modes of change associated with terminal addition, we are not claiming exact identity of mechanism in every case. In addition, this is a first attempt. As these issues are given further consideration, a better understanding of modes of change in body plan associated with terminal addition, and improvements in this classification of the modes of change, are likely.

MODES OF BILATERIAN EVOLUTION GIVEN TERMINAL ADDITION AS AN ANCESTRAL CONDITION

Although we argue for basal evolution of terminal addition in the Bilateria, it is certainly not universal in all bilaterian groups. Thus we are arguing that modification and loss of the terminal addition process has occurred frequently and has influenced many lineages. Furthermore, these changes occurred preferentially early in the Phanerozoic history. In order to explore this complex history we organize the ways that terminal addition appears to have been modified in metazoan history into a preliminary classification of 10 categories.

These 10 categories are listed and discussed below with examples of each. In many cases the polarity of modification, or character change is difficult to establish. However, in some cases the direction of character change seems apparent.

Although we list examples, these lists are by no means comprehensive.

(a) *Enhancement of the serial features* (“ENH” in Fig. 2)—Serial units become more completely integrated or obvious.

Terminal addition is most evident in animal phyla that are discretely segmented such as annelids, arthropods, onychophorans, and vertebrates. However, there are many intervening taxa on the tree where serial units are less easily recognized as strict segments. Loss of both morphologic features and developmental genes is a frequent phenomenon in the evolution of development (e.g., Jacobs and Gates 2003),

and there is much evidence of loss of the coordinated aspect in segmentation, as is discussed below. However, we leave open the possibility that enhancement of serial features, so that they become more obvious, coordinated, or “segment-like,” may have occurred independently in multiple lineages. For example, many annelids have coelomic compartments, that, in combination with the musculature, yield segments that serve as flexible hydrostatic units enabling locomotion, including burrowing (Clark 1964). Arthropods, on the other hand, lack internal segmental hydrostats; their segments are composed of rigid exoskeletal units requiring a more limb-focused form of locomotion given the rigid armor-like quality of the body wall architecture. Given these distinct functions and features of annelid and arthropod segmental units, it seems evident that some attributes of these segments must be derived and “enhanced” in the annelid and/or arthropod lineages relative to a common ancestor. The evolution of tergal rings in derived diplopods, in which dorsal and ventral aspects of segmentation became tightly coordinated (Enghoff et al. 1993), provides a more precise and taxon-specific example of such enhancement. Nevertheless in many cases it is difficult to infer the polarity and path of evolution in these features.

(b) *Increasing heteronomy or tagmosis* (“HET” in Fig. 2).

It has long been argued that an important component of body-plan evolution, and one likely controlled by Hox genes, was a trend toward a heteronomous series of units from an invariant or homonomous series, where perhaps only a few cephalar and genital bearing segments were distinct (e.g., Raff and Kaufman 1983). In arthropods, distinct sets of adjacent segments are often referred to as tagma. Tagma evolved in a number of lineages, including: the prosoma and opisthosoma in some chelicerate groups; the increased differentiation of the crustaceans relative to out-groups; the differentiation of malacostracan crustaceans relative to more basal Crustacea; and the differentiation of pterygote insects relative to basal hexapods, such as silverfish. In this regard, trilobites will be treated in more detail below. Nonarthropod examples include the differentiated features of some spionidan polychaetes (Rouse and Pleijel 2001). Chelicerates and myriapods have relatively simple overlapping posterior Hox gene expression, consistent with the terminal addition process and limited segment differentiation (Hughes and Kaufman 2002b). Similar results are suggested by study of *Chaetopterus* Hox genes (e.g., Irvine and Martindale 2000). Comparable, “tagmatization” of the vertebral column is an important component of gnathostome vertebrate evolution and diversification (e.g., Davis 1949), although limb development itself also involves a component of axial duplication (e.g., Metscher et al. 2005). With heteronomy comes an increased potential for homeotic evolution as is evident across crustacean orders (Jacobs 1986, 1987), and has been examined in terms of the mechanism of modification of Hox gene expression (e.g., Averof and Patel 1997; Deutsch

and Mouchel-Vielh 2003). Similar avenues of evolution are likely in vertebrates (e.g., Gaunt 2000). Heteronomy is most easily recognized in discretely segmented taxa such as annelids, arthropods, and in the vertebral architecture of vertebrates; however, chaetognaths show differentiation in the trunk, the tentacles of phoronids appear to interrupt the body posterior to the cephalar region, and hemichordates are heteronomous and show regionalized Hox gene expression (Lowe et al. 2003). Thus, greater regionalization of Hox gene expression appears to have evolved multiple times coincident with increased tagmosis/heteronomy.

(c) *Terminal addition becomes more stereotypic or comprehensive in the development of all tissue layers* (“COM” in Fig. 2)—For example, the evolution of comprehensive teloblastic growth, where the ectoderm as well as the mesoderm is produced in coordinated fashion by adjacent sets of teloblasts in the growth zone, appears to have evolved independently in the lineages leading to clitellates and malacostracans (e.g., Anderson 1973; Dohle and Scholtz 1997).

