The Evolution of Trilobite Body Patterning

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Key Words

Trilobita, trilobitomorph, segmentation, Cambrian, Ordovician,
diversification, body plan

Abstract

The good fossil record of trilobite exoskeletal anatomy and on-
togeny, coupled with information on their nonbiomineralized tis-
sues, permits analysis of how the trilobite body was organized and
developed, and the various evolutionary modifications of such pat-
terning within the group. In several respects trilobite development
and form appears comparable with that which may have charac-
terized the ancestor of most or all euarthropods, giving studies of
trilobite body organization special relevance in the light of recent
advances in the understanding of arthropod evolution and devel-
opment. The Cambrian diversification of trilobites displayed mod-
ifications in the patterning of the trunk region comparable with
those seen among the closest relatives of Trilobita. In contrast, the
Ordovician diversification of trilobites, although contributing
greatly to the overall diversity within the clade, did so within a nar-
rower range of trunk conditions. Trilobite evolution is consistent
with an increased premium on effective enrollment and protective
strategies, and with an evolutionary trade-off between the flexibility
to vary the number of trunk segments and the ability to regionalize
portions of the trunk.

INTRODUCTION

The rich record of the diversity and development of the trilobite exoskeleton (along with information on the geological occurrence, nonbiomineralized tissues, and associated trace fossils of trilobites) provides the best history of any Paleozoic arthropod group. The retention of features that may have characterized the most recent common ancestor of all living arthropods, which have been lost or obscured in most living forms, provides insights into the nature of the evolutionary radiation of the most diverse metazoan phylum alive today. Studies of phylogenetic stem-group taxa, of which Trilobita provide a prominent example, have special significance in the light of renewed interest in arthropod evolution prompted by comparative developmental genetics. Although we cannot hope to dissect the molecular controls operative within trilobites, the evolutionary developmental biology (evo-devo) approach permits a fresh perspective from which to examine the contributions that paleontology can make to evolutionary biology, which, in the context of the overall evolutionary history of Trilobita, is the subject of this review.

TRILOBITES: BODY PLAN AND ONTOGENY

Trilobites were a group of marine arthropods that appeared in the fossil record during the early Cambrian approximately 520 Ma and have not been reported from rocks younger than the close of the Permian, approximately 250 Ma. Roughly 15,000 species have been described to date, and although analysis of the occurrence of trilobite genera suggests that the known record is quite complete (Foote & Sepkoski 1999), many new species and genera continue to be established each year. The known diversity of trilobites results from their strongly biomineralized exoskeletons, made of two layers of low magnesium calcite, which was markedly more durable than the sclerites of most other arthropods. Because the exoskeleton was rich in morphological characters and was the only body structure preserved in the vast majority of specimens, skeletal form has figured prominently in the biological interpretation of trilobites.

Trilobite Body Plan

The name trilobite derives from the transverse division of the exoskeleton into a central axial region bounded by two lateral or pleural lobes (**Figure 1**). The sharp distinction of axial and pleural parts of the skeleton is a marked feature of trilobite body organization. In mature trilobites, the anterior-posterior (a-p) axis of the exoskeleton was also divided into three regions: the cephalon, thorax, and pygidium. Trilobites were constructed from a series of segmental building blocks evident within each of the three regions, but these regions differed in the degree to which segmentation was expressed. Segmentation was clearest in the thoracic region in which segments articulated against one another during life, placing a functional requirement for transverse joints that extended entirely across the exoskeleton. The posterior margin of the cephalon and anterior margin of the pygidium articulated against thoracic segments, explaining the clear segmental nature of the occipital or neck segment

Cephalon: the anteriormost or head division of the trilobite body composed of a set of conjoined segments whose identity is expressed axially

Thorax: the central portion of the trilobite body containing freely articulating trunk segments

Pygidium: the posterior tergite of the trilobite exoskeleton containing conjoined segments
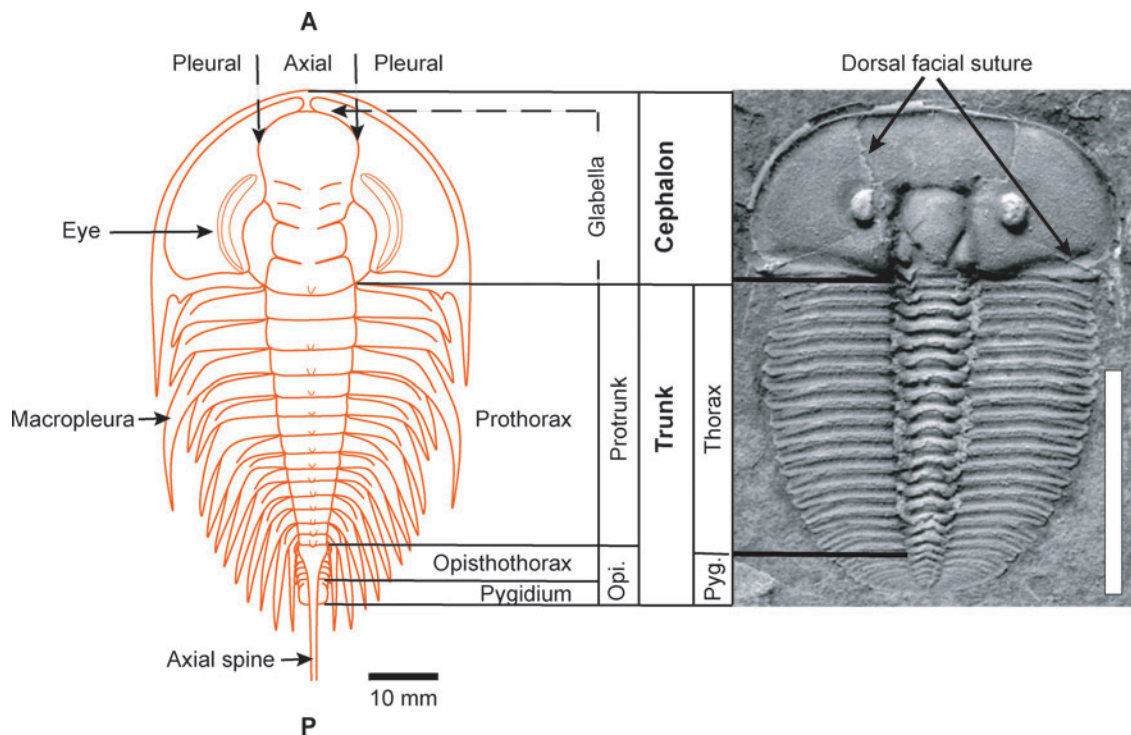
Figure 1

Basic anatomy of the dorsal surface of two trilobites. (*Left panel*) The figure is based on a generalized olenelloid trilobite, which had a boundary between two distinct or heteronomous batches of segments located within the thorax, dividing the protrunk from the opisthotrunk. (*Right panel*) *Aulacopleura konincki* displayed the homonomous trunk condition in which all trunk segments shared a similar morphology. A, anterior; Opi, opisthotrunk; P, posterior; Pyg, pygidium.

(Beecher 1897) and the anterior pygidial segment in trilobites. The same constraint did not exist in those parts of the cephalon and pygidium located away from the border with the thorax. Pleural and axial segmentation was also commonly evident in the pygidium, but pygidial segments were conjoined to one another and could not articulate. The similarity of thoracic and pygidial segments (see **Figure 1**) reflected their common site and manner of origin, as discussed below.

Where well-known, the cephalon had three pairs of postoral biramous appendages preceded by a pair of uniramous preoral antennae that possessed a sensory function in most trilobites. The number of segments—defined by furrows on the glabella that may have served as muscle attachment sites—commonly exceeded four, but the relationships of the anteriormost segments, including the ocular segment, remain obscure. There has been a long and contentious history of debate fueled by hints of segmental boundaries in the anterior part of the trilobite cephalon (e.g., Bergström 1973, Chatterton & Speyer 1997, Hupé 1953, Stubblefield 1936). Whatever the

Glabella: central inflated portion of the cephalic axis that served as the stomach capsule

Trunk: the postcephalic region of the trilobite body comprising a set of segments whose identity is clearly expressed both axially and pleurally

Homonomous: two or more segments identical or closely comparable in shape

Heteronomous: two or more segments distinctly different in shape

solution, trilobites evidently shared a basic complement of ocular and appendage-bearing segments similar to that of other basal euarthropods (Scholtz & Edgecombe 2005, Waloszek et al. 2005). Sutures within the cephalic region apparently functioned to permit ecdysis (molting of the exoskeleton) and are not easily interpreted in terms of segmental boundaries. Trilobites are commonly illustrated in dorsal view, but some calcified sclerites were confined to the ventral surface, most notably the hypostome, an axial plate that underlays a portion of the glabella. Morphological differentiation between adjacent exoskeletal segments was generally most marked within the cephalon, with the cephalic-thoracic junction marking the principal division along the a-p axis of the trilobite exoskeleton.

The thorax and pygidium together constituted the trunk of the trilobite body, with the sequential appearance of new trunk segments evident during postembryonic ontogeny. Unlike the cephalic region (in which the number of segments was apparently static both during the ontogenies of individual species and across the clade as a whole), the number of segments in the trunk, and the proportions allocated to the thorax and pygidium, was variable both ontogenetically and among taxa. The form of trunk segments was either homonomous, in which case trunk exoskeletal segments differed only in relative size or articulation pattern, or heteronomous, in which case the trunk contained more than one segmental morphotype (see **Figure 1**). The heteronomous condition encompassed individualized segments with markedly expanded pleurae or axial spines, in addition to the division of the trunk into two or more batches of discrete segment morphotypes, with segments within a batch similar in form and markedly different from those in other batches.

Any functional requirement for the expression of serially iterated segmental building blocks (Bergström 1973) was clearly relaxed, if ever operative, at the anterior of the cephalon. This was the locus of some striking morphological innovations among trilobites, including, for example, the extraordinary projecting trident of the Devonian phacopid *Walliserops trifurcatus*. In some trilobites, the posterior of the pygidium also showed a departure from the expression of segmentation with the development of unique spines.

