Evolving Form and Function: Fossils and Development

Proceedings of a symposium honoring
Adolf Seilacher for his contributions to paleontology,
in celebration of his 80th birthday

Derek E. G. Briggs, Editor

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Trilobite Construction: Building a Bridge across the Micro- and Macroevolutionary Divide

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Abstract
Studies of trilobites conducted at a variety of taxonomic levels record how an early euarthropod clade modified aspects of its body patterning as it evolved. There is little indication that early trilobites species were unusually plastic in all or most of their characters per se, but at least one feature, the number of thoracic segments at maturity, was markedly variable among basal trilobites, common in the Cambrian. The ability to vary segment numbers may have been surrendered for the advantages of greater degrees of trunk regionalization in some derived clades, but the phyletic trend toward more stable numbers of thoracic segments was not irreversible in all cases. Specific case studies show that controls of different aspects of body construction in trilobites could be complex, but this complexity offers the promise of a deeper knowledge of the developmental evolution of this extinct clade.

Keywords
Trilobite, evolution, development, segmentation, tagmosis, regionalization, plasticity, Cambrian, Paleozoic.

Introduction

Trilobites have a good fossil record. Their strongly biomineralized exoskeleton was prone to preservation and well over 10,000 species have been described, a proportion of which are known from articulated material. Because trilobite exoskeletons, calcified shortly after hatching, were repeatedly molted, ontogenetic series spanning all portions of postembryonic growth are available for many tens of species. Details of appendage morphology and other soft tissues are known for some 20 species, and the direct association of trilobite skeletons with trace fossils permits functional inferences about limb operation and behavior. The skeletal morphology of trilobites is complex and richly varied, and although not the ancestors of living arthropods, they nest within a diverse arthropod clade with many living representatives whose lives can be observed directly. The trilobite fossil record, which begins in the early Cambrian and ends at the close of the Permian, spans important episodes in metazoan history, including the tail end of the Cambrian ra-

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diation. With these advantages Trilobita offers the promise of insights into both the empirical history of evolution during this time and into modes of evolutionary change.

Investigations of trilobites have made important contributions to evolutionary paleobiology. Empirical studies of microevolutionary patterns based on trilobites provide classic examples of both stasis and prolonged gradual change in morphology over geologic timescales. Broad scale studies of morphological and taxonomic diversity have showed the primary historical architecture of the clade, and its associations with particular episodes of geologic change. Functional analyses have used various lines of evidence, including analogy with specific living organisms, to infer the life habits of organisms extinct for hundreds of millions of years. Yet, important as these studies are, they treat fossil taxa as the equivalents of living species: we use the fossil record as a proxy to assess how living species might evolve over geologic time, and living species for inferences on the biology of extinct forms. This paper focuses on the differences between fossil and living taxa and, specifically, on efforts in my lab and others to compare and contrast trilobite development with living arthropods. I am interested in investigating what insights trilobites provide into the developmental modes of basal euarthropods, the ways in which trilobites experimented with the structure of their body plan, and the empirical basis of arguments for increased developmental canalization during the evolutionary history of trilobites and other early arthropods in what could be quipped the ”warm afterglow” of the Cambrian radiation. All these questions require consideration of the extent to which trilobites differed from some or all living arthropods. As detailed below, the exceptional wealth of trilobite fossils presents a unique opportunity to identify and explore detailed case studies that can test explanations for patterns seen at broader taxonomic levels. This, then, is a special strength of the trilobite fossil record, as it offers the prospect of bridging the gap between processes of evolution operative at the species level with patterns seen at the clade scale.

Developmental Evolution and the Cambrian Radiation

Metazoan body and trace fossils from early Cambrian rocks (about 520 Ma) suggest that Cambrian marine organisms and ecosystems were structured in a way broadly comparable to extant species and environments (Hughes 2000). Cambrian life apparently differed significantly from late Neoproterozoic life; the Ediacaran–Cambrian transition was an important one, regardless of the date of divergence of major metazoan clades. No clear representative of arthropods is known from the Ediacaran fauna. Morphological features, however, such as division of macroscopic, bilaterally symmetrical bodies into a distinct anterior region that was markedly caecate, and a segmented posterior region that grew hemianamorphically, suggest aspects of body architecture and construction comparable to those of Arthropoda, among other organisms. In hemianamorphic growth an early anamorphic phase of postembryonic growth, characterized by the sequential appearance of new body segments, is succeeded by a growth phase invariant in the numbers of segments (Enghoff and others 1993). An ontogenetic series for *Spriggina,* for which tens of high quality specimens are available, reportedly shows two distinct growth phases. During the early phase the width of the body increased from 3 to 11 mm and the number of segments within the trunk increased from fewer than eight (Gehling 1991, pl. 4.3) to about 30 or 40 (Glaessner 1984:62). Growth thereafter did not involve the expression of additional trunk segments, and was thus hemianamorphic. The commonality of many aspects of developmental genetics among metazoans, and the broad consistency of patterns within phyla, suggest that the basic regulatory mechanics required to build and maintain complex body organization in metazoans had been established before the appearance of arthropods or animals that resembled them (Valentine 1995). Hence, when the form of a fossil allies it unquestionably to a crown group, it is reasonable to assume that the developmental regulation that produced that form was fundamentally similar to that of its living relatives.

Although recent phylogenies agree that onychophorans are the sister taxa to extant arthropods, those that include fossils present radically different hypotheses of relationship and character evolution (Wills and others 1994; Edgecombe and Ramsköld 1999; Budd 2002; Cotton and

Braddy 2004). A major difficulty lies in determining the nature and significance of character states not seen among extant arthropods. Some of these, such as enhanced sclerotization (Budd 1998), may have occurred within the lineage that led to the common ancestor of all euarthropods. Others, such the caudal plate of trilobitomorphs, are likely synapomorphic for major extinct clades (Edgecombe and Ramsköld 1999). There is considerable uncertainty in the phylogenetic significance of several features, such as the "great appendage" and the numbers of segments in the cephalon, and these have led to much controversy in assessments of early arthropod evolution. The cephalic regions of the major groups of living arthropods are characterized by consistent suites of appendage types and segment numbers, despite variations within some clades. In contrast, some fossil arthropods show marked variation in the numbers of conjoined segments in the cephalon and in the form of one or more of the appendages.

Early variation in such characters followed by later stability despite profound within-group diversification was the basis for Gould's (1989:230) support for an innate asymmetry in arthropod evolution that he related to the "aging" of genetic systems. Gould posited that developmental networks in early arthropods were simpler than those in extant forms, so that change in one gene or pattern of gene expression had more limited ramifications because of low levels of pleiotropy (the number of functions performed by individual genes). This model sought to explain the marked diversity of novel characters seen among the Burgess Shale fauna and predicted that once canalization of an aspect of development occurred it would not be reversed later.