(d) *Invariant serial-element/segment number* (“INV” in Fig. 2)—The adults in an evolutionary lineage attain an invariant number of serial units in the terminal addition context. This is a derived feature in leeches within the annelids (Anderson 1973), malacostracan crustaceans (e.g., Schram 1986), and possibly in the kinorhynch (Neuhaus 1995). Variability in mature segment numbers occurs in myriapods, but in both Chilopoda and Diplopoda some groups exhibit a derived epimorphic condition with constant segment number after hatching (Minelli and Bortoletto 1988; Enghoff et al. 1993). Parallel transition to a fixed segment number in later evolving trilobite groups is discussed below. Constant segment number at maturity is a derived condition in these groups. Conversely, it is suggested that the ancestral mode of terminal addition was permissive of variation in segment/serial-element number.

(e) *Truncation* (“TRU” in Fig. 2)—The terminal addition process can be partially or completely eliminated, reducing the number of serial units or segments to a small set of anterior segments that develop roughly simultaneously. In some cases only a few repeated units are present, and the addition of repeated units is no longer evident. In other cases only one or two posterior elements are added.

Brachiopod larvae are trimerous and bear repeated bundles of setae (e.g., Freeman 2003) that render them similar in many respects to spiralian larvae such as those of polychaetes (e.g., Zimmer 1997), suggesting that brachiopods evolved through truncation of terminal addition from a polychaete-like ancestor. In phoronid larvae repeated muscle and nerve elements of the trunk form in the posterior region (Freeman and Martindale 2002), suggesting terminal addition, and providing some limited support within this related group of lophophorates for the evolution of brachiopods via truncation of terminal addition. Recently Cohen et al. (2003) proposed a

model based on fossil data where medially folding provides a path from an elongate, possibly halkierid-like body plan, to a shortened form with a folded gut contained within shells. Similar scenarios yielding brachiopod morphology involve reduction of an elongate body-plan combined with retention of anterior and posterior shells inferred on the basis of the valve-like Cambrian sclerites, *Micrina* and *Mickwitzia* (e.g., Holmer et al. 2002).

Fossil data, such as presence of terminal shells with an intervening set of repeated sclerites in Cambrian *Halkieria* (Conway Morris and Peel 1990) and recent discoveries of vermiform molluscs with plates and spicules in carefully “sectioned” Silurian carbonates (Sutton et al. 2001, 2004), as well as reports of fossil chitons with three rather than a single row of plates (Vendrasco et al. 2004) provide novel combinations of characters not found in modern molluscs. These fossils suggest potential intermediates between vermiform taxa with terminal addition, and modern molluscs and brachiopods, as discussed above. In modern chitons the eighth plate field is generated following the formation of the first seven (e.g., Kniprath 1980) suggesting terminal addition (Jacobs et al. 2000), although not discrete metamerism (e.g., Friedrich et al. 2002). Reports of the addition of posterior dermal pattern elements during the development of neominiomorph Aplousobranchia (Baba 1940) have also been interpreted as evidence for terminal addition (Jacobs et al. 2000). Substantial fossil evidence supports the independent reduction of the number of metameric units in different classes of conchiferan molluscs such as gastropods and cephalopods (Wingstrand 1985; Peel 1991), although this may involve additional reduction of anterior metameric units that were not part of a terminal addition program. Thus molluscan morphology and development suggests a history of terminal addition outside the annelids within the lophotrochozoa, and also suggests a sequence of truncation events that have reduced the number of repeated units relative to monoplacophora, as argued by Wingstrand (1985) and supported by Cambrian fossil data (e.g., Peel 1991). In addition, such units become less discretely metameric as discussed below in (g).

Truncation appears to have occurred several times within the Ecdysozoa. Terminal addition/germ-band extension processes are thought to be ancestral in onychophorans and arthropods (e.g., Anderson 1973). However the related tardigrades (Fig. 2) have only five segments and lack an obvious growth zone (Hejnol and Schnabel 2005). Relative to other Crustacea, barnacles have a reduced abdomen; furthermore, Blin et al. (2003) document loss of *abdA*, a homeotic selector gene responsible for abdominal differentiation, providing a molecular correlate of the reduction/truncation of the terminally added segments.

Nematodes have little recognizable repeated architecture, although there is some evidence of patterning of the cuticle (Decraemer et al. 2003), suggesting that truncation, as well as

reduction (mode (g) discussed below) of repeated units has occurred. In this context some nematodes appear to have lost some combination of *Antp*, *Ubx*, *abdA* type selector gene homologues, relative to other nematodes, nematomorphs, priapulids, and panarthropods (Aboobaker and Blaxter 2003). These observations appear consistent with a “truncation” of terminally added posterior units, and may be comparable with the loss of abdominal segments and the *abdA* homologue in barnacles mentioned above.

(f) “Long germ-band development” (“SIM” in Fig. 2)—Terminal addition can be modified so that it is no longer sequential but simultaneous.

The most celebrated case of loss of terminal addition is the extensively studied syncytial development found in fruit flies. Here, genes controlling patterning of the whole segmented body-plan deploy in a virtually simultaneous manner in the 14th cell cycle. This rapid “long germ-band” development evolved within holometabolous insects well after the hexapod lineage came onto land and allows larvae to exploit ephemeral resources such as rotting fruit. Even in *Drosophila* the simple regulatory hierarchy of anterior Hox genes (e.g., Mahaffey et al. 1989), as opposed to the complex regulation of thoracic and abdominal Hox genes, likely reflects derivation from an ancestor where terminal addition of posterior segments required the reassignment of posterior segment fates as segments were added. In addition to the fly lineage, long-germ-band-like development has been reported within a group of South African Onychophora (Walker 1995; but see Mayer et al. 2005 for conflicting interpretation of a related species). Lastly, patterns of cell division in the development of the trunk of amphipods are not confined to the terminal region, and have a long germ-band aspect to them in a derived form of development relative to other Malacostraca (e.g., Scholtz et al. 1994).