Exceptional preservation provides a record of the external form of the appendages and some other body tissues for approximately 20 species (summarized by Hughes 2003a, but also see Hou & Bergström 1997). These cases span a variety of geological ages and clades, but they do not provide an adequate sample of the group as a whole, and they do not detail the ontogeny of the appendages. Nevertheless, a striking feature of trilobite limb construction is the overall similarity of the form of the leg-like endopods, which are composed of numerous short podomeres, and of the lamellate exopods (Hughes 2003a) along the length of the body, regardless of whether they were situated in the cephalon, thorax, or pygidium. Where known differences appear to be largely matters of scale or spinosity, rather than fundamental structure. The number of appendages and exoskeletal segments matched exactly in the thorax (in which segments articulated) and in those portions of the cephalon and pygidium closest to the thorax, but became mismatched toward both axial extremities in some trilobites. In several cases, the number of appendages in the pygidium greatly exceeded that expressed in the dorsal exoskeleton.
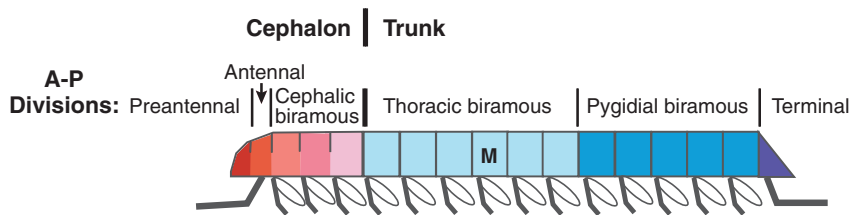
Figure 2

Major divisions of the anterior-posterior (a-p) body axis in trilobites. The letter M indicates an individualized segment morphotype. Colors indicate major morphological divisions along the axis, with shading approximating the degree of morphological difference between adjacent segments. Segments in red are cephalic, those in light blue are thoracic, those in dark blue are pygidial, and the terminal piece is in purple. Thoracic segments articulate with one another, whereas those in the cephalon and pygidium are conjoined. Figure modified from Hughes (2003b, 2005).

The form of the biramous limb varied among trilobites, but mainly in the relative proportions of various parts of the exopods and of the endopods. A pair of uniramous antennae-like appendages was evident as the last appendage pair in one Cambrian species (**Figure 2**).

Trilobite Ontogeny

The embryonic stages of trilobites are unknown, but trilobites appear to have calcified at or shortly after hatching. Similar to all arthropods, trilobite development was accomplished through a series of instars, each separated by an ecdysis (molt) during which the exoskeleton of the previous instar was shed (Whittington 1957). The combination of this developmental habit and the generally modest morphological changes between sequential molts enables the reconstruction of molt series for individual species. All trilobites may have displayed a hemianamorphic pattern of development in which instars characterized by the sequential appearance of additional trunk segments were succeeded by a sequence of instars invariant in the number of segments expressed in the dorsal exoskeleton in what is known as the epimorphic phase (Hughes et al. 2006) (**Figure 3**). The appearance and fate of individualized segments show that the site at which new segments first appeared was subterminal, adjacent to the anterior of the last body unit of the trunk (Stubblefield 1926).

The development of articulations provided criteria for the recognition of the traditional phases of trilobite ontogeny: the protaspid, meraspid and holaspid stages (see Whittington 1957). The development of the facial suture marked the onset of the protaspid phase, followed by the separation of the cephalon and the trunk at the neck joint, marking onset of the meraspid phase (Hughes et al. 2006). Additional articulations then developed sequentially at the rear of the leading segment of the meraspid pygidium until a specific number of segments had been released, marking the onset of the mature, holaspid phase. A consequence of this pattern of segment release was that the meraspid pygidium comprised a dynamically changing complement of segments. Few, if any, modern arthropods develop articulations in this manner.

Anamorphic development: development in which molting was accompanied by the sequential appearance of additional segments

Heminanamorphic development: in which an anamorphic phase of development is followed by an epimorphic phase

Epimorphic development: development in which sequential molts retained a constant number of segments

THE PHYLOGENETIC STATUS AND RELATIONSHIPS OF TRILOBITES

Currently it is generally agreed that all trilobites belong in a monophyletic group, defined by characters relating to the exoskeletal mineralogy, the vaulted axis, the structure and position of the eyes, and the attachment of the hypostome (Edgecombe
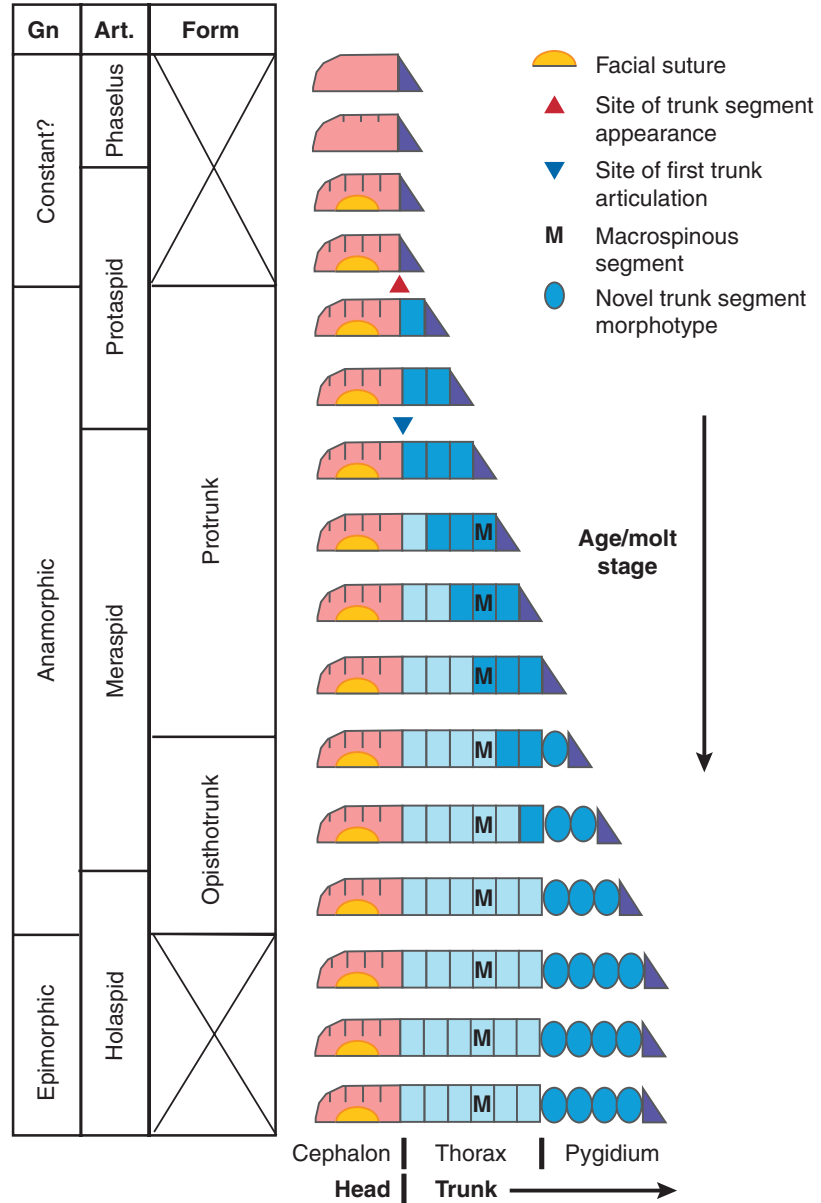
& Ramsköld 1999, Fortey & Whittington 1989, Ramsköld & Edgecombe 1991). As biomineralization appears to have been a definitive feature of trilobites, it is unlikely the group had a substantial existence, in terms of geological time, prior to their appearance in the fossil record, although the lineage leading to them may have. Despite the apparent coherence of the group, the placement of the diverse, diminutive, and blind agnostinid arthropods (common in the Cambrian and Ordovician) remains debated. In skeletal biomineralization, the number and general form of cephalic limbs, and the a-p body plan, agnostinids resemble other trilobites, particularly the similarly diminutive but sighted eodiscids, which are often considered to be their closest relatives (Cotton & Fortey 2005). However, supremely well-preserved immature individuals of *Agnostus pisiformis* from the late Cambrian Orsten deposits of Sweden (Müller & Walossek 1987) reveal a wealth of morphological detail unsurpassed in any other fossil considered to be a trilobite. Many of the details of the appendages and soft integument contrast with those known in other trilobites, particularly in the feeding function of the antennae, the nonlamellate nature of the exopod, and the form of the hypostome (Walossek & Müller 1990). Importantly, these and other characters resemble features known in some non–trilobite arthropods, particularly those of basal crustaceans (Stein et al. 2005). This resemblance implies that agnostinids share a more recent common ancestor with the crustaceans than they do with other trilobites. Further knowledge of the limb ontogeny of other early arthropods, and particularly of eodiscinid trilobites, will be helpful in resolving these issues. Some features shared between agnostinids and basal crustaceans have parallels in other arthropod groups (such as the trilobitomorph naraoiids), and similarities may be most marked among ontogenetically younger specimens (Chen et al. 1997). However, it seems unlikely that agnostinids are the plesiomorphic stem lineage to other Trilobita.