A variety of studies have addressed aspects of Gould's (1989) interpretations of the Burgess Shale fauna. Some studies explored whether the diversity of form represented among Cambrian arthropods was as great as he supposed (Wills and others 1994); others questioned the existence of developmental constraints of the type Gould invoked by highlighting the subsequent prevalence of convergent evolution (Conway Morris 1998). Such studies show that Cambrian arthropods were indeed diverse, perhaps surprisingly so in comparison to a wide range of living arthropods, but that many Cambrian arthropods apparently lay within the stem group of euarthropods. Arguments over the interpretation of the Burgess Shale have persisted but have not been fully resolved (Hughes 1998). Few studies have sought to explore whether developmental regulation of early arthropods was different in important ways from that of living forms. The record of early arthropod evolution is too sparse, and phylogenetic relationships too poorly resolved, to permit this issue to be explored much further among the group as a whole.

Trilobites: Primitive and Plastic?

The good fossil record of trilobites offers several avenues of approach to this issue. Traditionally, trilobites have been considered to root near the base of the euarthropods. With the discovery that the earliest trilobite is not significantly older than many nontrilobite arthropods, basing this view on the geologic antiquity of trilobites is no longer valid. Arguments for a basal position must relate to morphology. Interestingly, several key observations were made in this context before the formalization of a modern evolutionary concept. Burmeister (1846:37-38), for example, comparing trilobites with living arthropods, stated that "The earlier types…seem to present the various peculiarities of several groups passing into one another, resulting in forms which exhibit in association, although incompletely, the peculiarities now found detached and characteristic of very distinct groups." Burmeister illustrated his principle with the number of thoracic segments, a point to which I return later. Such observations are important in suggesting that the patterns observed have a validity that is independent of a specific, causal model for their origin.

Whether trilobites root among basal Euarthropoda (Budd 2002), basal arachnates (Cotton and Braddy 2004) or basal mandibulates (Scholtz and Edgecombe 2005) remains controversial. Most recent analyses suggest that trilobites belong to an arachnate clade that was established after the split between arachnate and mandibulate lineages (Edgecombe and Ramsköld 1999; Cotton and Braddy 2004). Indeed, several cladograms of Cambrian and modern arthropods place trilobites in positions far removed from the base of the ingroup (Wills and others 1994). Such arrangements suggest that trilobites appeared after the common ancestors of other euarthropod clades, but they provide limited information on the extent to which trilobites diverged form the common ancestor of all arthropods. Consideration of branch lengths suggests that trilobites may have diverged less from the common ancestor than other arachnates (Cotton and Braddy 2004).

For this discussion the fact that trilobites show features apparently plesiomorphic in several extant arthropod clades is more important than identifying their sister taxa. This is because these plesiomorphic features can provide insights into the form of the ancestral Euarthropoda. Such features include the following:

1. First pair of appendages uniramous and possibly antennal (see Scholtz and Edgecombe 2005);
2. Subsequent appendages biramous with exopodite and endopodite attached to basis, homonomous (that is, similar) in form throughout head and trunk (although the size and relative development of exopodite and endopodite varied along the anterior–posterior axis).
3. Head comprised of conjoined exoskeletal segments with four appendage-bearing segments (and thus conforming to Walossek and Müller's [1998] "head larva" type).
4. Hemianamorphic postembryonic growth, with an anamorphic phase of trunk construction from a subterminal growth zone followed by a segment invariant growth phase.
5. Cephalic–trunk junction marked by an articulating joint at maturity.
6. Morphological changes gradual and progressive over a prolonged series of postembryonic instars.

This list is not intended to imply that these features are synapomorphic for Euarthropoda, although some of them could be. Despite their taxonomic diversity, long history and varied modifications of developmental routines, all trilobites apparently maintained these aspects of body construction and growth mode. This is in marked contrast to other major euarthropod clades, all of which show significant departures from these conditions. Hence trilobites were "primitive" within Euarthropoda in the sense that all members of the clade remained relatively close to the basal euarthropod condition. These observations do not suggest that a high degree of developmental flexibility characterized trilobites at any point in their evolutionary history.

Is there reason to suppose that trilobites displayed unusual patterns of variation of any kind? Here the availability of large numbers of individuals from multiple collections becomes relevant for studies of morphological variation within species or species lineages. What is most striking, regardless of the mode of morphological change described, is the constancy of morphology: change, when it did occur, was of degree rather than kind. Studies of microevolutionary patterns within lineages of trilobites provide few insights into the evolution of morphological novelty. Where profound changes in morphology, involving dramatic modifications of whole organs, have been documented they relate to the loss of structures, rather than the appearance of novel ones (Feist and Clarkson 1989). In the face of overall stability in exoskeletal shape Eldredge's (1972) work on species of the Devonian genus *Phacops* (now assigned to *Eldredgeops*), a core empirical example of punctuated change, concentrated on variations in eye structure. The numbers of rows of lenses varied in *Eldredgeops,* but not the form of each lens. Sheldon's (1987) documentation of anagenetic change in several lineages of Ordovician trilobites showed variation in the number of segments in the pygidium and other differences in the relative sizes of characters. Such was also the case in the classic early studies of Kaufmann (1933) that showed iterative evolution of pygidial form.

Work by my former students showed comparable patterns. Mark Webster documented variation in cephalic shape in a lineage of *Bristolia* species from the early Cambrian of the western United States. While the modification of cephalic outline was quite profound and apparently achieved relatively rapidly, there were prominent reversals and differences in proportions. Brenda Hunda showed periods of both stasis and gradual change in the position of the eye of the Late Ordovician trilobite *Flexicalymene* in the Cincinnati region within a lineage of species that were defined based on the variations in other characters over a period of roughly three million years (Hanke 2004). My work on the late Cambrian genus *Dikelocephalus* (Hughes 1991, 1994; Labandeira and Hughes 1994) suggested more profound morphological variation within a species. Variation occurred in both proportions and in discrete characters, and apparently in a mosaic pattern. These conclusions merit further investigation in light of advances in geometric morphometrics and improved stratigraphic control, as the unusually high variability in *Dikelocephalus* may be related to a nearshore setting that experienced relatively frequent fluctuations in ambient conditions.

Based largely on the contrast between *Dikelocephalus* and other trilobites such as *Eldredgeops,* I suggested that morphology could have varied more plastically in Cambrian trilobite species than in later ones (Hughes 1991), and this example was mentioned by Gould (1993) as support for the notion of early plasticity in arthropods. To date there is little additional evidence to support this suggestion (see Smith 1998), but a rigorous test of the idea requires a stringent set of phylogenetic and paleoenvironmental controls, an adequate methodology for comparing patterns of variation, and strong arguments for the homology of at least some of the characters being compared. It now seems that the degree of variation in *Dikelocephalus* may not be remarkable when compared to short-term evolutionary changes in morphology in living species (Reznick and others 1997). Hence my current view lays less emphasis on the putative plasticity of early trilobites, and more on the stability of form within trilobite species and species lineages. This does not imply that morphological plasticity within trilobite species was trivial, or that it had no relationship to phylogenetic history, but that, as yet, there is no strong evidence that it was uniquely prevalent at any point during the Cambrian. Furthermore, the relationship between morphological plasticity and evolutionary change is complex and remains strongly contested (see West-Eberhard 2003).