(g) *Reduction of metamerism* (“RED” in Fig. 2)—If obvious repeated features are diminished, terminal addition may persist, but the lack of obvious morphologic correlates would make it more difficult to recognize.

Elongate bilaterians with limited metamerism often retain some evidence of terminal addition. These include lophotrochozoan taxa generally accorded phylum status that are currently thought to be derived annelids, or even derivatives of specific polychaete groups, such as the pogonophoran/vestmentiferan clade (Siboglinidae), as well as echiurans (Fig. 2; McHugh 2000; Bleidorn et al. 2003). In these taxa terminal addition appears to persist, but may be difficult to recognize because of limited external and ectodermal patterning. Pogonophorans/vestmentifereans grow posteriorly and form posterior coelomic cavities. In echiurans there is a posterior growth zone in the developing larvae (Newby 1902), followed by anterior to posterior addition of nerves (Hessling and Westheide 2002). Four-day cell-derived teloblasts give rise to nerves, mesoderm and ectoderm in the leech, the best-studied example of terminal addition in the Lophotrochozoa

(e.g., Weisblat and Shankland 1985). Partially teloblastic growth involving the generation of bands of mesoderm characterizes the development of sipunculans (Pilger 1997), and as other spiralian taxa such as nemerteans (Henry and Martindale 1998), suggesting that they too derived from an ancestor that expressed some form of terminal addition.

In Mollusca, in addition to reduction in numbers of repeated units discussed above in (d), muscle scars in early Paleozoic fossils document the independent parallel reduction and loss of serial organization in the stem of each of the major conchiferan clades (cephalopods, gastropods, and bivalves) (e.g., Peel 1991).

The Scalidophora, a group containing priapulids, loriciferans, and kinorhynchs (Fig. 2), have a substantial Cambrian fossil record (e.g., Dong et al. 2004) and, along with a Panarthropoda and Nematoida, comprise the Ecdysozoa. The Scalidophora have an overall radial organization and an introvert bearing concentric sets of hardened dermal elements referred to as scalids, from which the group derives its name. As opposed to the other scalidophorans, kinorhynchs have a clear overall bilateral organization posterior to the introvert, as well as a segmented organization with a fixed number of 11 segments, a posterior growth zone and terminal addition (Neuhaus 1995; Neuhaus and Higgins 2002). Unfortunately, few details of priapulid development are known; priapulids are largely radially symmetric around the oral–aboral axis, as are the even less understood loriciferans. Radial symmetry is thought to be a derived state associated with the infaunal mode of life (Nebelsick 1993; Adrianov and Malakhov 2001). Priapulids have numerous dermal elements, but serial elements are much less discrete than kinorhynch segments. Figures of loriciferan development indicate more discrete dermal units that increase to a fixed number, but whether a posterior growth zone is present is not obvious (e.g., Warwick 2000; Gad 2005). Thus priapulids may have experienced a reduction in the discreteness of units, whereas loriciferans and kinorhynch lineages may have experienced the evolution of more invariant segment numbers ((c) above) with and without the assumption of radial architecture, respectively. On the other hand, it has been argued that loriciferans are paedomorphic derivatives of the priapulids (Warwick 2000). Clearly, more information on the development of these groups and more confidence in their phylogenetic relationships would allow greater confidence in inferences regarding the character transformations touched upon here.

The Nematoida appear to have the least expression of repetition in ectodermal architecture of the three major ecdysozoan groups. Nevertheless, there are some hints of repeated elements in Nematomorpha, especially in the ectoderm of early stages of development (e.g., Muller et al. 2004). The relationships of nematodes with nematomorphs, and ultimately with Scaladiphora and Panarthropoda, implies a loss of both segmental units perhaps via truncation, as discussed

above, as well as reduction of the morphologic aspect of repeated units.

(h) *Replication of axes* (“REP” in Fig. 2)—Replicated axes may confound the comparison with simpler single-axis bilaterian designs.

A variety of lines of evidence support the argument that certain deuterostomes derive from a basal condition in which a single bilaterian axis generated the body-plan with a contribution from terminal addition. Most workers view early Paleozoic stylophorans with a single ambulacron as representative of a basal, singularly ambulacrate, echinoderm (Mooi, 2005). All modern echinoderms have 5-fold symmetry with five ambulacra. The expression patterns of *engrailed* (*en*) at the ends of ambulacra in developing brittle stars are consistent with the supposition that these growing ends are comparable with bilaterian axes (Lowe and Wray 1997). Mooi (2005) argues for the terminal addition of ambulacral elements in echinoids, documenting support for terminal addition even in this derived condition. Thus, each ambulacron undergoes a terminal addition process that appears derived from an ancestral bilaterian axis through a replication process.

It may be that in the history of chordates, the body plan was once largely reduced to the pharyngeal basket, the rest of the axis having been lost or perhaps reduced to a modest structure with larval function. Re-evolution of a posterior axis present in the adults would perhaps have retained or co-opted some but not all of the features typical of terminal addition, hence the function of *eve* and *cad* in the posterior combined with the absence of posterior metameric *en* expression early in the terminal addition process. In addition, replication of axes also occurs in the pectoral and pelvic limbs of gnathostome vertebrates (e.g., Metscher et al. 2005). These gnathostome limb axes incorporate copies of some but not all *Hox* genes expressed on the A/P axis complemented with additional duplicates of the most posterior axial *Hox* gene (*Abd B* homologues). The development of these axes can also be said to proceed from anterior to posterior in the apical ectodermal ridge. Thus, some aspects of the terminal addition process are likely maintained here in the development of these supernumerary axes.