There is general agreement that trilobites were closely related to a group of non-biomineralized arthropods whose first cephalic appendage pair comprised sensory

Plesiomorphic sister taxa: closest relative of a monophyletic group lacking evolutionarily derived features

←——————————————————————————————

Figure 3

Generalized trilobite ontogeny showing the boundaries of ontogenetic stages based on three aspects of the development of trunk segments: generation (Gn), articulation (Art), and morphology (Form). The generation state contains a poorly known initial stage that may have had a constant set of cephalic segments, the anamorphic phase during which new segments appeared in the trunk, and the epimorphic phase after which the exoskeletal segment number was constant despite continued molting. The articulation state is based on dorsal sclerite articulation pattern, with the onset of the protaspid stage marked by the development of the dorsal facial suture, onset of the meraspid stage marked by the onset of trunk articulation, and the onset of the holaspid stage marked by the completion of trunk articulation. The morphology state refers to the form of trunk segments, which in some trilobites are divided into discrete, heteronomous batches of anterior (protrunk) and posterior (opisthotrunk) segments. The site of the appearance of new trunk segments is shown for the first trunk segment only. Segment color scheme as in **Figure 2**. Individualized segments, such as those that bore unusually large axial or pleural spines (i.e., a macrospinous condition), retained the same position relative to the cephalic margin following their first appearance, indicating that the site of appearance of new segments was subterminal, and the boundary between articulating and conjoined segments migrated posteriorly during the meraspid phase (Stubblefield 1926). Modified from Hughes et al. (2006).
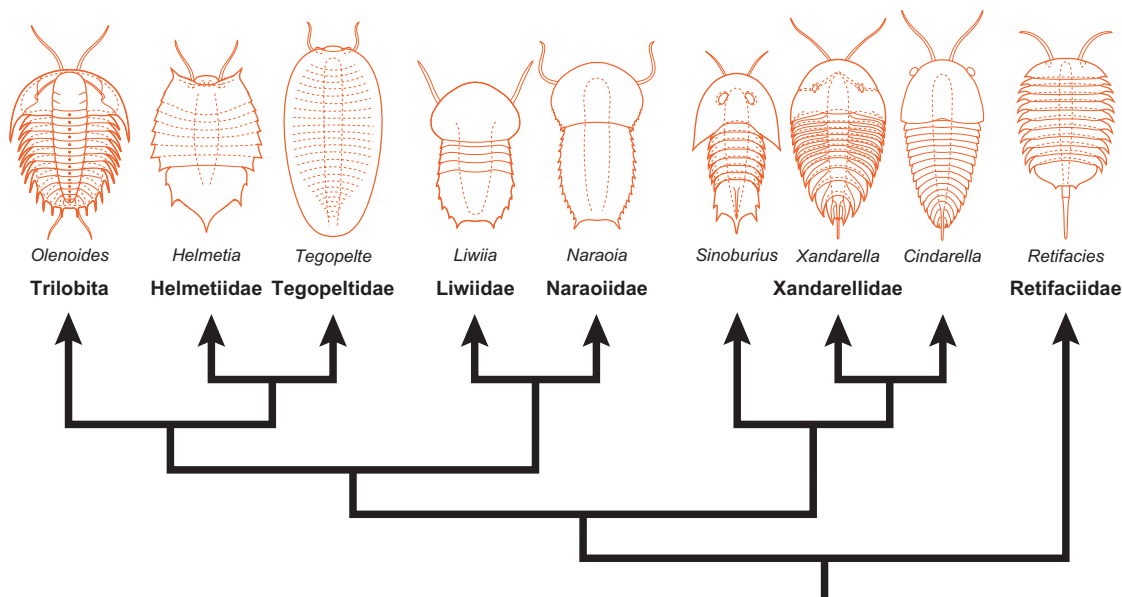
Figure 4

Form, relationship, and major modes of trunk-segment articulation among trilobites and
Trilobitomorpha. Figure based on phylogenetic schemes of Edgecombe & Ramsköld (1999)
and Cotton & Braddy (2004).

Euarthropoda: group of
arthropods with derived
cephalic structure,
containing all living
arthropods

antennae, subsequent pairs bearing biramous appendages with lamellate exopods
(Cotton & Braddy 2004, Edgecombe & Ramsköld 1999, Hou & Bergström 1997).
These are referred to informally as trilobitomorphs (sensu Cotton & Braddy 2004)
(**Figure 4**). The organization of many trilobitomorphs is similar to that of trilobites,
with one pair of antennae followed by biramous appendages of similar structure in
the cephalon and trunk, a cephalic shield that covered several appendage pairs, and
a trunk comprising largely homonomous exoskeletal segments commonly divided
into an anterior region of freely articulating segments and a posterior pygidium-like
structure (**Figures 1** and **4**).

The placement of trilobites (and now also trilobitomorphs) with respect to living
and other fossil arthropods has been the subject of debate for 200 years and remains
contentious. In recent years, a monophyletic view of Arthropoda has been generally
accepted, partly due to evidence from molecular phylogeny (Aguinaldo et al. 1997,
Giribet et al. 2001) and developmental genetics (Popadic et al. 1996, Akam 2000),
but also due to the realization that many Cambrian arthropod fossils constitute stem-
group lineages located en route to living arthropods. These Cambrian arthropods
possessed characteristics that were intermediate between living arthropods and living
arthropod-like animals such as modern onychophorans (Budd 1998). Trilobites and
their trilobitomorph allies are considered to belong to the Euarthropoda, a derived
clade characterized by multiple conjoined segments in the cephalon (**Figure 5**), but
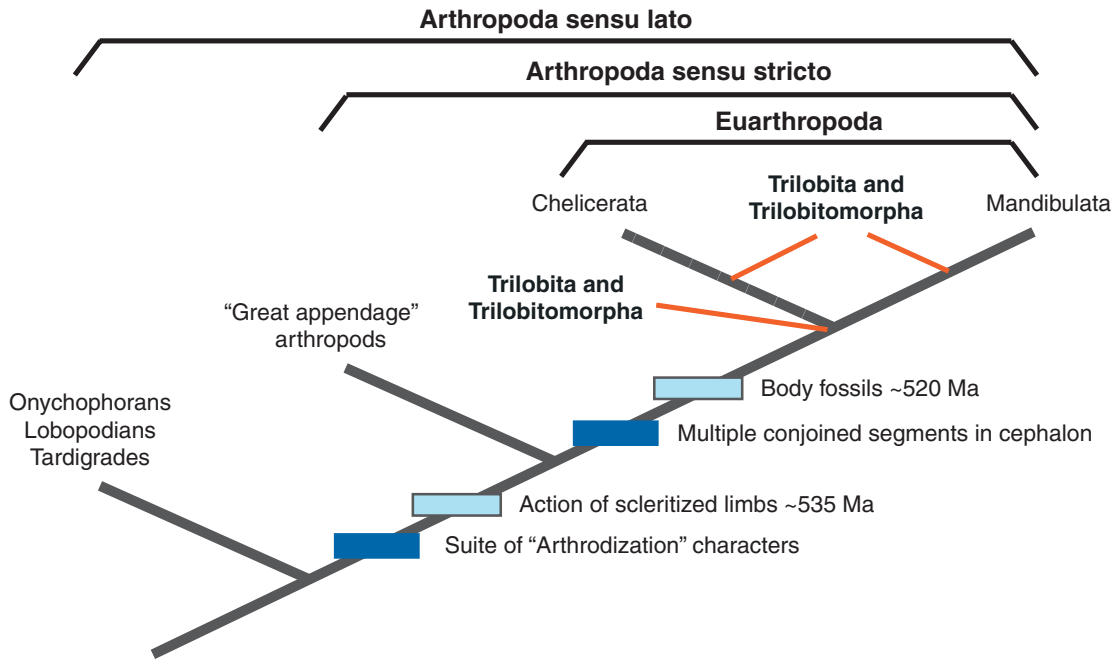affinities within this clade remain debated. Recently, most authors have allied trilobites

Figure 5

Placement of Trilobita among the Arthropoda. Figure shows three possible locations for the placement of trilobites and trilobitomorphs and two fossil-constrained minimum ages for features characteristic of particular groups. Evidence from trace fossils indicates the presence and action of scleritized limbs prior to the appearance of body fossils. Modified from Waloszek et al. (2005).

with chelicerates (e.g., horseshoe crabs, spiders, scorpions, and mites) (e.g., Cotton & Braddy 2004, Wills et al. 1994) or placed them in an unresolved position with respect to both the chelicerates and the other great clade of modern arthropods, the mandibulates (Budd 2002). An intriguing argument links trilobites to mandibulates based on the view that the euarthropod antennae is a synapomorphy for a broadly defined Mandibulata (Scholtz & Edgecombe 2005, 2006, Waloszek et al. 2005). The implications of this new view for issues such as agnostinid affinities await detailed consideration.

The difficulty of resolving the affinities of the trilobites, although frustrating from a taxonomic viewpoint, offers promise from another perspective. Characters unique to trilobites mostly reflect their biomineralization. With regard to basic body organization and ontogenetic mode, trilobites apparently resemble both chelicerates (Størmer 1939) and mandibulates (Garstang & Gurney 1938, Hessler & Newman 1975) in the characters general to both groups, or to basal members of both groups (Hughes 2005). Remarkably, despite their diversity and long evolutionary history, trilobites apparently did not deviate widely from characteristics that may have been possessed by the common ancestor of all living arthropods, which is suggested by the highly serial nature, broadly homonomous segmentation of the dorsal exoskeleton

and limbs, and hemianamorphic development with modest morphological transitions between instars (Hughes et al. 2006). In this respect, Trilobita are of value as a well-documented euarthropod stem group chronicling an episode of evolutionary diversification, decline, and extinction in a major clade that never developed the radical departures from the ancestral morphology that characterize living arthropod groups.

EVOLUTION WITHIN TRILOBITA

The abundance of trilobites in the fossil record permits diverse approaches to the analysis of their evolution. Broad summaries spanning a variety of perspectives are provided by many studies (Fortey 1990, 2000; Šnajdr 1990; Whittington 1992; Whittington et al. 1997) and by a comprehensive web site administered by Dr. Sam Gon III (**http://www.trilobites.info/**). Here I emphasize key aspects of trilobite evolution, many of which have been known for years, from the perspective of evolutionary trends in body patterning.

A Brief History of the Clade Trilobita

One can view the evolutionary history of trilobites from a variety of perspectives, including diversity across a range of taxonomic levels, abundances of taxa and individuals within and among collections, collection occurrences, morphological disparity as assessed by phenetic or phylogenetic methods, and inferences on the ecological roles of particular morphologies. At a broad scale the results of these different approaches correlate with one another, reflecting the fact that all relate essentially to the variety of form. The overall history of the Trilobita consists of approximately 100 million years of the net expansion in their taxonomic, phenetic, and ecological diversity (through the Cambrian up until to the later part of the Ordovician), followed by a prolonged decline lasting approximately 200 million years, with the last trilobites resembling morphologies that persisted since early in the Cambrian (Foote 1993, Fortey & Owens 1990b, Stubblefield 1959). These prolonged phases of expansion and contraction provide an opportunity to explore the adaptive and environmental context of a major diversity fluctuation in an early euarthropod group over an extended interval of geological time.