Synoptic studies of trilobite evolution suggest that the maximum diversity of cranidial shape was reached in the later Ordovician (Foote 1991), and that phenetic distances between Ordovician species were, on average, greater than between Cambrian ones (Foote 1990). These studies are complemented by others suggesting that the widest array of trilobite “morphotypes” was present in the later Ordovician (Fortey and Owens 1990, 1999), as well as by traditional assessments of taxonomic diversity (Stubblefield 1959). Morphotypes are recognized as distinctive morphologies reflecting particular lifestyles that often were derived convergently from different clades. Each of these approaches suggests that the early Paleozoic witnessed an overall expansion in the morphological diversity of trilobites that extended well beyond the end of the Cambrian. Much of the expansion of diversity was driven by the appearance of trilobites with distinctive mature morphologies during the earlier part of the Ordovician (Foote 1991; Adrain and others 1998). While the phylogenetic origins of these clades has been obscure (Whittington 1981), recent work on the early phylogenies of Cambrian trilobites is elucidating the primitive sister taxa of many of these groups (for example, Adrain and Westrop 2004). The picture is one of expanding variety of form, rather than one of depletion. Thus, trilobite evolutionary history reflects the broader transitions in skeletonized faunas occurring during the early part of the Paleozoic.

Trilobite Segmentation and Its Variation

Trilobites offer the exciting potential to explore morphological variation at scales ranging from the population level to the overall history of the clade. The origin of morphological novelties in trilobites must have had first expression within individual species. Hence, it is disappointing, although perhaps not surprising, that microevolutionary studies show stability of form and provide little direct insight into the origins of morphological diversity within the Trilobita. However, variation in a set of features related to segmentation within some species does mirror major macroevolutionary transitions in trilobite history. This has led me from trying to quantify phenetic variability within trilobite species towards a focus on the evolution of segmentation in trilobites as a whole. Studies of trilobite segmentation offer the dual advantage of linking micro- and macroevolution in trilobites, and an opportunity to dissect and assess constructional and functional aspects of development chronicled within the fossil record. Furthermore, an understanding of trilobite segmentation offers insights into the conundrum of the plasticity of some characters early in their evolutionary histories followed by their later stabilization as recognized by Burmeister (1846) and Gould (1989), reconciling it with a more conventional evolutionary narrative.

Useful aspects of trilobite segmentation

SEGMENTATION WAS FUNDAMENTAL TO THE TRILOBITE BODY PLAN AND ITS CONSTRUCTION. Although segment expression can differ among organs or tissues of the same animal (Budd 2001; Minelli and Fusco 2004), trilobites were clearly constructed from a series of segments repeated serially along the anterior–posterior (AP) axis of the animal. Aspects of the genetic controls on the definition and specialization of arthropod segments are becoming reasonably well known among euarthropod clades (Akam 2000), offering the promise of a richer understanding of patterns of variation in segmentation. Despite great progress much remains to be learned about how segments are specified and how similar structural patterns can have markedly different developmental programs even within the same individual. It is clear, however, that within any particular organ or tissue under observation cell populations follow segment-specific fates. Hence the boundaries between segments (however they are expressed morphologically) represent the fundamental construction of the organism. In trilobites, segments appeared as serially homologous units of body construction that were specified early in ontogeny, at or near the top of a hierarchy of subsequent development. The extent to which structural variation in trilobites was coincident with segment boundaries can be explored from adaptive and constructional viewpoints. Furthermore, there were multiple different components of segmentation itself, including the form of individual segments, patterns of regionalization among segments, and the overall number of segments. Trilobites present opportunities to explore covariation in these components, permitting insights into possible controls (Fusco and others 2004).

THE RELATIONSHIPS AMONG SEGMENTS SERVED TO DEFINE THE MAJOR DIVISIONS OF THE TRILOBITE ANTERIOR–POSTERIOR BODY AXIS. Interestingly, different divisions of the AP axis were suggested by appendages and by exoskeletal segments (Hughes 2003a; Figure 1). Differences in appendage structure were concentrated at the extreme ends of the AP axis, while the principal differences in exoskeletal segment structure occurred within the main body of the animal. Appendages between the extreme ends were biramous and apparently largely homonomous in form throughout individual animals (Hughes 2003b). Although differences in the structures of these biramous appendages occurred among trilobites, these differences were modest compared to those among many other arthropods. Similarly trilobites, unlike many arthropods, apparently showed relatively few deviations from the correlation of one appendage pair for each segment expressed in the dorsal exoskeleton. These observations suggest that patterns of variation expressed among exoskeletal segments represented the most significant differences between segments along the main portion of the AP axis.

Trilobite development involved changes in segmentation. The trilobite cephalon bore paired antennae plus three pairs of appendages. A reasonable speculation, based on patterns in other arthropods, is that the boundary between the trilobite cephalon and trunk also marked a boundary in the mode of segment expression during embryogenesis. The postembryonic growth of all trilobites was evidently hemianamorphic in all well documented cases (Fusco and others 2004). Early postembryonic growth was characterized by the anamorphic appearance of new segments at the anterior of a subterminal growth zone (Stubblefield 1926; Chatterton 1994; Zhang and Pratt 1999), followed by a later phase with a constant number of trunk segments. Throughout ontogeny the trunk contained a caudal plate made up of segments that were rigidly conjoined one to another (Figure 2). Release of freely articulating thoracic segments from the anterior of the developing caudal plate began when the trunk had accumulated several segments, and continued for several instars. Maturity of segment articulation was reached when the number of freely articulating thoracic segments stabilized, after which molting of the trilobite continued. All segments were conjoined at first appearance but only some of them were later released to become freely ar-

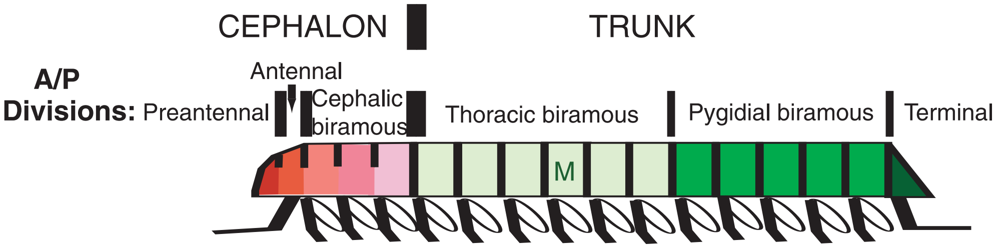

Figure 1. Major divisions of the anterior–posterior body axis in trilobites. M is an individualized segment morphotype. Colors approximate the degree of morphological difference between adjacent segments of the major morphological divisions along the axis. Modified from Hughes (2003a).

ticulating. Thus each exoskeletal segment had one of two distinct fates. One possible case of euanamorphosis (adding segments throughout life) is the early Cambrian trilobite *Balcoracania dailyi* (Paterson and Edgecombe, in press), but this has yet to be shown conclusively.