(i) *Loss of co-terminal gut and body axes* (“SEP” in Fig. 2)—The body axis or axes add units beyond the position of the anus. In deuterostomes, a post-anal structure, or separation of the anus and the terminus of the body axis appears to have occurred in the stem lineage of the chordates. Hemichordates have a terminal gut opening in both the larva and adult, which is not the case within their presumptive sister taxon, Echinodermata. Cambrian stylophoran morphology suggests that the anus and the ends of the ambulacron were already well separated in the stem prior to the radiation of the living echinoderms (e.g., Lefebvre 2003). In echinoids, it appears likely that the anus and the termini of the ambulacral

axes are secondarily coordinated on the dorsal/aboral surface and this may account for the coaxial Hox gene expression (Arenas-Mena et al. 2000). Given the presence of a terminal anus in hemichordates and the currently accepted tree topology, multiple losses of this condition in the deuterostomes seems the most likely interpretation.

Outside of currently accepted deuterostomes, chaetognaths have a post-anal tail, and phoronids have a terminal anus as larvae (e.g., Freeman and Martindale 2002), but a curved gut develops later in life to accommodate their residence in a blind-ended burrow. This need for a recurved gut in closed structures, be they burrows in phoronids, exoskeletons in chonchiferan mollusks, and brachiopods, or endoskeletons in echinoderms, is a recurrent evolutionary theme in Metazoa. In the classes of conchiferan mollusks, there is fossil evidence for the independent loss of serial repetition of structures roughly coincident with the transition from a metamericly organized monoplacophoran body-plan to a torted gastropod, a folded cephalopod, and a confined bivalve. In each case the loss of serial musculature is evident in the muscle scars found in an evolutionary succession (e.g., Wingstrand 1985; Peel 1991). In cephalopods, modification of Hox gene specification of axial structures is evident during this process and the exact nature of the axial organization becomes difficult to compare with more elongate bilaterians (Lee et al. 2003).

(j) *Limitation of terminal addition to fewer tissue layers or teloblasts* (“DIF” in Fig. 2)—Terminal addition can become less stereotypic involving fewer tissue layers—in some cases becoming more diffuse or less localized to the posterior growth zone.

In flatworms undifferentiated neoblast cells are no longer localized in a growth zone. Thus flatworms grow through differentiation of neoblast cells that are located throughout the body. Current work places the majority of flatworms within the Lophotrochozoa, rather than basal in the protostomes. If this is the case then flatworms represent a derived condition involving loss of terminal addition (*i*), and diffusion of blast cell function. Whether neoblasts in flatworms are an evolutionary derivative of teloblasts (which occur in other Lophotrochozoa), is an open question. Recent molecular-phylogenetic findings placing acoels as basal in the Bilateria, suggest they might be an important group useful in characterizing the basal bilaterian condition (e.g., Ruiz-Trillo et al. 2004).

TERMINAL ADDITION IN THE FOSSIL RECORD OF EARLY METAZOANS

Terminal addition as a morphological and developmental pattern is detected in both fossil and living organisms. Evidence of terminal addition in fossils supports several aspects of our argument. Evidence from the latest Precambrian Ed-

iacaran forms supports terminal addition in the stem of the bilaterian clade, whereas evidence from Cambrian trilobite lineages supports the parallel departure from a certain form of terminal addition. These observations are consistent with our theme of a radiation and predictions. We discuss these examples and then treat the fossil record more broadly addressing the interplay between evolution of the terminal addition mode of development and ecological and adaptive influences that, in combination, have generated global diversity patterns.

Body patterning among Ediacaran/Vendozoan organisms

Late Proterozoic fossil assemblages referred to as Ediacaran or Vendian (after localities in Australia and on the Russian platform, respectively) represent a diverse range of fossil morphotypes subject to a variety of taxonomic interpretations. Some argue that these fossils represent an extinct clade of multicellular organisms defined by unique constructional properties and potentially separate from the Metazoa (Seilacher 1984, 1989). On the other hand traditionalists (Glaessner and Wade 1971; Glaessner 1984) interpret these forms as members of extant, metazoan clades (Runnegar 1995). Claims of specific homologies are limited by lack of preservation of sufficient morphologic detail. Most forms have been considered “diploblastic” but this interpretation is not universal, and some forms such as *Kimberella* (Fedonkin and Waggoner 1997) do suggest a triploblastic condition. The fossils in question range from radial to roughly bilateral in overall form and possess repeated units interpretable as an ontogenetic series. Given these attributes, and the plausible interpretation that these forms are branches off the stems of basal metazoan clades (e.g., Buss and Seilacher 1994), possibly including the Bilateria, it seems reasonable to consider these forms in the terminal addition context.