Higher-level systematics within Trilobita remains in flux, as it has been for much of the past 200 years. The scheme currently utilized by most specialists can be found in Chatterton & Speyer (1997); Fortey (1990, 1997, 2001); Fortey & Chatterton (1988). This phylogeny forms the basis for the arrangement shown in **Figure 6**, which attempts to convey a general impression of the phylogenetic structure, and the overall morphological diversity and stratigraphic history of the Trilobita. The earliest known trilobites, the fallotaspids, lacked dorsal facial sutures, as do early Cambrian olenelloid trilobites and all agnostinids. Conventionally, the earliest trilobites with dorsal facial sutures are classified as belonging to the Redlichiina, a paraphyletic group at best (**Figure 6**), which apparently encompassed basal members of other groups originating early in the trilobite-bearing Cambrian, such as the Agnostida (with or without the true agnostids, the Agnostina), the Corynexochiida, and the
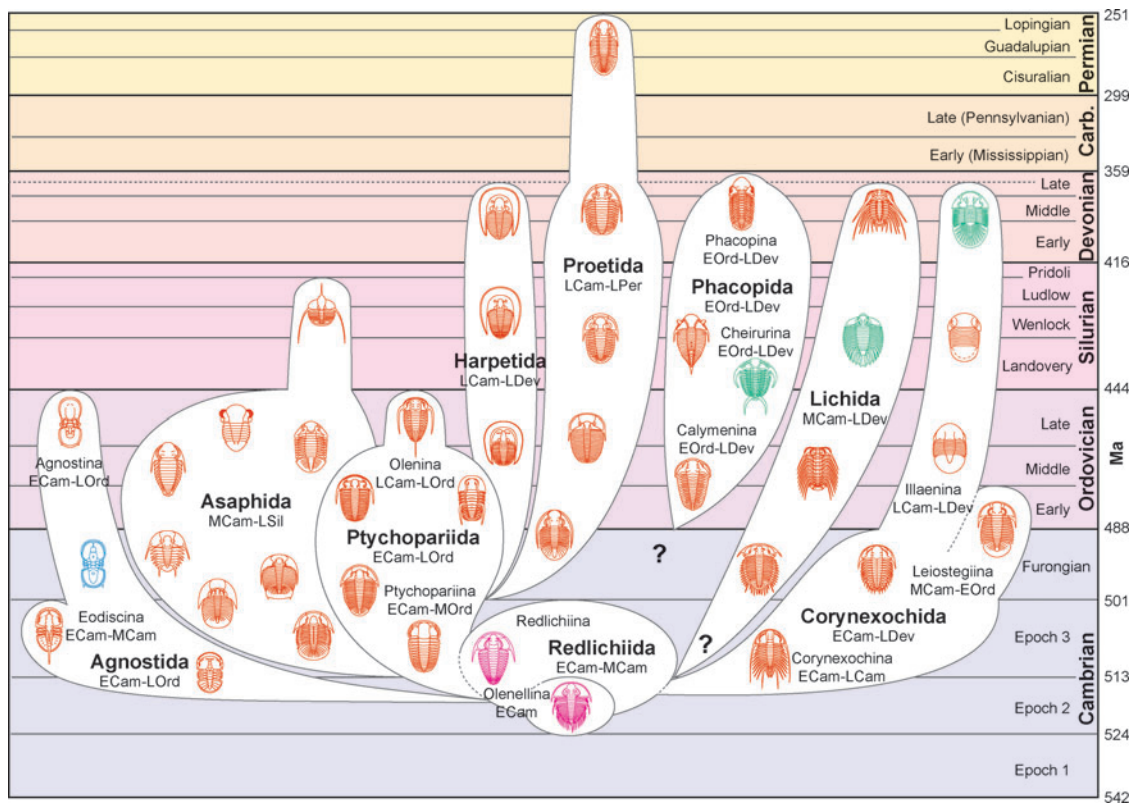
Phenetic: an approach to the estimation of diversity based on the overall similarity of form among individuals

Paraphyletic: a taxonomic group containing some but not all the descendants of a common ancestor

Figure 6

Summary of the evolutionary history of the major trilobite clades plotted against stratigraphic time. The *y*-axis scale approximates a log scale to permit the more detailed illustration of the Cambrian and Ordovician diversifications. Numbers refer to age in millions of years (Ma). Although the spread along the *x* axis approximates the morphological diversity within a clade at any given stratigraphic level, horizontal distances between groups should not be interpreted to suggest degrees of phenetic difference. The diagram is not meant to imply that maximal phenetic variance was present in the early part of the Cambrian, even though groups such as Agnostida and Corynexochida form the extremes along the *x* axis. This is an artifact of the mode of representation. Trilobite color represents the condition of dorsal exoskeletal trunk tagmosis: orange is the homonomous condition, pink is the heteronomous condition in which the batch boundary occurs within the holaspid thorax, blue is where this boundary occurs within the holaspid pygidium, and green where it occurs at the thoracic/holaspid pygidial boundary. The representation is schematic and not meant to imply that all members of these clades younger than the image shown had that condition.

Ptychopariida. The later two groups are both apparently paraphyletic, containing the plesiomorphic members of derived clades that originated later. Fortey (1990, 1997) recognized the Libristomata, to which the Ptychopariida and several derived clades belonged, on the basis of the natant hypostomal condition in which the hypostome was detached from the rest of the calcified ventral cephalic shield. The validity of this

Tagmosis: division of the body into structurally and functionally distinct segments or batches of segments

characteristic as a synapomorphy for this group is contested, as is the notion that the dorsal cephalic suture evolved only once (Jell 2003).

The origins of the major post-Cambrian trilobite clades have also long been problematic. Although most of the major groups are defined by a set of characters clearly distinctive of that group and are thus apparently monophyletic, their similarities to other trilobites are predominantly those that were general to all trilobites (Eldredge 1977). This has hindered the recognition of the plesiomorphic sister taxa of the derived clades, yielding the cryptogenesis problem, which is the unresolved phylogenetic connection between these derived groups and their unknown ancestors (Stubblefield 1959, Whittington 1981). Characters of the early ontogenetic stages of some trilobites unite forms markedly different in maturity, such as the form of the phacopide protaspis, which apparently allies the Calymenina, Cheirurina, and Phacopina (Whittington 1954). Ongoing analysis of the ontogenies of silicified specimens from the Cambrian (by J.M. Adrain, B.D.E. Chatterton, S.R. Westrop, and others) is shedding light on the Cambrian roots of the derived clades that dominated the post-Cambrian history of trilobites.

The limited resolution of trilobite higher-level phylogeny impedes the analysis of evolutionary trends within the Trilobita but it does not prohibit it. Indeed, the problems of trilobite phylogeny illustrate a critical aspect of trilobite evolution that is highlighted herein: differences between two major pulses of trilobite diversification, one in the Cambrian, the other in the Ordovician.

As this review is concerned with examining the ways in which trilobites modified their body patterning, I emphasize diversification rather than extinction, but particularly important extinction events characterized the end of the Ordovician period and much of the middle-late Devonian interval (Feist 1991). In both cases profound environmental changes, perhaps involving modifications of ocean-water oxygen levels, may have been involved (Adrain et al. 1998, Chatterton & Speyer 1989). The ultimate demise of trilobites at or near the end of the Permian removed a group whose diversity had been dwindling for a considerable period. In the later part of their history, trilobites did not generate taxic diversity quickly enough to withstand events at the close of the Permian: Their extinction thus apparently resulted from bad genes rather than bad luck (Raup 1981).

Two Major Diversifications

Appreciation of the differences between these two radiations in terms of the evolution of trilobite body patterning requires a consideration of the characters that contributed to the morphological diversification in each case. Here I propose that the two diversifications differed in the range of characters modified. Both involved changes that embellished pre-existing structures along with novel innovations. However, the Cambrian diversification featured evolutionary experiments with the constructional framework for the trilobite trunk including the mode and number of segments generated, and the development of articulations, whereas the Ordovician diversification recorded a greater emphasis on the morphological embellishment of a stabilized complement of body segments. Below I lay out an argument for this idea in the context

of a general review of trilobite evolution. Compilation of data to test this view is in progress elsewhere.

The Cambrian Diversification

Segmental variation concerns several interrelated aspects of segmentation, including the number of trunk segments, the mode of trunk-segment addition, the nature and development of articulations between tergites, and the form of individual trunk segments. The greatest range in mature trunk-segment numbers was displayed within the first trilobite-bearing interval of the Cambrian (Hughes 2003a). Extremes include eodiscid trilobites with 10 or fewer trunk segments such as *Neocobboldia chinlinica* (Zhang 1989) and even fewer if agnostinids are trilobites, and emuellid trilobites such as *Balcoracania dailyi* with 103 trunk segments (Paterson & Edgecombe 2006). Variation in trunk-segment number apparently occurred among close relatives. The plesiomorphic sister taxa of emuellid trilobites apparently possessed approximately 15–25 trunk segments at maturity, and if Jell's (2003) view of eodiscinids origins is correct, then the segment-poor eodiscinid (and possibly all Agnostida) and segment-rich emueliid clades may have been phylogenetically adjacent (Paterson & Edgecombe 2006, figure 2). Other radical and independent excursions in the number of trunk segments apparently characterized some early Cambrian olenelloid (with up to approximately 45 trunk segments) (Palmer 1998) and early middle Cambrian corynexochid (with approximately 10 trunk segments) (Robison & Campbell 1974) trilobites.

Although all trilobites apparently added segments after hatching (and therefore show a phase of anamorphic development) (Hughes et al. 2006), the maximum number of trunk segments in *B. dailyi* was so high that the normal pattern of hemianamorphic development might not have applied in this case. Whatever the developmental mode, the posterior trunk segments likely appeared at a rate that greatly exceeded one or two segments per instar, which is the rate of anamorphic segment addition in most other trilobites (see Hughes et al. 2006, Pocock 1970).

Just as the generation of trilobite trunk segments usually achieved a stable, mature phase, so too did the development of trunk articulation at the onset of the holaspid phase. Among Cambrian trilobites, both the overall number of holaspid thoracic and pygidial segments and the proportions allocated to these different body regions varied markedly. In emuellids, less than 5% of the number of trunk segments and an even smaller proportion of the trunk exoskeletal area were occupied by the pygidium. In some eodiscids, the proportion of pygidial segments exceeded 65% of the trunk segments, and the pygidium encompassed a similar portion of trunk area (see Fortey & Owens 1997 for a metric relating to pygidial dimensions, broadly reflecting the number of segments within the pygidium). Hence the early trilobite-bearing Cambrian witnessed wide variation in the allocation of trunk segments between the thorax and pygidium.