The functional context of segmentation. The extent to which segments were evident along the trilobite AP axis, and to which aspects of segmentation were integrated in the dorsoventral and axial–peripheral dimensions, can be interpreted in functional terms. Segments in the cephalic region were rigidly attached to each other (which presumably provided stability during the manipulation of food particles as they entered the mouth). Here segments were evinced only by glabellar furrows that likely served as apodemes for muscles attached to the cephalic appendages. Segmentation was not readily apparent in the pleural region of the cephalon and its inferred course has been the subject of much unresolved controversy (Stubblefield 1936; Raw 1953; Palmer 1957). The course of the dorsal suture did not seemingly relate to cephalic segmentation in any direct way. This is shown by the genal spine or angle, which was apparently associated with the posteriormost and most clearly demarcated cephalic segment. The genal angle was separated from the cranidium by the dorsal suture in trilobites with an opisthoparian suture, but conjoined to the cranidium in proparian trilobites. Hence development of the suture and the cephalic segmentation were evidently decoupled, with no obvious hierarchical relationship between the two.

Sutures within the dorsal cephalon were used in ecdysis only, but those within the trunk served as articulating surfaces that permitted flexure. Because flexure required articulation, the sutures necessarily crossed both axial and pleural parts of the exoskeleton. Thus, variation in the associations between sutures and segments can be understood in functional terms. The relationship between segment expression and sutures was not as precise in all trilobitomorphs (sensu Cotton and Braddy 2004). For example, the ratio of articulations to numbers of appendages was variable along the trunk of *Xandarella spectaculum,* with a one-to-one ratio in the anterior of the mature trunk, but a variable ratio with higher numbers of appendages per articulation toward the rear (Hou and Bergström 1997). The early Cambrian *Phytophilaspis pergemena* (Ivantsov 1999) had an even more discordant relationship, with a profound disjunction between the course of sutures and segment boundaries in the pleural, but not the axial, parts of the anterior trunk. Segmentation was also expressed in the posterior pleural part of the cephalon of this animal. These cephalic pleural segments, which could correlate with those in the posterior of the glabella, were apparently compressed behind the eye. This observation, coupled with the posterior and abaxial migration of the eye that commonly occurred in trilobite ontogeny, suggests that much of the pleural part of the trilobitomorph cephalon was allied to the ocular segment or regions anterior to it.

The number of exoskeletal segments and trunk appendages was exactly matched within the thoracic region, but the match became less exact in those portions of the animal that did not articulate (see Figure 1). This can also be interpreted in functional terms, as rotation and enrollment required particular concordance between external and internal structures at the sites of maximum flexure (see Bruton and Haas 1997; Budd 1999). The boundary between the articulating thoracic segments and the rigidly conjoined caudal segments differed in significant ways from that of the cephalic–trunk boundary. In almost all trilobites (excluding those with high effaced exoskeletons) differences across the boundary between thoracic and caudal segments were significantly less prominent, with segments clearly expressed in the axial and pleural regions of both the thorax and caudal plate.

Three scales of segmental variation. The different fates of segments that first appeared at a common point of origin (the subterminal growth zone) offer interesting possibilities for exploring the relationship between a common mode of body construction and the differential development of trunk segments. The scales of variation are (1) the form of individual segments, (2) the regionalization of batches of segments into distinct morphological sets and (3) the overall number of trunk segments and the numbers allocated to the mature thorax and caudal plate. Beginning with individual segments, there are two distinct styles of variation. In the first case the forms of individual segments in a conserved position along the AP axis may have varied between individuals and taxa. In the second case the relative position of a distinctive segment may have varied within the AP sequence.

The trunk segment shape was either homonomous throughout the trunk, or heteronomous (that is, it varied) (Figure 3). Hence a second aspect of segmental variation was that of regionalization into sets or "batches" of segments, with each batch defined by sharing a similar form that differs from that in other parts of the trunk (Hughes 2003a, 2003b). Similarities between segments can be assessed using a geometric morphometric approach to whether individual segments varied in form or pattern of growth (Simpson and others 2005). The "two-batch" condition is clearly exemplified by trilobites such as *Planiscutellum planum* (see Figure 3B), in which the proportions of the individual segments in mature individuals, as defined by the course of the pleural, interpleural and axial furrows, varied markedly across a specific segmental boundary within the trunk. *Hox* genes are known to have an important role in the division of arthropod bodies into discrete sets of segments (Akam 2000), and the control of similar regionalization in trilobites could have been achieved in a comparable manner. Whatever these controls, they were operative in more than a single segment (Hughes 2003b; in that paper I discussed models of *Hox* gene expression in trilobites and outlined one model attributed to Sundberg [2000]. Here I clarify that Sundberg's model of Hox gene expression in trilobites was implied, rather than specifically articulated, in his paper).

The third style of variation among trilobite segments was in their number. In this regard there was a clear distinction between the cephalon and the trunk. Despite marked differences in the shape of adjacent cephalic segments, the number of segments in the cephalon was apparently quite constant. The number of cephalic appendages seems to have been constant in all trilobites in which it can be assessed (Hughes 2003b), and the apparent excess in the number of exoskeletal segments over appendages in some trilobites is difficult to interpet. In marked contrast the trunk region showed considerable ontogenetic and phylogenetic variation in the numbers of segments. Among Trilobita the mature trunk region ranged from about 8 to over 100 trunk segments (see Paterson and Edgecombe, in press). The developmental controls on the numbers of segments among modern arthropods are not yet well known, but a key transition in the postembryonic development of all trilobites was the switch from the appearance of additional segments to the segment invariant phase. The relationship between segment numbers and segment form may have been hierarchical. In some cases regionalization into two batches of trunk segments was evident before the appearance of the last trunk segment.

In summary, the trilobite exoskeleton expressed segments that show marked AP differentiation that can be related to ontogeny, construction and functional differentiation. Segments were expressed as discrete units of construction that contained multiple characters. The covariance of segments and characters can be assessed at a variety of scales ranging from individual segments to the morphological integration of the exoskeleton as a whole.

The Evolutionary History of Trilobite Segmentation

The fossil record of trilobites presents opportunities to explore variation in segmentation across different taxonomic scales. This section considers some of these variations in trunk segment regionalization and the number of trunk segments. The interplay of characters related to different aspects of segmentation, when seen in constructional and functional contexts, offers promise for unraveling the record of evolution within this group and how it may have proceeded.

Individualized segments

The pattern of evolution of individualized trunk segments in homologous serial position is akin to that seen in some of the classic studies of morphological evolution within trilobite species lineages (see above): variation was confined to a single morphological entity, with limited intraspecific variation. I know of no cases in which variation among individuals of a single species approaches that commonly used to designate differences between species. Certain segments, such as the macropleural segments of olenelloids (Palmer 1998) or shumardiids (Peng and others 2003), were clearly individualized along the trilobite trunk. The specific form and position of such segments, however, are widely variable among taxa and, considered across Trilobita as a whole, apparently occurred at any position within the trunk, whether thoracic or caudal. A thorough review of the forms and positions of individualized segments is beyond the scope of this contribution, but no striking patterns are evident from a casual survey. Nor is the functional significance of individualized trunk segments well known. Whatever was controlling their formation was apparently specific to particular segments. There were presumably different controls that specified shape differences between positionally homologous segments and determined the different positions of individualized segments in a sequence of otherwise similar ones.