The earliest Ediacaran assemblages (565 Ma) contain “rangeomorphs,” frond-like forms that branch in a self-similar manner at two and possibly three hierarchical levels giving them a “fractal” quality (Narbonne, 2004). Later Ediacaran assemblages include flat organisms constructed from homonomous units that are organized along one (or more) axes (Gehling 1991) and have a bilaterian aspect. Among these forms, *Spriggina*, *Praecambridium*, *Vendia*, and *Marywadea* are divided into a distinct “anterior/cephalic” region and serially constructed “posterior/trunk” (Glaessner and Wade 1971; Glaessner 1984; Gehling 1991; Ivantsov 2001). The metameric nature of the “trunk” is controversial because of the apparent (although possibly preservation-related) asymmetry of unit boundaries across the midline yielding an “offset” appearance to the “segments.” However, in grasshopper terminal addition left/right asynchrony in the expression of the “segment polarity” gene *engrailed* is evident in a percentage of individuals (Patel et al. 1989). Thus some degree of

bilateral asynchrony/asymmetry need not preclude an interpretation of terminal addition.

Ontogenetic change in Ediacaran taxa has only been minimally discussed, although some information about growth is available in the “cephalized” taxa mentioned above, as well as for *Dickinsonia* (Wade 1972), a “metameric” organism (Gehling 1991), that lacks a clear bipartite “head/trunk” divide. Tens of high quality specimens, by Ediacaran standards, document an ontogenetic series for *Spriggina*, and they reportedly show two distinct growth phases. First, width increases from 3 to 11 mm whereas the number of “trunk” segments increases from less than 8 (Gehling 1991, pl. 4.3) to 30 or 40 (Glaessner 1984, p. 62). Subsequent growth does not involve additional trunk elements (Glaessner 1984) as is the case in trilobites. This pattern of an early, “anamorphic” growth phase characterized by sequential addition of trunk units/segments followed by size increase exclusively through growth of previously formed “segments,” is referred to as “hemianamorphic” (Enghoff et al. 1993). Fusco (2005) documents that hemianamorphic growth is the basal condition in myriapods. Confirmation of the presence of hemianamorphic growth in *Spriggina* would suggest potential for this form of development in stem group Bilateria. Anamorphic growth apparently also characterized *Praecambridium*, but more work is needed as the variation in the relationship between size and segment number seems high (Glaessner and Wade 1971; Ivantsov 2001).

In *Dickinsonia* progressive addition of repeated units is evident (Wade 1972), although varied preservation hinders documentation of the balance between “segment” accretion and growth. That *Dickinsonia* was hemianamorphic, as is reported for *Spriggina*, seems unlikely given the presence of hundreds of segments in large specimens. This large segment number suggests euanamorphic growth where “segment” addition continued through the life history (Enghoff et al. 1993). Wade (1972, p. 177) wrote regarding *Dickinsonia* that, “As the animals enlarged, the pygidium and pre-pygidial area where new segments were budded off must have increased in overall size also,” suggesting terminal addition. However, the position of “segment addition” and the presence of a terminal “pygidium” has yet to be formally addressed in *Dickinsonia* or any other Ediacaran taxon. *Spriggina*, with its large size range, relatively good representation, and hemianamorphic growth appears to offer the most promising candidate for establishing the presence of terminal addition in the Proterozoic. Until this is achieved, alternative modes for the increase in trunk segments, such as intercalation, remain possible. These limitations notwithstanding, the “metameric” construction of Ediacaran organisms coupled with the reported pattern of hemianamorphic growth, hints at the Neoproterozoic advent of the cephalization and terminal addition aspects of the bilaterian condition. This, combined with the developmental homologue of the bilaterian dorso-

ventral axis recently established in the anemone *Nematostella* (Finnerty et al. 2004), implies that bilaterian development had evolutionary antecedents that had evolved in the latest Proterozoic.

Terminal addition in the Trilobita

Trilobites are of critical interest in that they record the evolution of terminal addition starting early in the Cambrian shortly after the inception of the Cambrian radiation, close enough in time to reflect the evolutionary dynamics following the initial evolution of terminal addition, but also extending through 100s of millions of years of subsequent Paleozoic evolution. Ontogenetic sequences spanning early post-embryonic growth to maturity provide a record of segment development for numerous trilobite species. In these taxa the cephalic region remains stable in segment number although the trunk shows hemianamorphic growth—segment accretion followed by segment-number-invariant growth (Fig. 3). Certain trilobites bear trunk segments with unique features—such as an enlarged axial or pleural spine. By tracking the position of these “marker” segments in ontogeny, the site of segment addition can be located at the anterior of a subterminal segment (Fig. 3) documenting “terminal addition” in this fossil group.

Basal trilobites are homonomous in the trunk region and vary in number of trunk segments at maturity; such variation occurs at low taxonomic rank and sometimes within species (McNamara 1983). Later evolving trilobites display several of the modes of variation of terminal addition, categorized as (a)–(j) above, making them uniquely suitable fossils for analysis of the evolution of terminal addition. Examples of such modifications are given below:

Evolution of trilobite tagma (b). The trilobite trunk has long been recognized as containing separate caudal (pygidial) and thoracic “tagma” (see Hughes 2003a, b). However, unique among euarthropods, the pygidium is not composed of a single segment, and segments that originate in the pygidium are incorporated into the thorax during ontogeny, leading some workers to question whether the trilobite pygidium is a separate tagma (Minelli et al. 2003). Several trilobite clades independently evolved two morphologically distinct sets of trunk segments (Fig. 4). In several, but not all, cases the boundary between sets coincides with the boundary between the mature thorax and pygidium (Hughes 2003a, b). Trilobite evolution was thus characterized by the repeated evolution of more complex regional patterning from a simple and basal homonomous condition.