The onset of the segment-invariant phase of development and the stable thoracic articulation phase could occur synchronously or offset from one another. Examples of synchronous transition in both phases (synarthromeric mode), the onset of the holaspid phase preceding the onset of the segment-invariant phase (protarthrous

Tergite: sclerotized subdivision of the dorsal exoskeleton bounded by an articulating joint

Caudalization: the tendency in derived groups for a larger proportion of trunk segments to be assigned to the holaspid pygidium

mode), and the onset of the segment-invariant phase preceding the onset of the holaspid phase (protomeric mode) are all known among early Cambrian eodiscid trilobites, with modes apparently varying intraspecifically in the case of *N. chinlinica* (Hughes et al. 2006). It may be noteworthy that extreme protomeric development occurred in the late Cambrian burlingiid trilobite *Schmalenseeia fusilis*, which did not develop trunk articulation and thus never progressed beyond the protaspid stage (see Hughes et al. 2006, Peng et al. 2005).

Variation in the number of thoracic segments in the holaspid stage has been reported in a number of trilobite species, the great majority of which were Cambrian taxa belonging to basal clades (Hughes et al. 1999). The apparent temporal reduction in the number of cases of such variation has been related to a general trend toward the stabilization of the number of holaspid thoracic segments at progressively higher taxonomic levels (McNamara 1983, 1986), with the derived clades characterized by stable numbers of segments. Examples of such stability from a variety of major clades include the Calymenidae (with 13 segments), Phacopina and (most) Lichidae (with 11), Phillipsidae (with 9), Asaphidae (with 8), and Trinucleidae (with 6), and this stability was evidently derived independently in these clades (i.e., sister taxa to each of these clades differed in segment number). This trend was interpreted to imply progressive canalization of phenotypic variation as a general feature of trilobite evolution (McNamara 1983), but such a trend was apparently reversible in some aulacopleurid trilobites (a group whose morphology resembles that common among Cambrian ptychopariids) (Hughes et al. 1999). The increased stability in thoracic segment numbers may relate to another important tendency in trilobite evolution: the allocation of an increased proportion of the trunk segments to the holaspid pygidium, a trend known as caudalization (Raymond 1920, Stubblefield 1936). Although many Cambrian trilobites clearly showed low degrees of caudalization, others were strongly caudalized, such as Agnostida and various corynexochid and ptychopariid groups.

Another striking variation in the segmentation pattern among some Cambrian trilobites was that although the majority of trilobites showed a homonomous trunk-segment condition, some taxa developed trunk segments with distinctly different forms. These distinctions fall into two categories: (*a*) cases in which individual segments differed from others within the trunk in unique ways, and (*b*) cases in which segments were organized into distinctive batches of similar segments (Hughes 2003a). In the latter case, the trunk is divided into two (or possibly more) regions, known as the protrunk and opisthotrunk (**Figure 1**). The most striking cases of such heteronomy in Cambrian trilobites occur in those forms with a small pygidium, such as the olenelloid *Bristolia bristolensis* and emuellid *Balcoracania dailyi* (Paterson & Edgecombe 2006). Here the boundary between protrunk and opisthotrunk segments occurred within the thorax. When such a condition occurred, the degree of differentiation was limited by the requirement for functional articulation between segments. Hence differences were confined to the pleural region (see **Figure 1**), and the strict one-to-one associations between pleural and axial regions of each segment were maintained. Notable transitions in the segment morphotype occurred within the pygidium in some forms in which a greater proportion of trunk segments were allocated to the holaspid

pygidium (e.g., Matthew 1896). In these cases, the functional requirement for transverse articulation did not apply.

Variations in the development of trunk segmentation seen in the Cambrian diversification of trilobites are comparable with those seen among the trilobitomorphs. The variability in patterns of trunk tergite articulation is striking: Conditions range from forms such as *Primicaris larvaformis* (Zhang et al. 2003) and possibly also species of *Skania* (Lin et al. 2006), which, similar to *Schmalenseeia fusilis*, apparently never developed trunk articulations, although these nontrilobite forms apparently lacked the facial sutures characteristic of the trilobite protaspid phase. The phylogenetic position of parvancorinomorph taxa such as *P. larvaformis* and *Skania* has not been resolved in detail, but a recent analysis placed them as basal to naraoiids (Lin et al. 2006), a group whose trunk articulation pattern is comparable to that of a trilobite meraspid degree 0 in that only a neck joint was developed. Other trilobitomorphs lacking any trunk articulation are the Tegopeltidae (**Figure 4**).

Trilobitomorphs such as *Cindarella eucalla* showed a pattern of trunk articulation similar to that of most redlichiid trilobites in that articulations were present throughout most of the trunk. However, the cephalon of this form and of *Xandarella spectaculum* apparently encompassed more appendages than that typical of trilobites, and both these xandarellids are extraordinary in that the relationship between tergal boundaries and appendages varied along the length of the trunk. The anterior parts of the trunk of *X. spectaculum* displayed a one-to-one relationship between the two, but more posterior tergites apparently encompassed a progressively larger number of appendages. This was accomplished by a decline in the size of appendage pairs toward the rear coupled with an expansion of the length of each tergite (Hou & Bergström 1997). In *C. eucalla*, tergite length remained approximately constant rearward as appendage size declined (Ramsköld et al. 1997).

The presence of a trilobite-like pygidium that succeeded a trilobite-like thorax (with a one-to-one relationship between appendage pairs and tergites) is evident in a variety of trilobitomorphs, such as Liwiidae, Helmetiidae (although the articulating capability of tergite boundaries is unclear in some cases), and apparently also in the basal xandarellid *Sinoburius* (**Figure 4**). In all these cases, the pygidium encompassed a considerable proportion of the total area of the trunk and a significant proportion of the total number of trunk segments, and appears to be the plesiomorphic (primitive) condition (Edgecombe & Ramsköld 1999). The lack of well-preserved early ontogenetic stages of any trilobitomorph in which the trunk was divided into the thorax and pygidium precludes analysis of whether trunk articulations developed progressively in a trilobite-like manner, but multiple large specimens with apparently constant segment numbers may suggest a segment-invariant phase. Hence it is possible that hemianamorphic development was the basal condition throughout the clade and that thoracic articulation, where developed, generally accrued in a trilobite-like manner.

Ivantsov (1999) reported an extraordinary relationship between segment boundaries and articulations in the trilobite-like arthropod *Phytophilaspis pergamena*, which bore a phosphatic exoskeleton. Here two specimens indicate that the articulation boundary between the thorax and pygidium apparently cut across several trunk segments. If this pattern is vindicated by additional specimens, and cannot be interpreted

as a taphonomic artifact (possibly the result of compaction-related deformation of a common ecdysial posture), this species indicates a peculiar disassociation of the relationship between exoskeletal segments and articulation-bound tergites within the trunk. A close parallel in trilobites may be the dorsal facial suture in opisthoparian trilobites in which the suture apparently cuts across at least one segment boundary.

Most trilobitomorphs had homonomous exoskeletal trunk segments. In some cases trunk segments were also homonomous with the posterior cephalic segments. The distinction of the trunk into regionalized batches of segments, or the presence of individual segments of unique form, occurred in such stem-group Arthropoda sensu stricto as *Fuxianhuia* (Chen et al. 1995, Hou & Bergström 1997), indicating that the ability to regionalize the trunk existed early in arthropod evolution. These observations of the segmentation patterns within nontrilobite trilobitomorphs suggest that the variety of patterns evident within early trilobites has parallels among trilobite sister taxa: There is no indication that trilobites were unusually variable in these aspects of body construction.

However, the evolution of Cambrian trilobites involved considerably more than variations in the number, articulation, and form of trunk segments. Taxa are also differentiated by a host of other characters, including tergal shape and the relative proportions of structures within tergites, and by novel characters ranging from discrete structures, such as spines, to subtle differences in surface ornament. Hence the argument is not that the variation among Cambrian trilobites was fundamentally different from that of later clades, but that variation in the number of trunk segments and their allocation to the thorax and pygidium played a larger role early in trilobite history.

The Ordovician Diversification

A diversification that became marked from near the base of the middle Ordovician onwards resulted in the rise to prominence in terms of abundance and taxic, morphological, and ecological diversity of a set of derived trilobite clades. Most of these had mature body forms distinct both from one another and from those common among Cambrian trilobites (Adrain et al. 1998, Foote 1991, Fortey & Owens 1990b, Stubblefield 1959, Whittington 1981) (**Figure 6**). Beecher (1895, 1897) noted the increased disparity among Ordovician clades and argued that early postembryonic stages of these derived trilobites had a richer array of characters than those trilobites belonging to Cambrian clades and that the degree of morphological change accomplished during their ontogenies was greater than that of Cambrian trilobites. He interpreted this transition as an example of recapitulatory evolution, whereby novel characters were added at the termini of the ontogenetic trajectories of their ancestors (see Gould 1977). This view has long been abandoned as general evolutionary principle, but the suggestion that Ordovician clades were commonly peramorphic (in the sense of moving morphological development along a common ontogenetic trajectory beyond the terminal point of the ancestor) with respect to Cambrian ones has continued to be defended (McNamara 1986). The idea that per-molt growth increments were larger among the clades that dominated the Ordovician diversification
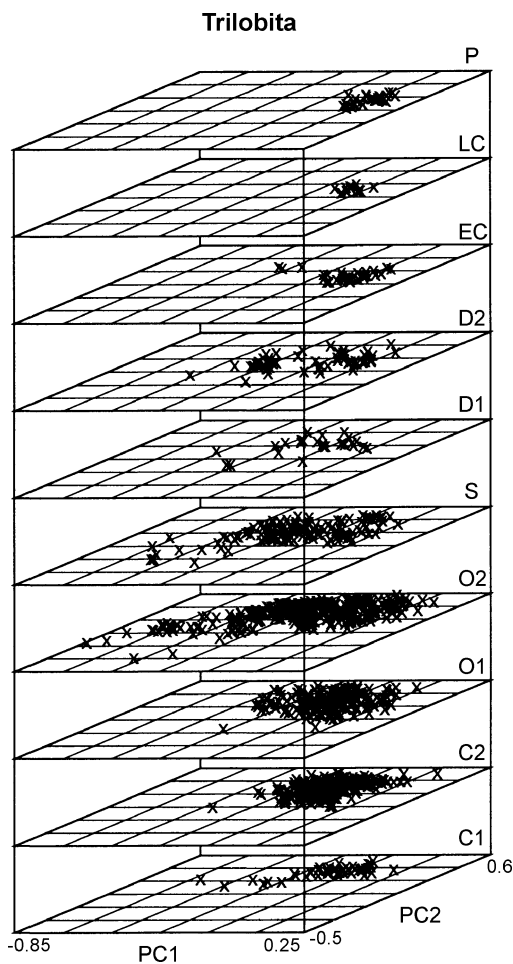
Trilobita

Figure 7

Summary of trilobite cranidial (or cephalic outline forms lacking a dorsal facial suture) outline morphospace occupation for a successive series of time slices throughout the evolutionary history of Trilobita. Figure modified by M.J. Foote from Foote (1991). PC, principal component axes; C, Cambrian; O, Ordovician; S, Silurian; D, Devonian; EC, Early Carboniferous; LC, late Carboniferous; P, Permian.