Batches of regionalized segments

The degree to which tagmosis is evident in the trilobite exoskeleton was correlated with both ontogenetic mode and with sclerite function. Cephalic exoskeletal tagmosis was stable from hatching onward, while trunk tagmosis was not. From a constructional viewpoint (Seilacher 1970) trunk growth was achieved through the periodic anamorphic addition of serial building blocks. Any causal relationship between the temporal molt cycles and the spatial periodicity of trilobite segments remains unknown, and modern arthropods show that the two are not contingent on each other. In many arthropods all body segments are specified before hatching, as in such peracarid crustacean clades as cumaceans, tanidaceans, mysidaceans, and in most amphipods and isopods (Williamson 1982; Schram 1986), in addition to many myriapods (Enghoff and others 1993); in some all segments are specified synchronously, as in long germ band insects such as *Drosophila* (Patel 1994). In Trilobita transitions between anamorphic instars were characterized by the appearance of segments in increments of whole integers, although at different points in anamorphic ontogeny the numbers per molt could vary (McNamara and others 2003). Trilobite ontogeny can be characterized as “track-like” compared to that of many living arthropods, in that postembryonic development took place over an extended series of anamorphic molts during which characters generally changed in small, progressive increments (Hughes and Chapman 1995; Hughes 2003b). I will present more detailed arguments elsewhere to suggest that trilobite growth approximates the basal developmental condition of Euarthropoda. Trilobites experienced a protracted period of body construction in which free-living juveniles interacted directly with the environment.

While anamorphic construction of the trunk was common to all trilobites, the extent to which the trunk segments were regionalized was highly variable, and different conditions were apparently derived independently in various clades. The basal condition of the trunk in Trilobita is not certain, and some nontrilobite trilobitomorphs show clear regionalization of the trunk (such as *Sinoburius lunaris*; see Hou and Bergström 1997). The position of the boundary between batches of segments in Trilobita was not stable for either segment number or articulation state.

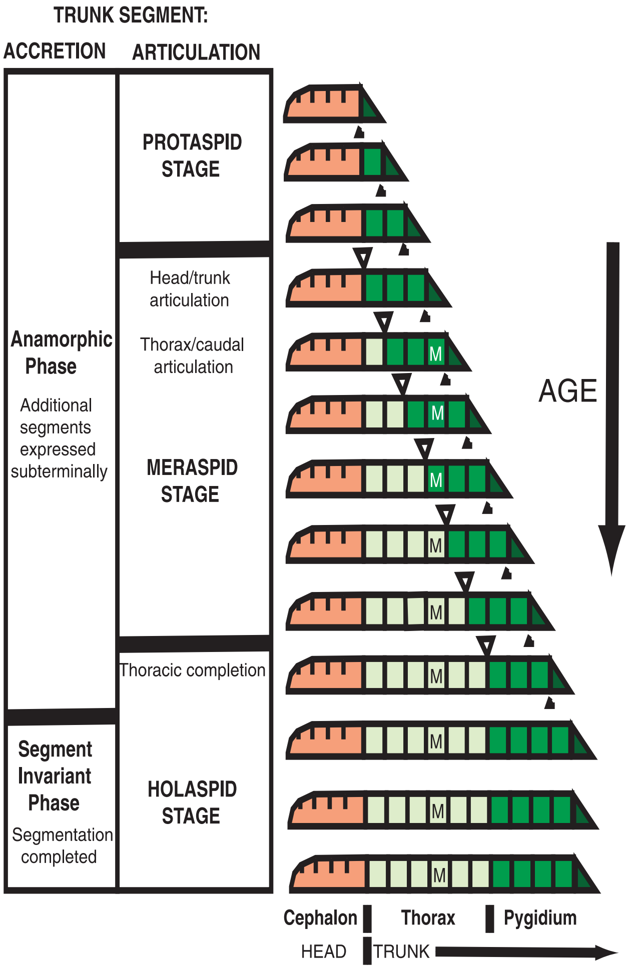

Figure 2. The ontogeny of a trilobite dorsal exoskeleton. A small, solid upright triangle marks where additional segments were first expressed; a larger, open downward triangle are sites of developing articulation. Major developmental events and stages are on the left. Depending on the species, the meraspid– holaspid transition could precede, coincide with or follow the anamorphosis–segment invariant phase transition. New segments were first expressed at the anterior of the posterior trunk growth zone (black right triangle). Conjoined trunk segments are shown in dark green anterior to this; freely articulating trunk segments are shown in light green. The increase in absolute size of individual segments between molts is not represented. M is a distinctive segment that passes from the caudal plate into the thorax during meraspid ontogeny.

For example, the boundary was coincident with the mature thoracic or caudal boundary in scutelluid trilobites, but lay within the thorax of mature olenelloids (Hughes 2003a, 2003b). Similarly, the nature of the boundary between batches of segments was variable. In some cases it was sharply defined along a single surface, in others the transition in segment form was gradational over several segments.

The relationship between the heteronomous condition and the development of segments is particularly interesting. In some trilobites the distinct identity of trunk segments was evident from their first appearance near the rear of the developing caudal plate. Such was evidently the condition in the scutelluids *Dentaloscutellum hudsoni* and *Scutellum calvum* (see Chatterton 1971). However, in others, such as *Breviscutellum* (*Meridioscutellum*) (see Feist 1970) and

Kosovopeltis svobodai (see Kácha and Šarič 1991), at first appearance all trunk segments shared a similar morphology of the furrows that marked the boundaries between, and structures within, segments. The distinctive form of the posterior of the thorax developed sequentially during later meraspid growth. Similar patterns also occurred among encrinurid trilobites, a clade that varied greatly in the extent to which the two-batch condition was developed. In addition to developing out-of-register segmentation schemes in the axial and pleural segmentation of the segments that were to form the mature caudal plate, *Encrinurus* (*Encrinurus*) *macrourus* showed a progressive anagenetic trend toward reduction in the number of axial rings (Ramsköld 1986). This Silurian species from Sweden also showed the development of a longer mucro, a posterior spinose projection apparently made from several conjoined segments, that possibly equated to a third batch of trunk segments.