Evolution of invariant or determinant segment numbers (d). The number of adult segments seen among Early Cambrian trilobites ranged from 8 to 103 (see Hughes 2003a; Paterson and Edgecombe in press). Subsequent extinction of segment-poor clades, as well as loss of forms with very large

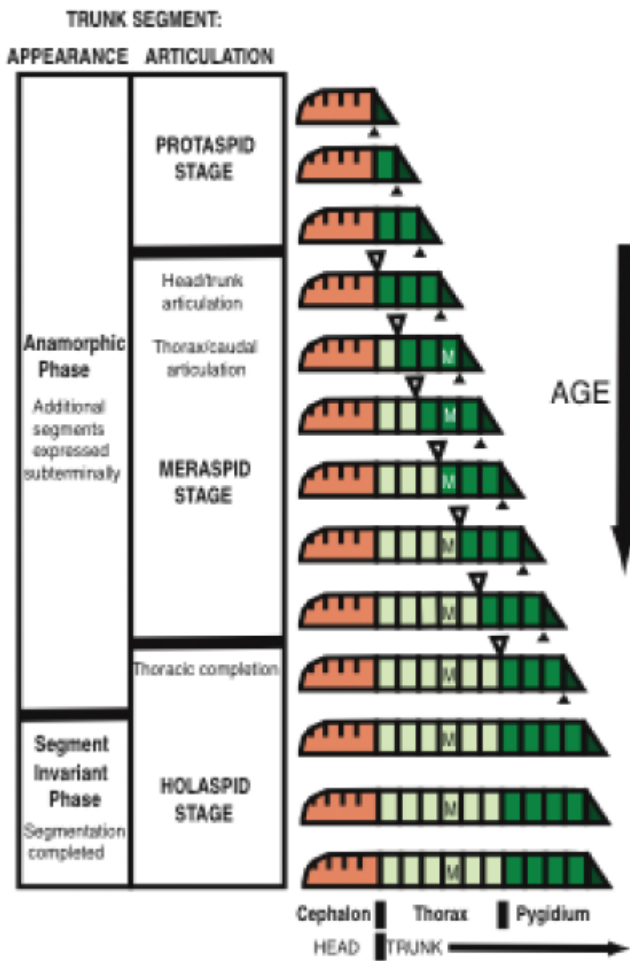


Fig. 3. Schematic representation of the ontogeny of a trilobite dorsal exoskeleton. A small solid triangle marks the location at where new segments appeared, a larger open triangle marks site of developing articulation. “M” represents a distinctive segment illustrating the passage of a segment from the caudal plate into the thorax during meraspid ontogeny and the site at which new segments first appeared by subterminal addition at the anterior of the posterior trunk segment, shown here as the dark green triangle. Major developmental events and stages are shown to the left. Conjoined trunk segments are shown in green, freely articulating trunk segments are shown in lightest green. The increase in absolute size of individual segments between molts is not represented.

numbers of segments reduced this range. By the Late Ordovician, near the peak of trilobite taxic diversity and other morphologic disparity, a range of only six to 35 segments is observed. This long-noted pattern of diminished range and variance in trunk segment numbers (Raymond 1920) has recently been attributed to increasing developmental constraint on segment numbers among derived clades (McNamara 1983; McKinney and McNamara 1991). This has clear parallels among Euarthropoda as a whole (Schram 1986), as discussed above, and is complemented by a shift in the taxonomic level

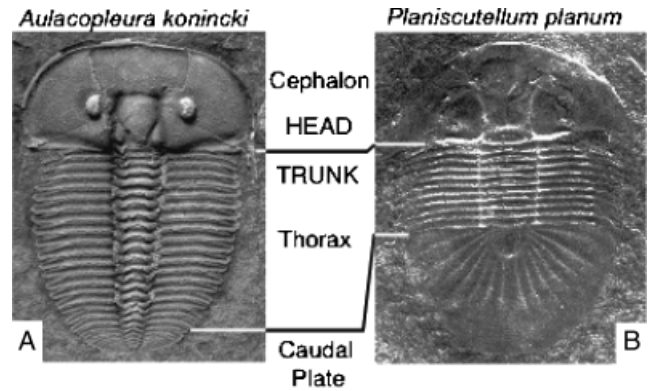


Fig. 4. Examples of the homonomous and heteronomous trunk conditions in trilobites. The trunk region is divided into the freely articulating segments of the thorax and the fused segments of the caudal plate. In (A), *Aulacopleura konincki*, the segments of the mature thorax and caudal plate were similar in morphology and size (the specimen is about 2 cm long). This species typifies the homonomous trunk segment condition. In (B), *Planiscutellum planum*, mature thoracic and caudal segments bear strikingly different morphologies and sizes (the specimen is about 10 cm long). This species typifies trilobite trunk heteronomy with two distinct “sets” of trunk segments forming what are often referred to as “tagma.” Both specimens are from Silurian rocks near Lodenice in the Czech Republic. See Hughes (2003a).

in which variation in the number of mature thoracic segments occurred. Many Cambrian species commonly exhibit intra-specific variation in mature thoracic segment number (Hughes et al. 1999) whereas later forms are typically consistent in segment number at the family level or higher. Stability of thoracic segment number in derived clades is striking—all cheirurids had 11 thoracic segments, all scutelluids had 10, all odontopleurids had nine, all raphiophorids had six, etc., but the underlying cause of this pattern is less clear and individual exceptions, or “reversions” are known (Hughes et al. 1999). Intriguingly, constancy of thoracic segment numbers correlates with degree of regionalization of the trunk (Hughes, 2003a). Variation in the number of mature thoracic segments apparently occurs only in forms with homonomous trunk segments. Selection may play a role here as changes in number might lead to incorporation of segments of inconsistent type into a “tagma,” potentially reducing its performance in protective enrolment or other functions. In addition, parallels can be drawn to the stereotypic segment number and increased “regionalization” exhibited by Malacostraca relative to more basal crustaceans.

