The ontogeny of trilobite segmentation: a comparative approach

Nigel C. Hughes, Alessandro Minelli, and Giuseppe Fusco

Abstract.—Ontogenetic stages of trilobites have traditionally been recognized on the basis of the development of exoskeletal segmentation. The established protaspid, meraspid, and holaspid phases relate specifically to the development of articulated joints between exoskeletal elements. Transitions between these phases were marked by the first and last appearances of new trunk segment articulations. Here we propose an additional and complementary ontogenetic scheme based on the generation of new trunk segments. It includes an anamorphic phase during which new trunk segments appeared, and an epimorphic phase during which the number of segments in the trunk remained constant. In some trilobites an ontogenetic boundary can also be recognized at the first appearance of morphologically distinct posterior trunk segments. Comparison of the phase boundaries of these different aspects of segment ontogeny highlights rich variation in the segmentation process among Trilobita. Cases in which the onset of the holaspid phase preceded onset of the epimorphic phase are here termed *protarthrous,* synchronous onset of both phases is termed *synarthromeric,* and onset of the epimorphic phase before onset of the holaspid phase is termed *protomeric.* Although these conditions varied among close relatives and perhaps even intraspecifically in some cases, particular conditions may have been prevalent within some clades.

Trilobites displayed hemianamorphic development that was accomplished over an extended series of juvenile and mature free-living instars. Although developmental schedules varied markedly among species, morphological transitions during trilobite development were generally regular, limited in scope, and extended over a large number of instars when compared with those of many living arthropods. Hemianamorphic, direct development with modest change between instars is also seen among basal members of the Crustacea, basal myriapods, pycnogonids, and in some fossil chelicerates. This mode may represent the ancestral condition of euarthropod development.

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Introduction

Progressive changes during the postembryonic development of the trilobite exoskeleton related to three aspects of segmentation: the number of segments, the articulations between segments, and the shape of segments. Changes in segment articulation provide the basis for the conventional stages of trilobite ontogeny: the protaspid, meraspid, and holaspid phases (Beecher 1895; Chatterton and Speyer 1997; Raw 1925; Whittington 1959). Changes in number and shape of segments and their relations to changes in segment articulation have received comparably little attention. As part of a separate study of trilobite growth increments we have compiled a database of 65 trilobite species for which quantitative data on putative successive instars have been published. Thirty-five of the species in this data set yielded ontogenetic sequences complete enough for us to examine the developmental schedules of segmentation for a substantial portion of ontogeny (Table 1). These schedules illustrate significant diversity in the interrelationships between different aspects of segmentation among members of the group. We present an integrated segmentation scheme that expresses these variations. Our purpose is to provide character information of potential value for trilobite phylogeny, to explore the ways in which trilobites varied aspects of their segmental development, and to provide a richer descriptive framework for trilobite development that can facilitate comparisons with living arthropods. The ultimate aim of such an approach is a clearer view of the evolution of segmentation across Arthropoda, and a basis for the evaluation of the comparative development of ancient and modern arthropods.

The Importance of Trilobite Development.— Current interest in the evolution of arthropod body patterning requires comparative analyses of developmental processes, highlighting both the common and the unique aspects of body patterning within each major arthropod clade. The principal value of trilobite ontogeny from this evolutionary developmental biology (evo-devo) perspective is as an empirical record of the postembryonic development of multiple representatives of an early euarthropod clade (for phylogenetic assessment see Budd 2002; Cotton and Braddy 2004; Edgecombe and Ramsköld 1999; Scholtz and Edgecombe 2005; Walossek and Müller 1990). To date only trilobites and the Orsten-type arthropod faunas (e.g., Müller and Walossek 1986; Walossek 1993; Waloszek and Maas 2005) offer detailed paleontological information in this regard. The particular strengths of the trilobite fossil record have been outlined elsewhere (Hughes 2003b), as have arguments that aspects of trilobite form and development may have been quite close to the basal euarthropod condition (Hughes 2003b, 2005).

Segments and Segmentation.—The evo-devo approach to the study of arthropod segmentation is revealing an unexpected variety of patterns and processes (Fusco 2005; Minelli and Fusco 2004). Comparative (Minelli and Fusco 2004) and experimental (Janssen et al. 2004, 2006) evidence suggests that the concept of segmentation applies to organs or structures, rather than to whole organisms (Budd 2001). The concept of segment as a unit repeated along the main body axis can provide a useful element for description, but this unit is not necessarily the same across the whole phylum. A recent study of the developmental genetics of the pill millipede *Glomeris* (Janssen et al. 2004) shows that dorsal and ventral series of repetitive units are independently established during embryogenesis.