These observations can be viewed both in constructional and functional terms. Growth from a subterminal budding zone may have imposed structural limits on variability in the shape of segments when their cellular progenitors were defined. For example, the initial shape of segment boundaries might have mirrored some aspect of the terminal zone, such as the shape of its anterior margin (the site of the subterminal appearance of new segments). However, it is not clear that the initial specification of segments at a cellular level coincided with the appearance of segments in the exoskeleton (Minelli and others 2003). Hence, although the subterminal appearance of segments in trilobites has commonly been called "teloblastic" (Størmer 1942; Hessler 1962), this was not based on evidence of teloblastic stem cells. The development of the terminal zone itself has yet to be adequately documented in trilobites. It is interesting from a functional perspective to note that all trunk segments were conjoined at first appearance, but a certain portion of them were destined to become freely articulating thoracic segments later in life. In segments to be released, tight integration between axial and pleural aspects, and between dorsoventral aspects (that is, exoskeletal segments and appendages), would ultimately become a functional requirement, but only at the point at which they became freely articulated, several instars after their initial appearance. Posterior segments, destined to remain part of the mature caudal shield, did not face the same constraint. We could therefore predict that the degree of integration of aspects of segmentation would increase with transition into the thorax, but would not apply to segments destined to form the mature caudal plate. The disassociation of pleural and axial aspects of segmentation in the mature caudal plate, as documented above (see also Richter 1925), could indicate a toleration of variability in boundaries between exoskeletal segments destined to remain conjoined. Selection on these segments could have favored features of the form of the caudal plate as an integrated structure, such as its outline shape or the relative volumes of its axial and pleural components, rather than on segments as individual units. The high quality of preservation of ontogenies of several pertinent trilobite taxa will aid such investigations.

The two-batch pattern was independently derived in several different clades of trilobites, and the manner of its expression was also highly variable. Its convergent acquisition may point to the selective advantage of a regionalized posterior trunk region (evident in many crustaceans, for example). The frequency of its occurrence, in contrast to the rarity of "three-batch" conditions (but see the discussion of *Encrinurus* above), suggests that developing two-batch modularity was accomplished (or lost) relatively easily in trilobites, but that the development of additional trunk regionalization was less easy (see Minelli 2003). The repeated occurrence of the two-batch condition could provide an example of the developmental channeling advanced by Gould (2002) as an explanation for cases of parallel evolution. Testing such a notion will be difficult; the variety of styles of the two-batch condition suggests significant differences in its genetic basis in different groups.

Few studies have yet shown significant intraspecific variation in regionalization among trunk segments, but the encrinurid study of Ramsköld (1986), which showed a temporal trend in the loss of axial rings and development of the mucro, shows the promise of such an approach. Recent work on a new species of the Ordovician pliomerid trilobite *Hintzeia* used a morphometric approach to assess the descriptive basis of homonomy–heteronomy distinction (Simpson and others 2005), in an attempt to determine whether the shapes of segments are homonomous or not.

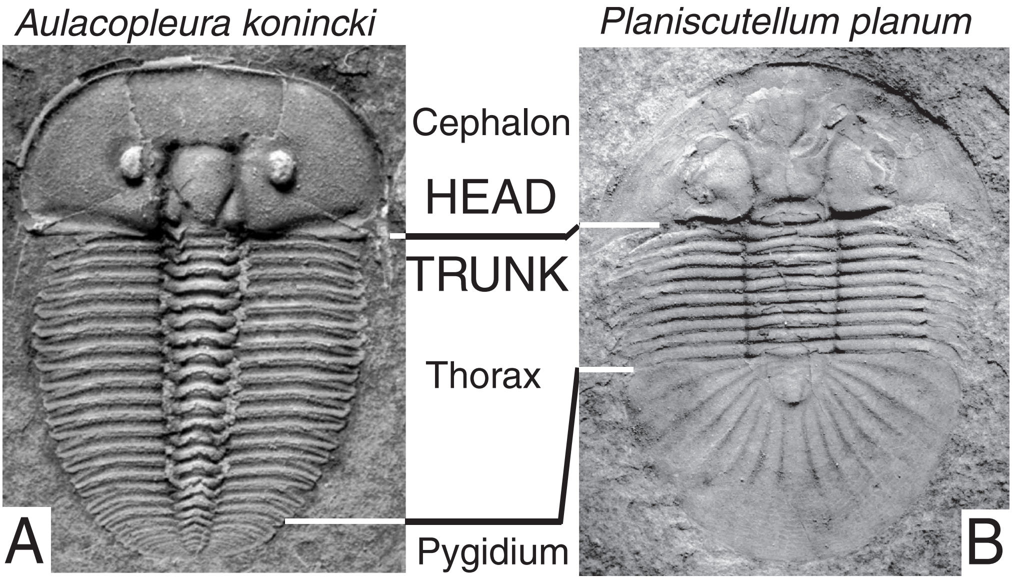

FIGURE 3. Major anterior–posterior articulation divisions of exoskeletons of mature trilobites. The trunk is divided into the freely articulating segments of the thorax and the fused segments of the caudal plate. **A,** In *Aulacopleura konincki* the segments of the mature thorax and caudal plate were similar in morphology and size (the specimen is about 2 cm long). This species typifies the homonomous trunk segment condition. **B,** In *Planiscutellum planum* mature thoracic and caudal segments bear strikingly different morphologies and sizes (the specimen is about 10 cm long). This species typifies the "two batch" trunk condition. Both specimens are from Silurian rocks near Loděnice in the Czech Republic. See Hughes 2003a.

Tracing the appearance or loss of the two-batch condition within well-constrained species-level phylogenies could be possible in some groups, such as olenelloids and cheirurids.

Numbers of trunk segments

Co-occurrent, mature individuals identical in other respects can differ by as many as five thoracic segments within what are considered to be single trilobite species. For several reasons, the aulacopleurid trilobite *Aulacopleura konincki* (see Figure 3A) in particular has received attention (Hughes and Chapman 1995, 2001; Hughes and others 1999; Fusco and others 2004). Meristic variation of this kind has long been of interest to evolutionary biologists because it mimics that between species (Bateson 1894) and thus provides insights into the microevolutionary origins of differences between taxa. The number of thoracic segments at maturity was commonly species specific among trilobites, and thus intraspecific variability of this character in other species is a direct link between studies at the population level and those between taxa—bridging the microevolutionary–macroevolutionary divide. Furthermore, one of the most topical areas of research in evolutionary developmental biology today is the study of the relationship between development and ecology, which seeks to illuminate how morphological novelties are established within populations.

The Silurian Lodenice trilobite assemblage, which contains *Aulacopleura konincki,* is a natural laboratory for studying several aspects of variation in segment numbers in trilobites. Only *A. konincki* among many trilobite taxa collected at the site shows high variability in segment numbers (see Figure 4), suggesting that the variation is related to something specific about this trilobite. Although *A. konincki* is markedly variable in segment number compared with other well-represented trilobites at the site, its overall shape was not anomalously variable (Hughes and others, 1999). This result, combined with studies of growth dynamics in *A. konincki,* suggests a form of compensatory growth such that the size of individual segments was adjusted to conserve the overall proportions of the animal at any particular size during maturity. This implies that the segmental variation in the *A. konincki* sample could reasonably be seen as intraspecific.