Long germ-band-like patterns in derived trilobites (f). The number of cephalic segments appears to have been broadly consistent throughout trilobites and the head/trunk divide appears to be the fundamental boundary within the trilobite body plan (Hughes 2003a) and may equate to the division between an anterior set of synchronously specified segments and a posterior set specified in a prolonged period of ana-

genetic segment accretion. In contrast to the long interval of anamorphic growth seen in most trilobites, almost all future trunk segments develop early, followed by differentiation of the thorax in derived cheirurid trilobites (Whittington and Evitt 1953). In other words, segments were defined early in ontogeny relative to the development of articulation patterns that define tagma. Thus these cheirurids evolved a mode of development somewhat akin to “long germ-band” arthropods.

Reduction of metamerism in trilobites (g). In some scutellid trilobites all prospective trunk segments initially shared a similar morphology. However, prospective pygidial segments soon acquire a distinct growth trajectory involving strong positive allometry in the axial and pleural growth. These later ontogenetic features mask the segmental nature of the pygidium, generating a lobate axial region lacking A/P subdivision. Segments apparently served as constructional units, but their exoskeletal expression diminished as the mature body plan was established (Hughes in press).

In several cases regionalization of the trilobite trunk was accompanied by a relaxation of strict axial–pleural (sternal–tergal) segmental integration in the mature pygidium. A striking case is that of some encrinurid trilobites in which the number of segments defined axially (ventrally) in the mature pygidium can be about 1.6 times the number defined pleurally, and it is impossible to assess which pleural segment “belongs” to which axial segment. Analogous dorso-ventral segmentation mismatches are known in cases where appendages are preserved. Of the 20 species for which soft parts are known there is one pair of ventral appendages for every clearly defined exoskeletal segment in the anterior part of the trunk. In the less well-defined posterior caudal region the dorso-ventral match was maintained in some species but in others the number of posterior ventral appendages greatly exceeded the number of dorsal segments (Hughes 2003b). This difference may reflect important differences in growth schedules—once dorsal exoskeletal development of segments achieved epimorphosis (the segment invariant phase), ventral structures including appendages may have continued to accrete in an anamorphic manner. This modification of typical segmental structure is comparable with the millipede condition where the ventral sternal condition has two segmental units including two pairs of legs for each dorsal tergite (Enghoff et al. 1993). However, the millipede example is consistent through much of ontogeny with all trunk segments bearing four legs.

Clearly, further detailed case studies of the controls of variation within trilobite taxa (e.g., Fusco et al. 2004) are needed. However, the good understanding of trilobite phylogeny and stratigraphic distribution, combined with known patterns of evolution of development in this group which initially diversified in the Cambrian, allows for a preliminary assessment of the temporal pattern of evolution of trilobite

development in the context of the ancestry of terminal addition. The observed pattern, developed in detail above, is broadly consistent with our major theme. Initially, Cambrian trilobites show a pattern of hemianomorphic growth with variable segment number even within species. Subsequently, as one goes into the Ordovician a number of groups independently evolve distinct trunk tagma and a stereotypic segment number. Other departures from the ancestral terminal addition condition involve an example of near simultaneous accretion of trunk segments as well as departures from “perfect” metameric organization. Thus, in some ways the trilobites serve as a model or microcosm for the evolution of metazoan terminal addition as a whole, the broad patterns of which are discussed below.

The temporal pattern of terminal addition as documented in the fossil record

Broad patterns of evolution of novel form are evident in the bilaterian fossil record. Jacobs (1990) distinguished patterns between taxa with and without a “serial/segmental” organization (Fig. 5). Ordinal origination in serially organized forms, dominated by arthropods in the fossil record, peaked in the Cambrian. Somewhat surprisingly, ordinal origination in nonserially organized taxa, taken in this past work to be indicative of novel body form, showed a peak in the Ordovician, not the Cambrian, and showed a subsidiary peak in the Triassic. Thus, nonserially organized forms continued to diversify morphologically and to respond to ecological factors induced by the Permo-Triassic mass extinction, and segmented taxa do not. Initial interpretation (Jacobs 1990) led to the inference that there was a form of developmental constraint experienced in serially organized forms that was not present in organisms that had lost or modified their serial organization. Overall there are parallels between this analysis and the argument regarding terminal addition presented here, as the data appear to capture an initial phase of evolutionary innovation in more serially organized forms, and a trend toward continued morphological diversification in groups such as molluscs, brachiopods, echinoderms, and gnathostome vertebrates. These latter groups were not viewed as being serially organized in Jacobs (1990), and here they are viewed as taxa that have experienced a significant degree of modification of terminal addition.