(Chatterton et al. 1990) has also been mooted. Although both these ideas require testing and are not necessarily commensurate, they attest to the view that at least some post-Cambrian trilobites differed from their ancestors in similar ways, although they possessed different suites of characters.

A contrast in the nature of the Cambrian and Ordovician diversifications is illustrated by the jump in cranidial shape diversity that occurred within the Ordovician (**Figure 7**). In the context of body-patterning evolution, Foote's (1991) analysis of cranidial shape included information on the course of the dorsal facial suture (except in those forms with a marginal suture), which varied relatively little among most Cambrian trilobites. The fact that Cambrian redlichiid, eodiscid, ptychopariid, and corynexochiid trilobites clustered together in a relatively small area of cranidial shape space (Foote 1991) suggests either a single evolutionary origin for the dorsal facial suture or a strong constraint on its site of origin, perhaps related to a segmental boundary (assuming trilobite monophyly and that the fallotaspid-like marginal suture was the

Cranidium: central portion of the cephalon bounded laterally by the dorsal facial suture

Dorsal facial suture: a line of weakness on the dorsal surface of the exoskeleton that facilitated molting and served to separate the axial portion from the marginal portions

basal condition). The constancy in position in early groups contrasts with the variety of sutural courses seen in later trilobites and hence the much larger area of morphospace occupied by later clades in Foote's analysis (**Figure 7**). This pattern exemplifies the difference between the Cambrian and Ordovician diversifications: The Ordovician diversification did not involve the origin of a new aspect of trilobite organization (in this case the dorsal facial suture), but it did involve significant novel deployment of a pre-existing structure, and it apparently did so independently in a number of clades. In contrast, radical modifications of the position of the facial suture did occur among Cambrian trilobites (e.g., Hughes et al. 1997, Whittington 1994), but taxa with such structures did not form a large component of Cambrian trilobite diversity.

Stubblefield (1959) anticipated a distinction in the pattern of Cambrian and Ordovician diversification based on estimates of taxonomic diversity. Further support for this view comes from attempts to compare the variety of ecological roles occupied by trilobites belonging to derived clades (Fortey & Owens 1990b) with those evident among Cambrian trilobites (Hughes 2000). Fortey & Owens (1990b) defined a set of trilobite morphotypes that they inferred to represent adaptations to particular lifestyles. Such functional inferences, when drawn from a range of morphological and geological evidence, can be compelling, such as arguments that mature, free-swimming forms occupied a variety of levels in the water column (Fortey 1985, McCormick & Fortey 1998). According to Fortey & Owen's (1990a,b) model, during the later Ordovician the largest number of clades contributed to the largest number of morphotypes, suggesting that the ecological diversity of trilobites peaked at that time (but also see Seilacher 1985 for a different view of trilobite ecology). Many Cambrian trilobites can also be assigned to these morphotypes, but commonly with a lower degree of confidence (see Fortey 1985 for an example involving pelagic trilobites). As morphotypes are defined by characters whose functional role can be inferred, the adaptations of Cambrian trilobites to these roles were evidently less distinct than those of their Ordovician counterparts (Fortey & Owens 1990b, Hughes 2000). This is consistent with the idea that Cambrian trilobites were, en masse, more generalized (Fortey & Owens 1990a).

From a body-patterning perspective, the contrast between the Cambrian and Ordovician trilobite diversifications is that the Ordovician diversification may have yielded trilobites of greater distinction in terms of overall character richness, but apparently within a narrower range of conditions of trunk segmentation. What did such a transition represent?

Flexure, Enrollment, and the Adaptive Context of Trilobite Diversification

The notion that the Cambrian and Ordovician trilobite diversifications differed in important ways preceded the formalization of evolutionary theory. Burmeister (1846, pp. 37–38) noted increased disparity among stratigraphically later trilobite groups and interpreted this to indicate the progression toward more perfect matches to idealized types. This was based on the view that early forms were unable to achieve a sealed capsule upon enrollment, whereas a variety of later forms were able to do so. The view of

significantly improved protective efficiency of enrollment during trilobite evolution has received substantial support in the subsequent literature (e.g., Bergström 1973; Chatterton & Campbell 1993; Clarkson & Henry 1973; Whittington 1989, 1990), and it provides a useful framework for exploring the adaptive context in changes in trilobite body organization through time, as discussed below.

In addition to roles in the organization of development (Minelli 2003) and as a substrate for muscle attachment (Budd 2001), the exoskeleton evidently served a protective function throughout trilobite history (Babcock 2003). Adjustments to overall body proportions that permitted efficient enrollment were matched by innovations within individual tergites that aided the articulation efficiency, and these are most easily interpreted as protective responses to predators. The overall organization of the exoskeleton reflected the need to optimize the functionality of this protective role within the context of other demands, such as feeding and reproduction.

Detailed information on the junctions between tergites permits the reconstruction of how they articulated (Chatterton & Campbell 1993, Whittington 1990). A suite of characters were involved in this process, which assisted in guiding the route of flexure and in preventing the exposure of soft tissues. The number and form of such characters varied among trilobite clades. Trilobites belonging to derived groups, such as harpetids, and some trinucleids had articulating surfaces comparable with or simpler than those of many early Cambrian trilobites. Nevertheless, the appearance of a suite of features associated with the articulating surface (such as ball-and-socket connections, the fulcrum (a geniculation on the anterior margin of the pleurae), and faceted and ornamented contact surfaces between distal pleurae) is a striking feature of many derived trilobite clades, when compared with the simple flanged hinge present in most early Cambrian trilobites. Such novel structures may have guided the course of flexure more effectively or strengthened joints between adjacent segments (Clarkson & Whittington 1997, Whittington 1990).

A characteristic closely related to articulation process was the ability of trilobites to perform complete enrollment (Clarkson & Whittington 1997), which is when dorsal flexure permitted the pygidial shield to come in contact with the cephalic shield. Spheroidal enrollment was the condition in which the rim of the pygidium and the tips of the thoracic segments came into contact with the rim of the cephalic shield (Bergström 1973, Harrington 1959) and is the type of enrollment that Burmeister (1846) considered to be more perfect. Such a condition was not possible for an early Cambrian trilobite such as *Balcoracania dailyi* because the posterior trunk segments would have been too narrow to effectively shield cephalic soft tissues. Some early Cambrian trilobites have been reconstructed as unable to enroll completely (Whittington 1989), with flexure limited to a cylindrical C shape, with gaps between the pleural tips providing access to the interior of coiled animal. Given that the posterior of the trunk was much narrower than the cephalon in most multisegmented early trilobites, exoskeletal protection provided by enrollment in such forms was limited compared with that in many derived trilobites. Complete enrollment has been documented in a variety of Cambrian trilobites (Chatterton & Campbell 1993, Stitt 1983) and is thought to have occurred even in forms lacking the fulcrum (Clarkson & Whittington 1997). Many of these were cases of spiral enrollment (Bergström 1973)

in which the pygidium (and commonly some posterior thoracic segments as well) were tucked inside the cephalic shield. Spherical enrollment did occur among Cambrian trilobites, particularly among eodiscinids and agnostinids. Cambrian trilobites that lacked trunk articulation, such as *Schmalenseeia fusilis*, could not have enrolled or flexed the trunk.

Complete enrollment was common among derived trilobites, either as an encapsulated sphere (as in many calymenids, phacopinids, illaenids, asaphids, and proetids) or as a cylindrical form with lateral gapes protected by extended pleural spines (as in some odontopleurids) (Clarkson & Whittington 1997). Hence the manner of enrollment varied markedly among trilobites, and different styles apparently imposed different constraints on further variation. Spheroidal enrollment required a precisely coordinated scaling of the body proportions. This degree of precision is emphasized by the occurrence of vincular notches, grooves in the cephalic rim that exactly accommodated portions of the rim of the pygidium and the tips of thoracic pleurae during enrollment. Vincular structures are an example of a suite of characters called coaptative devices that interlocked when the exoskeleton was completely enrolled (e.g., Chatterton & Campbell 1993, Clarkson & Henry 1973, Henry 1968). Such embellishments, of which there are numerous kinds, hindered the opening of the enrolled trilobite through shearing motion. Coaptative structures that differ in morphological detail but that apparently served similar purposes were derived independently in several clades, such as the various Panderian structures of phacopids, protetids, illaenids, and nileids (Chatterton & Campbell 1993). Although some coaptative structures are evident among Cambrian trilobites, they were developed most prominently among post-Cambrian trilobites. Examples of putative evolutionary trends in such characters, in particular species lineages, have been reviewed elsewhere (Chatterton & Campbell 1993, Fortey & Owens 1990b).

In summary, although the earliest trilobites were able to flex their exoskeletons efficiently, there is evidence that derived groups elaborated the structures associated with flexure and evolved efficient exoskeletal coverage during enrollment. Hence although trilobites apparently suffered predation throughout their geological history, their patterns of evolution are consistent with the idea of an evolutionary arms race between trilobite prey and increasing effective predators (Vermeij 1987).

Enrollment and Segmentation

Although the trend toward more efficient enrollment was characteristic of derived trilobites, relatively little is known of the detailed functional morphology of enrollment. Overall body shape is predicted to be constrained in forms with spheroidal enrollment because of the necessarily precise fit of the cephalon and trunk. The trunk morphology of spheroidal enrolling forms conformed to that prediction. Thoracic segments were similar in width to the cephalon (Bruton & Haas 1997). The curvature of the pygidium matched that of the anterior of the cephalon. The number of trunk segments was constant in the holaspid thorax and commonly also in the holaspid pygidium. The ability to enroll spherically does not seem to have required a particular number of segments, as small and trunk-segment-poor trilobites (such as

the early Cambrian eodiscinid *Tsunyidiscus longquanensis*) may have been able to en-roll from the first meraspid instar onward, without any free thoracic segments (Zhang & Clarkson 1993). Degree 0 meraspid *A. pisiformis*, lacking any thoracic segments, certainly enrolled (Müller & Walossek 1987). Similarly, the ontogenies of some caly-menids suggest that the development of coaptative structures preceded the develop-ment of trunk articulation and the possibility of usage for that purpose (Chatterton et al. 1990). This may also suggest the capacity for complete enrollment from early meraspid stages onward. Therefore it does not seem that a specific complement of segments was required to permit enrollment.