Aulacopelura konincki is distinguished from other trilobites in the assemblage by its striking homeomorphy in shape with basal libristomate trilobites such as *Alokistocare idahoense,* common in the Cambrian and also known to have variable segment numbers within collections from individual beds (see Hughes and others 1999). Because *A. konincki* is phylogenetically separated from these homeomorphs by a considerable taxonomic distance, and because intermediates had markedly stable numbers of thoracic segments in maturity, the similar pattern of variation in thoracic segment numbers is clearly convergent. Hence a derived trilobite converged on a pattern of variation common in basal forms. The variability in thoracic segment numbers in *A. konincki,* which correlates directly with the total number of trunk segments, could have been related to fluctuating environmental conditions on the local seafloor. *A. konincki* is found in huge numbers on certain bedding plane surfaces and may have bloomed at times of oxygen stress. Flexibility in controlling the number of segments could have been adaptively advantageous in such settings, or simply have been a physiological response to adverse conditions (Hoffman and Parsons 1991). Whatever the reason, targeted growth in *A. konincki* (see below) suggests the operation of tight regulatory control during growth (Fusco and others 2004).

My interest in the variability of thoracic segment numbers was prompted not only by the opportunity to compare intraspecific variations with those that are transpecific, but also because of an important trend in the history of trilobite segmentation. Variation in the numbers of thoracic segments at maturity was common at the intraspecific, interspecific and generic levels in Cambrian trilobites, but was constant even at the family level and higher among later clades (McNamara 1983, 1986). Such a trend has been called "the paradigmatic example of developmental entrenchment associated with the Cambrian radiation" (Erwin 2000) and has been attributed to increased constraint or "hardening" of developmental systems in the aftermath of the Cambrian radiation (McNamara 1997). This is also a view that Gould (1989) advocated as an explanation of the riot of form among Cambrian arthropods. Since it posits a fundamental asymmetry in the evolution of development, it makes the dual prediction that (1) overall levels of variation should be unusually high in the Cambrian and (2) features once canalized should become irrevocably invariant. I used the *Aulacopleura konincki* assemblage as a natural experiment to test this hypothesis. Because *A. konincki* converged on an earlier abandoned pattern of variation, it overcame any general constraint on intraspecific variation in segment numbers. Thus the study of *Aulacopleura* showed that if a derived trilobite converged on a Cambrian morphotype (and thus presumably pursued a similar lifestyle) it could also evolve a similar pattern of segmental plasticity. This suggests that such plasticity was related to the ecologies of particular Cambrian species at that time, rather than to any general property of developmental systems common to all early trilobites.

The variance in the size distributions of successive instars during the anamorphic growth of *A. konincki* was constant, suggesting an active process of targeted growth. Fusco and co-workers (2004) investigated the transition from anamorphic growth into the segment invariant phase. They considered whether the final number of thoracic segments within an individual was determined late in ontogeny when a critical size threshold was reached (as in some modern arthropods), or whether the mature number of thoracic segments was determined earlier. They discovered that the latter was the case, raising the likelihood that the five mature segment morphotypes, from 18 to 22 thoracic segments, were polymorphs or sibling species. The implication of this result is that although growth of final thoracic segment numbers at maturity in *A. konincki* was flexible, size and apparently shape were tightly controlled. "Plasticity" in trilobites can be a complex phenomenon, and there is little evidence that development in *A. konincki* was "sloppy" in any sense. It will be interesting to see whether similar patterns pertained in Cambrian trilobites that also show intraspecific variation in thoracic segment numbers at maturity.

The patterns of trunk segmentation discussed so far relate specifically to the numbers of tho-

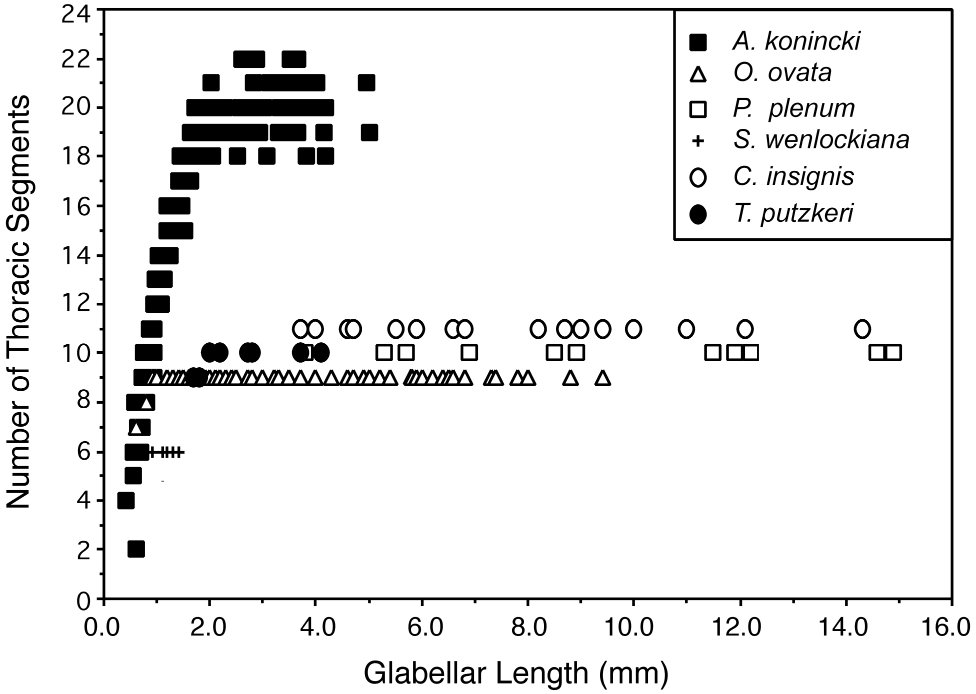

FIGURE 4. Relationship of the number of thoracic segments to overall size, as represented by glabellar length in six trilobite species from the Silurian Loděnice assemblage: *Aulacopleura konincki, Odontopleura ovata, Planiscutellum plenum, Scharyia wenlockiana, Cheirurus insignis* and *Thebanaspis putzkeri.* Note the marked variability in mature segment numbers in *A. konincki,* the only taxon to show this variation after termination of the anamorphic growth phase. Modified from Hughes and others 1999.

racic segments at maturity. Trilobite taxa differed markedly in the proportion of trunk segments allocated to the mature caudal plate, and so the history of thoracic segmentation is not a direct proxy for that of the trunk as a whole. Despite the trend in the Ordovician toward maximal diversity of cranidial shape, the maximum range of total trunk segments (thoracic and caudal combined) peaked in the early Cambrian. A comprehensive analysis of the history of trunk segmentation in trilobites has yet to be attempted, but the net trend was apparently (and surprisingly) one of increasing overall numbers of trunk segments through the history of the group (Raymond 1920; F. A. Sundberg, pers. comm.). This trend may have been influenced more by the extinction of segment-poor forms than by the later evolution of segment-rich ones. Concomitantly, there was a tendency in several derived clades for the allocation of a greater proportion of mature trunk segments to the caudal plate, leading to trunk "caudalization" (Raymond 1920). This trend explains the increased relative size of the caudal plate documented in later trilobites (Fortey and Owens 1997).