Since 1990 there has been an increasing emphasis on measures of disparity that are independent of taxonomy (e.g., Foote 1999). Understanding of taxonomy of fossils and modern groups has improved dramatically, and interpretation of articulated halkieriids, among other forms has provided more evidence suggestive of the evolutionary loss of serial organization early in some major groups such as molluscs and brachiopods. In addition, if larger patterns of diversity and disparity are to be understood, examination of evolutionary

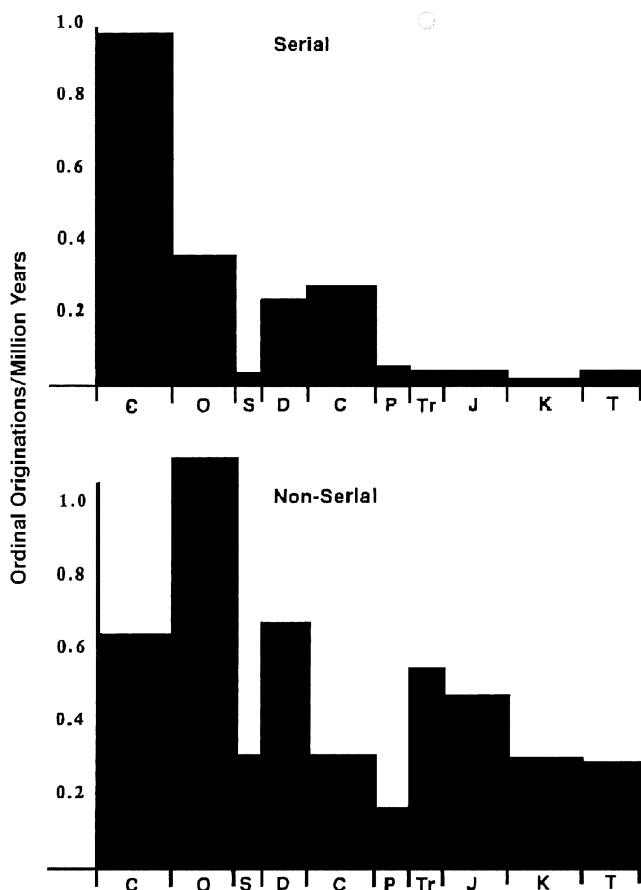


Fig. 5. Ordinal Origination is expressed as a rate in two graphs: one for serially organized phyla such as arthropods, and one for taxa where the organization of the body-plan has become more complex. Orders recognized as of uncertain higher taxonomic affinity are shown in a hatched pattern. Conversely, the shaded portion of the “serial” histogram and the unshaded portion of the “nonserial” histogram document orders of known higher taxonomic relationship. “Serial” forms evolve earlier and “nonserial” forms radiate later into the Ordovician and rebound after the Permo-Triassic. This is consistent with the early evolution of terminal addition recorded in serial forms and departure from this condition and further modification of these lineages in the “nonserial” group.

novelty and constraint cannot be examined independent of ecological context and adaptive function. For example, the repeated evolution of the stereotypic segment number and thoracic and pygidial tagma in trilobites involves a loss of ancestral aspects of terminal addition, but also permits enrollment of the trilobite into a defensive posture. Thus the evolutionary departure from terminal addition has a developmental component, but a selective component where defense against predation is important (a potential increase in the importance of defense strategies is also implicated).

Arguments relating changes in mode of terminal addition and axial architecture also appear to influence the relative importance of living groups of animals. Evolution of the bi-

lateral bivalved shell in clams, the flexure of the gut in cephalopods, scaphopods, and gastropods effect greater protection in combination with improved penetration of soft substrates, sessile filter-feeding, or locomotor design. Paleozoic diversity increases in these groups roughly coincides with the evolution of their novel axial organizations in the Ordovician. Furthermore, the numerical and ecological dominance of these molluscan classes today is staggering relative to their unmodified sister taxa which are all monoplacophoran-like groups that are either extinct or are minimally diverse. Similar arguments could be made for brachiopods relative to their putative halkieriid ancestors. Singly ambulacrate, “stylophoran” echinoderms were never diverse and are extinct, whereas following axial duplication, pentamer architecture has proved excellent for filter feeding, particle sorting, predation, as well as leading to architectures that permit grazing, such as Aristotle’s lantern, a secondary development that is dependent on the pentaradial organization. The axial complexity in gnathostome vertebrates seems to have permitted a radiation relative to out-groups such as cyclostomes or cephalochordates. Some arthropod groups such as cirripeds, which dominate some environments, and malacostracans, which have radiated dramatically and are the most conspicuous crustaceans today, appear to have benefited from changes in their axial organization. Less heteronomous forms such as anostracans (e.g., brine shrimp) are now restricted to ephemeral environments free of teleost predators. The diversification of malacostracans is roughly coincident with the diversification of teleosts during a regime of increased predation in the sea during the transition into the Cenozoic (e.g., Vermeij 1973). In addition to increased heteronomy, malacostracans appear to deal with increased predation through crypsis and armoring in the true crabs, and the evolution of tail flipping escape behavior evident across many of the other groups (e.g., shrimps and lobsters). Tail flipping may have evolved coincident with stereotypic segment number. In hexapod evolution a similar pattern can be seen where more homonomous apterygote forms are less diverse compared with the winged insects. As previously stated, long germ-band development is advantageous in situations that require rapid development. More broadly some might argue the holometabolous condition is related to evolution of the germ-band and terminal addition. Certainly holometabolous insect orders have evolved to become the most diverse groups of animals in the world. Beetles, at the pinnacle of this diversity, benefit from heteronomous “wings” with the elytra providing armored protection in an organism that can also fly.

Although a detailed account of the relationship of development to ecology through time is beyond the scope of this work, it should be clear from the above discussion that evolution of novel form through what we refer to as modes of terminal addition are intimately intertwined with the overall succession of marine faunas in the Phanerozoic (Sepkoski

1981), and the increasing escalation between predator and prey, especially toward the end of the Phanerozoic (Vermeij 1973).

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