Relationships between trunk-segment shape and number are harder to assess in forms with spiral enrollment because in that case the precise pattern of enrollment may have been less stereotyped. Nevertheless, it is unlikely that many of the trunk-segment-rich early Cambrian forms could have encapsulated upon enrollment be-cause the posterior trunk segments would have been too narrow to effectively shield cephalic soft tissues.

Many trilobites that enrolled spherically had cephala and pygidia of comparable size (the isopygous condition). Isopygy or even macropygy (when the pygidium was larger than the cephalon) could be achieved by a sharp increase in the size of py-gidial segments, as in species of the lichiid *Acanthopyge* (**Figure 8**), or by assigning a large proportion of the total number of trunk segments to the pygidium regardless
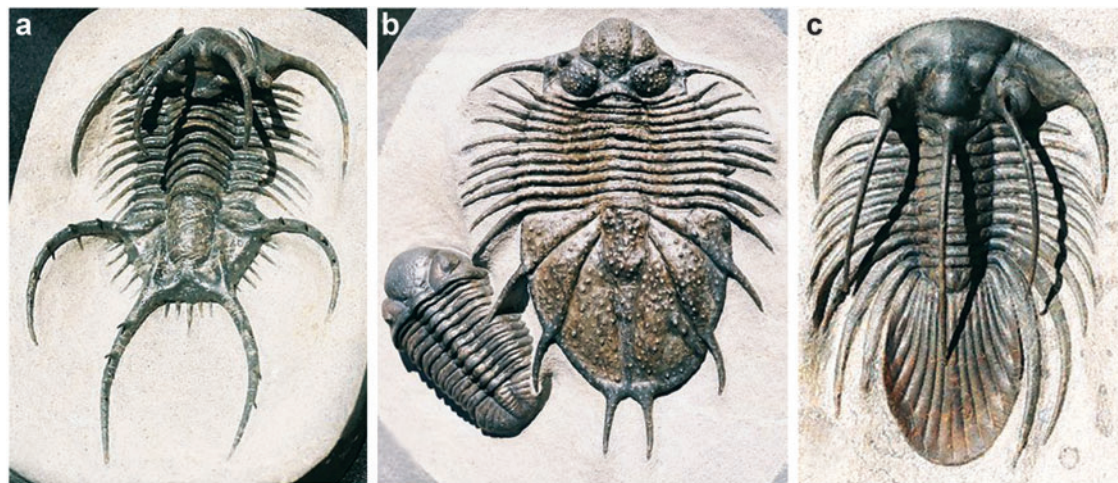
Figure 8

The "two-batch" heteronomous trunk condition, here with the mature thoracic and pygidial segments showing different morphologies, occurred in a variety of major post-Cambrian trilobite taxa, as illustrated by the large specimens in each of the three figures. All specimens are from the AM Limestone of the Devonian of Morocco. (*a*) *Ceratarges* sp. (Order Lichida), length 8.4 cm. (*b*) The larger specimen is the lichiid trilobite *Acanthopyge* sp. (Order Lichida), length 8.4 cm. The smaller trilobite (Order Phacopida, species undescribed) shows the homonomous trunk condition. (*c*) *Kolihapeltis* sp. (Order Corynexochida), length about 5 cm. See Hughes et al. (2007).

of the size of individual segments (caudalization). Isopygy occurred in several groups
with spherical enrollment and may have facilitated more precise control of enroll-
ment (Fortey 2001). Examples of isopygous spherical enrollers occur in Agnostida,
Proetida, Asaphida, Illaenina, and some Phacopida. It is not clear that all highly
caudalized trilobites enrolled spherically, and a more general explanation for caudal-
ization could be the reduction in the number of surfaces of potential rupture between
exoskeletal elements (Hughes 2003a). We need comparative analysis of the ontoge-
netic relationships between the number, size, form, and articulation between trunk
segments among species showing different patterns of growth and flexure.

Heteronomous Batches of Trunk Segments

A different aspect of trilobite trunk evolution, alluded to above, is the tendency for
trunk segments to become regionalized into batches of segments that shared similar
shapes but which differed in shape from those of other parts of the trunk (Hughes
2003a,b). This regionalization into sets of similar segments contrasts with individu-
alized segments such as macropleural or macrospinous segments, which are usually
embellished in a unique manner (Hughes 2005). The best examples show separation
of the trunk into two distinct batches of segments, although additional divisions may
have occurred. Regionalization of segment form within the trunk presumably implies
regionalization of function. Although no trunk appendages are known from trilobites
with the most marked heteronomous trunks, their relative sizes and perhaps also pro-
portions must have changed across batch boundaries in some cases (see **Figure 1**).
There was no consistent relationship between enrollment and heteronomy of seg-
ment form, partly because different styles of heteronomy occurred in different groups,
and heteronomy did not necessarily preclude spherical enrollment. Although some
heteronomous forms had large pygidial spines that would have projected anteriorly
on enrollment, heteronomy may have also been related to novel modes of propulsion
or feeding (Burmeister 1846, Raymond 1920).

Figure 9

Constraints on increasing mature thoracic segment number in some trilobites with a
heteronomous trunk. In the upper panel, all trunk segments are homonomous and an extra
thoracic segment can be achieved by developing one extra articulation, shown here as a switch
from synarthromeric to proteromeric development in forms maintaining a constant number of
trunk segments. In the lower panel, the trilobite has a heteronomous trunk, with the
thoracic-holaspid pygidial border marking the boundary between two batches of segments. A
similar switch from synarthromeric to protomeric development would result in an individual
with the last thoracic segment of pygidial morphotype, unlikely to integrate functionally with
the thoracic segments preceding it. This inferred nonviability is indicated by the red cross.
Achieving a functionally integrated form would require a developmental switch in the
specification of segment morphotype, shown by the red triangle, which anticipated the
ultimate position of the thoracic-holaspid pygidial boundary. The requirement for
independent, temporally displaced, yet integrated transitions in the onsets of the mature
phases of two different aspects of segmentation may explain why examples of such cases are
rare or unknown. Segment color scheme as in **Figure 2**.
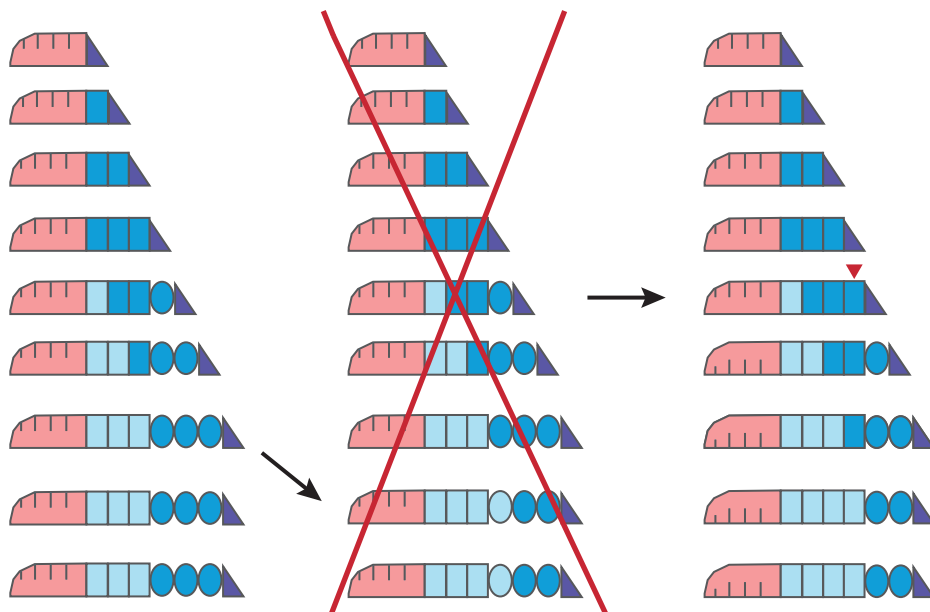
a
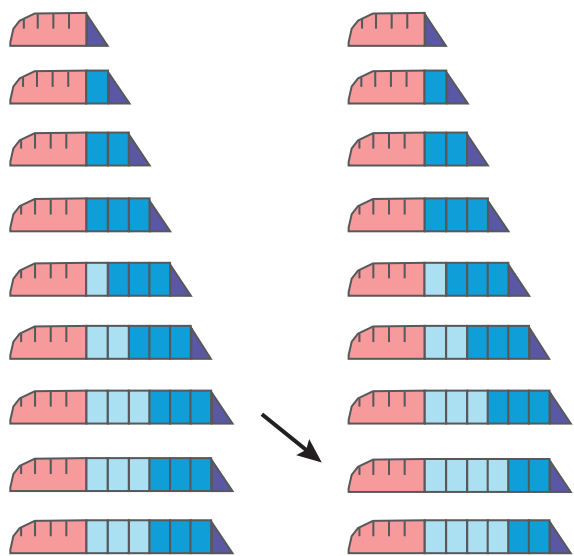
Synarthromeric ancestor   Protomeric descendant

b

Synarthromeric ancestor   Protomeric descendant   Protomeric descendant

The evolution of batches of heteronomous segments is interesting from a body-patterning perspective for several reasons. Unlike the development of segment articulation, which was apparently specific to trilobitomorphs, regionalization of batches of segments is a common theme throughout arthropod evolution. Indeed, the post-Cambrian evolution of arthropods appears largely to be the story of increased functional and morphological differentiation of segments (Abzhanov & Kaufman 2000, Budd 2000, Cisne 1974, Wills et al. 1997). Furthermore, such morphological regionalization among segments was likely under the control of those developmental genes responsible for such regionalization in all living arthropods: the *Hox* genes (Akam 2000; Hughes 2003a,b; Sundberg 2000).