What could have driven trends associated with trunk segmentation? The rise of increasingly effective predators provides an answer. Many derived trilobites show elaborate attempts to impede access to their soft internal tissues. These include various modifications of the exoskeleton such as intricate spines. Likewise, the evolution of caudalization could have limited the number of exoskeletal elements by reducing the total number of articulation surfaces (Hughes 2003b). The most notable trend was toward encapsulated enrollment, often accompanied by complex interlocking devices (Clarkson and Henry, 1973). This occurred in several derived clades and would have obstructed the opening of enrolled trilobites during a shearing motion. Encapsulated enrollment would have been a strong constraint on shape throughout the trilobite body. It was achieved in various ways among different clades of trilobites (Bergström 1973). Each method of enrollment exerted specific constraints on overall body shape. For example, the constraint on forms in which the ventral side of the caudal plate fitted exactly into the ventral side of the cephalon, as in spheroidal enrollment, likely differed from that on forms in which the posterior of the trunk was tucked inside the animal, as in spiral enrollment. These differences aside, the contrast with basal trilobites is clear. Many early trilobites could not have encapsulated on enrollment in any way: the shapes of their bodies and structure of their segments simply precluded this (Whittington 1989).

These observations predict that trilobites with encapsulated enrollment controlled their shapes with greater precision than early ones that did not form a closed capsule. *Aulacopleura konincki* enrolled in a spiral (see Hughes and Chapman 1995). The coordination of relationships among size, segment number and shape likely reflected this constraint. I am now examining trilobites that varied their segment numbers but apparently did not enroll, and predict that these attributes were not as strongly coordinated in such forms. The selective advantage of varying numbers of trunk segments is not well known, but if respiration were associated with appendages in *A. konincki,* the ability to vary segment numbers (and thus numbers of appendage pairs) could have been useful in an environment with fluctuating bottom-water chemistry.

Variation in thoracic segment numbers at the lowest taxonomic levels seems to have been restricted to those trilobites with homonomous trunk segments extending across the mature thoracic–caudal divide (Hughes 2003a). The relationship between variability of segment numbers and segment homonomy may be an example of an ancient evolutionary trade-off between the selective advantages of the ability to vary segment numbers and the regionalization of the trunk at the boundary between mature articulating and conjoined segments. Allocation of an homonomous segment to the alternative trunk region could have been achieved at low cost to fitness because it was similar in form to the segments of the other region. This may not have been the case in a heteronomous trunk in which a segment in the "wrong" region would have been morphologically highly distinct and unlikely to integrate functionally with equivalent ease. This may be an example of interactions between the different aspects of trilobite segmentation detailed above: the number of segments in relation to the regionalization of their shapes.

Trilobite Segmentation, Plasticity and the Evolution of Development

This discussion of trilobites segmentation may serve as a prospectus of opportunities for future research. It is presently too early to come to firm conclusions, but several themes are emerging.

1. Strong evidence of unusual variability at the species level in Cambrian trilobites is currently restricted to variation in the number of thoracic segments. This variation in trunk segment numbers is in marked contrast to the state in later trilobites (and most later arthropods), but is comparable to that seen in some extant species of arthropods (Bateson 1894) or other taxa such as salamanders (Jockusch 1997).

2. The trend toward more stable numbers of thoracic segments was accompanied by the rise of more efficient predators. It seems likely that changes in the allocation of segments between the thorax and caudal regions, in the context of roughly constant numbers of trunk segments, were related to the trend toward encapsulated enrollment. The relationships between these trends and trunk regionalization are unclear.

3. When evaluated on cranidial shape, the morphological, and by inference ecological, diversity of trilobites peaked in the Ordovician, but the greatest range of trunk segment numbers at maturity occurred in the early Cambrian. Thus, the evolutionary histories of cephalon and trunk are partially independent. The hemianamorphic postembryonic growth of trilobites likely made possible evolutionary changes based on changes to the controls of developmental timing. Various styles of ontogenetic modification, commonly embraced by the term "heterochrony," may have achieved more dramatic effects among Cambrian rather than later trilobites, as proposed previ-

ously (McNamara 1983, 1986), thus explaining the large range in segment numbers at that time. This was possibly related to the prevalent trunk segment homonomy among early trilobites. One avenue for research in this area would be to explore what information arthropod trace fossils might yield on the diversification of appendage form and modularity. Seilacher's classic work on arthropod trace fossils and their temporal distribution suggests that this approach would be promising (Seilacher 1955).

Based on these observations, we can consider the question of morphological plasticity in early metazoans. There is no strong evidence that, in general, early trilobite species had elevated levels of intraspecific variation compared with later trilobites or other Cambrian taxa. An evolutionary trend toward more constant thoracic segmentation was not inviolable, and departures from the trend could have used different mechanisms. Similar patterns of variation could have been achieved in a variety of ways.

The basic body plan of trilobites (see Figure 1) can be reconciled with scenarios for the evolution of arthropod body patterning genes based on extant arthropods (Hughes 2003b). Given the tremendous conservation of aspects of developmental controls among higher level taxa, Gould (2002) argued that any evolution of developmental systems in the Cambrian and thereafter involved "tinkering" with developmental programs established before Cambrian arthropods appeared.

The wealth of data that trilobites provide may illuminate the early evolution of euarthropod body patterning. Although trilobites are not ancestral to any living arthropod, their body patterning is close to the basal condition of the Euarthropoda. It has been suggested that trilobites diversified while retaining a basically homonomous body plan (Akam and others 1994), and the degree of tagmosis in trilobites clearly never achieved that in mandibulate arthropods (Hughes 2003a). However, levels of tagmosis in trilobites were comparable to those of other contemporary arthropods (Cisne 1974; Wills and others 1997; Budd 2000). Thus a major difference between trilobites and living forms is that trilobites never achieved the modularity so spectacularly characteristic of many extant arthropods. Since low degrees of tagmosis were characteristic of Cambrian arthropods in general, at some level trilobite evolution can be a proxy for understanding the evolution of arthropod body patterning as a whole. The transition in trilobites from variability in numbers of homonomous segments to a constant number of regionalized ones may have been paralleled at this time in other groups as their levels of tagmosis also rose. Seen in this context, the variations in Cambrian arthropods considered bizarre by Gould (1989) are likely plesiomorphic characters either in the stem groups of extant euarthropods, or in the depauperate basal members of crown group clades: these forms seem bizarre because they are extinct or rare. Hence, while there is little evidence that the fundamentals of developmental control were different in the Cambrian, the Phanerozoic record witnessed a significant change in the degree of arthropod modularity. The ways in which this was achieved might qualify as genetic "tinkering" but this, apparently, was how arthropod evolution unfolded.

If trilobites were similar to extant euarthropods in their basic architecture and development, why did they go extinct when others survived? This is currently unclear. Although the extent of trunk regionalization increased during trilobite evolution, it does not match the rise evident among Paleozoic crustaceans. There is no strong evidence to suggest that trilobites were prevented from developing greater regionalization by genetic constraints. Nevertheless, arachnate body patterning was less regionalized in general than that of mandibulates (Hughes 2003b). Maintenance of a relatively homonomous condition was perhaps adaptively favored by an aspect of life common to all trilobites. Further research on comparative developmental genetics and arthropod ecology should tell us.

Acknowledgments

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