Heteronomous batches of trunk segments evidently evolved independently in a number of clades (Beecher 1897, Hughes 2003a), such as olenelloids, emulellids, cheirurines, scutelluids, lichiids, odontopleurids, and agnostinids, if trilobites (**Figure 6**). As mentioned above, batch boundaries sometimes occurred within the mature trunk (as in various olenelloids and redlichinids), at the holaspid thoracic-pygidial boundary (as in scutelluids, lichiids, and cheirurids) (**Figure 8**), or within the pygidium (as in the agnostinid *Rhaptagnostus*). [Interestingly, Haeckel (1896) recognized the fundamental importance of the two-batch condition in trilobites and considered it to define his derived taxon Eutrilobita, an evidently polyphyletic group.] These different relationships between batch boundary and trunk-segment-articulation boundary placed different constraints on the ability of segments within each batch to vary in form. All segments within the thorax had to retain functional articulations between segments. Hence batch boundaries within the thorax were largely a matter of the relative size of the pleural region, and the transition in segment shape was either abrupt or graded over a series of segments. This constraint was not operative in those trilobites in which the batch boundary occurred within the holaspid pygidium. Those segments would not have been articulated at any point during their ontogenies, so the requirement of integrated axial and pleural boundaries was relaxed. Relaxation of this constraint led to a wide variety of segment morphologies (**Figure 8**).

The degree of heteronomy between segments in the holaspid thorax and pygidium was apparently correlated with the decreasing variability in the number of segments assigned to the thorax in derived groups. Variation in segment number occurred at low taxonomic levels, apparently even intraspecifically, in trilobites with a homonomous trunk (Fusco et al. 2004, Hughes & Chapman 2001, Hughes et al. 1999). This may be because all that was required in such forms was the generation of an additional articulation (**Figure 9**). All segments had similar form, so the transfer of an extra segment from the pygidium to the thorax may not have impeded normal thoracic function. Thus, if there was any selective advantage for an increased number of thoracic segments, such a transition might have been achieved relatively easily. Varying the number of segments allocated to the thorax of a form heteronomous across the holaspid thoracic-pygidial boundary would likely have presented a greater challenge because the result of a segment being misassigned to the wrong region could be a thoracic or pygidial segment distinctly different in shape from that of its associates. Because in a heteronomous trunk these two regions are functionally specialized, it seems unlikely that such a segment would offer a selective advantage. In such cases,

mutations operative at different points in ontogeny would be required to (*a*) vary the number of trunk segments to be assigned to each batch, the morphological expression of which occurred soon after the segment budded from the subterminal generative zone (Hughes 2003a), and (*b*) shift the position of the final articulation in a complementary manner at a later stage of ontogeny (**Figure 9**). The near constancy in the number of thoracic segments in such heteronomous forms suggests that integrated change of that kind was uncommon. This explanation is also consistent with the evident caudalization of many derived clades: As all thoracic segments were once part of a functional meraspid pygidium it may have been easier to evolve a reduction in thoracic segment number within a lineage than an increase.

SUMMARY

Improved knowledge of evolutionary relationships among Euarthropoda, and particularly the characteristics and placement of stem-group trilobitomorph taxa, provides a platform from which to evaluate trilobite evolution. Such work also highlights the relevance of data from Trilobita for evaluating major trends in arthropod evolution. Many of the modifications in the overall number of segments, allocation of segments to specific body regions, and regional differentiation of segments evident among Cambrian trilobites have parallels among contemporary relatives outside the group. It appears that modifications of the form and articulation of the trunk were a general characteristic of trilobitomorphs, just as the degree of cephalization was apparently variable at a larger taxonomic scale among stem-group Arthropoda. The Ordovician trilobite diversification, in contrast, involved a series of novelties that apparently embellished the functional performance of the trilobite exoskeleton, particularly in response to predation, but also with regional specialization within the trunk perhaps related to other functions.

The idea that different stages in phylogenetic history exhibited variations in different suites of characters dates back to Darwin and beyond, and does not suggest remarkable development plasticity per se during early euarthropod evolution. Nevertheless, major aspects of body patterning clearly had been stabilized prior to the appearance of trilobites in the early Cambrian. The variation in aspects of segmentation seen in the Cambrian diversification might be the warm afterglow of the initial radiation of Arthropoda. In that regard, trilobite evolution is consistent with that of several other major groups in that crown group clades were established during the Cambrian and became dominant thereafter (Budd & Jensen 2000).

Researchers have interpreted trilobite species lineages to show both long-term morphological stasis within species (Eldredge 1971, 1972) and gradual anagenetic change (Sheldon 1987), although providing statistical support for either such mode is challenging (McCormick & Fortey 2002). In fact, given both the rates of evolution theoretically possible (Gingerich 1993) and empirically observed among modern organisms (Reznick et al. 1997), studies of trilobite microevolution show remarkably slow rates of net change. However, this is a consequence of the manner in which the stratigraphic record accumulated (Sadler 1981): The ability to reconstruct progressive, small-scale morphological changes in species lineages from multiple horizons

in a stratigraphic sequence requires that observed rates of evolution be slow. There is no evidence that such evolution was fundamentally different from that responsible for the generation of the major aspects of trilobite diversity. Indeed, one of the exciting opportunities afforded by trilobites is that microevolutionary studies of trilobite segment ontogeny and variation conducted at high stratigraphic resolution may yield insights into the mechanisms controlling the evolution of major aspects of trilobite body patterning (Fusco et al. 2004, Hughes 2005).

Given that a biomineralized dorsal exoskeleton is a trilobite synapomorphy it seems unlikely that the clade had a geologically long history prior to their appearance in the rock record. Likewise, there is no strong evidence for a prolonged history of trilobitomorphs prior to the appearance of trilobites. The earliest scratch marks produced by an appendage comparable with those from sclerotized arthropods predate the first appearance of trilobites by only approximately 15 million years (**Figure 5**), and could have been made by arthropods considerably more basal than any euarthropod. Taken at face value, this evidence suggests that much of arthropod stem group evolution was accomplished during this interval. Hence, evolutionary rates in features associated with body patterning appear to have been higher during the earliest Cambrian than thereafter (Jacobs et al. 2005). Fossil evidence for arthropods prior to the Cambrian is equivocal: Even the most striking putative homologies between arthropods and Ediacaran organisms, while plausible, are inconclusive.

Jablonski (2000, pp. 18–19) has proposed some challenges for paleontologists seeking to understand the developmental evolution of fossil groups. These include (*a*) "to pinpoint some of the phenotypic changes most likely to be underlain by large-effect genes, and then to test whether these changes can predict the evolutionary trajectories of clades in the fossil record," and (*b*) to examine "how well the ontogeny of individual organisms can predict the extent of morphological diversification of their descendent clades." This review of the evolution of trilobite body patterning suggests that the clade provides opportunities for addressing both issues.

The repeated and evidently convergent differentiation of the trunk into distinct batches of segments, evident in trilobites and in other arthropods, may have been facilitated by what Gould (2002) termed a "homologous underlying organizer," in this case the convergent differentiated expression of posterior *Hox* genes. The morphological impact of such deployments, and their potential for further embellishment, depended on the context of the deployment site with respect to the holaspid articulation boundary: The opportunity for modification of posterior segment morphology was much higher if such segments were confined to the holaspid pygidium, isolated from functional constraints required by articulation. It would be useful to document the evolution of the two-batch condition in multiple cases to test this idea.

Jablonski's (2000) second challenge was anticipated by Beecher (1897), who pointed out that the lack of significant larval modification or drastic character predisplacement in trilobite ontogeny provides a good basis for comparing it with trilobite phylogeny. Compared with the radical changes evident in the ontogenies of many mandibulate arthropods, trilobite ontogeny involved gradual character transformations accomplished over an extended series of free-living instars (Hughes & Chapman 1995). Such a condition may be a general characteristic of basal euarthropods

(Hughes et al. 2006). There is a parallel between the track-like ontogenies of trilobites and the relatively modest modification of body patterning evident within the clade as a whole. In contrast to other euarthropods, and particularly to mandibulates, the repeated experiments in trunk-segment heteronomy do not appear to have conferred long-term success to trilobite clades: It was the homonomous trunk that was ubiquitous throughout trilobite evolutionary history. Why? The generally homonomous forms of both limbs and exoskeletal segments might be the consequence of a life mode common to all trilobites (Hughes 2005), perhaps that associated with a particular burrowing feeding habit (Seilacher 1985). However, other views of trilobite ecology suggest that the clade pursued many of the modes of life known today among free-living marine arthropods (Fortey 1985; Fortey & Owens 1990b, 1999). The difference between these views is of fundamental significance, with Seilacher's view providing a selective reason for the maintenance of homonomy, and Fortey and Owens' view raising the question of why trilobites did not fair as well as did other euarthropods while pursuing a comparable range of lifestyles. The evolution of heteronomy appears to have been linked to long-term evolutionary success in other clades of euarthropods. Sadly, that was not the case in trilobites.

SUMMARY POINTS

1. The good preservation of trilobite diversity and ontogeny, coupled with the retention of features that may have characterized the basal euarthropod, gives trilobites renewed significance in the context of recent advances in arthropod evolutionary biology.

2. The Cambrian diversification of trilobites displayed modifications of the patterning of the trunk region comparable with those seen among the closest relatives of Trilobita, the trilobitomorphs.

3. The Ordovician diversification of trilobites, although contributing greatly to the overall diversity within the clade, did so within a narrower range of trunk modifications.

4. Trilobite evolution surrendered the ability evident among early trilobites to vary the number and articulation state of trunk segments for increasingly effective enrollment and protective strategies.

5. The trunk region repeatedly became regionalized into sets of morphologically distinct segments among different trilobite clades. Such modifications apparently did not contribute to the long-term success of the clade as they did in some other groups of arthropods.

FUTURE ISSUES

1. There is a need for an improved dataset on trilobite diversity and ontogeny, with a particular focus on exceptionally preserved material to improve fundamental knowledge.

2. Well-supported phylogenies need to be established for trilobite clades, and characters distributions mapped onto these, in combination with the use of a variety of methods of analysis of morphological variation, including independent contrasts methods, to test specific hypothesis about evolution of trilobite body patterning.

3. There is a need for computer-generated dynamic models of trilobite exoskeletons to define the limits of flexure and articulation among different morphotypes.

4. Detailed morphometric analyses and modeling of trilobite ontogenetic trajectories to discern principles governing trilobite development should be conducted.

5. Integration of the understanding of trilobite paleobiology with that of other arthropods, both fossil and living, will allow the uniquely important attributes of the trilobite fossil record to be more fully realized.

ACKNOWLEDGMENTS

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