The description of trilobite segmentation is typically limited to a postembryonic, exoskeletal, dorsal, axial view. In this paper, pragmatically, the term ''segment'' applies to the dorsal segmental structures of the cephalon and the trunk, the latter including both the articulated sclerites of the thorax and their non-articulated serial homologues within the pygidium. There is evidence for correspondence between the numbers of dorsal exoskeletal segments and ventral appendages in the trilobite thorax, but the same correspondence did not extend to the pygidium in all cases (see Hughes 2003b; Minelli et al. 2003).

In this paper we are concerned with segmentation of the dorsal exoskeleton alone and our approach aims to develop a descriptive framework that is not committed to specific interpretations of segmentation processes. We acknowledge that (1) the expression of segmentation may differ between ventral and dorsal surfaces of the exoskeleton (particularly within the pygidium), and (2) counts of the numbers of segments in the pygidium are commonly imprecise because of the small size of the posteriormost trunk region. Although these factors are important and are noted, the magnitude of variation within the species we discuss is small compared to the major differences among the taxa that we illustrate.

Outline of Trilobite Development and Tagmosis

Like all arthropods trilobites repeatedly molted their exoskeleton as they grew. Where well known, the growth rate between putative successive instars was apparently constant across multiple molts (conforming to the so-called Dyar's rule), and comparable to that of many living arthropods (Fusco et al. 2004). During early postembryonic development new trunk segments originated sequentially from a subterminal growth zone (Stubblefield 1926). Shape changes were commonly concentrated among these early free-living instars, whereas the final period of growth, characterized by constancy in segment numbers, often approximated isometry, although the greatest change in size commonly occurred during this terminal phase of growth (e.g., Hughes 1994). It is not known whether trilobites had a terminal molt and thus definite growth, but large specimens covered by encrusting organisms while alive suggest that rates of molting diminished in later ontogeny (Brandt 1996).

Trilobite tagmosis, in the sense of differentiation along the anterior-posterior axis into batches of similar segments, included a significant distinction between a set of cephalic

TABLE 1. Thirty-five trilobite species for which the developmental mode of trunk segmentation can be inferred with some confidence. Taxa are selected from a database of 65 species for which quantitative data for growth increments between successive instars have been published. Note that in the first two species it is not possible to designate a specific type of protomeric developmental mode, partly because agnostid stages prior to the development of trunk articulation are unknown. The putative mixed-mode development of *Neocobboldia chinlinica* is discussed in the text.

Species name	Order/suborder and family	Age	Developmental mode	Reference
Agnostus pisiformis (Linnaeus 1757)	Agnostina, Agnostidae	Late Cambrian	Protomeric	Müller and Walossek 1987
Trinodus elspethi (Raymond 1925)	Agnostina, Metagnostidae	Middle Ordovician	Protomeric	Hunt 1967
Tsunyidiscus longquanensis (Zhang and Zhu in Zhang et al. 1980)	Eodiscina, Tsynidiscidae	Early Cambrian	Protarthrous	Zhang and Clarkson 1993
Neocobboldia chinlinica Lee 1963	Eodiscina, Calodiscidae	Early Cambrian	Synarthromeric/Hypoprotomeric	Zhang 1989
Pagatia prolata Jell 1975	Eodiscina, Eodiscidae	Middle Cambrian	Hypoprotomeric	Jell 1975
Aphelaspis brachyphasis Palmer 1962	Ptychopariida, Aphelaspididae	Late Cambrian	Hypoprotomeric	Palmer 1962; Lee and Chatterton 2005
Ctenopyge (Eoctenopyge) angusta Westergård 1922	Ptychopariida, Olenidae	Late Cambrian	Hypoprotomeric	Clarkson et al. 2003
Ctenopyge gracilis Henningsmoen 1957	Ptychopariida, Olenidae	Late Cambrian	Hypoprotomeric	Clarkson et al. 2003
Ctenopyge ceciliae Clarkson and Ahlberg 2002	Ptychopariida, Olenidae	Late Cambrian	Protarthrous	Clarkson and Ahlberg 2002
Peltura scarabaeoides westergaardi Henningsmoen 1957	Ptychopariida, Olenidae	Late Cambrian	Hypoprotomeric	Bird and Clarkson 2003
Triarthrus eatoni (Hall 1838)	Ptychopariida, Olenidae	Late Ordovician	Synarthromeric	Whittington 1957; Cisne 1973
Ogygopsis klotzi (Rominger 1887)	Corynexochida, Dolichometopidae	Middle Cambrian	Protarthrous	Walcott 1916; McNamara and Rudkin 1984
Bathyuriscus fimbriatus Robison 1964	Corynexochida, Dolichometopidae	Middle Cambrian	Protarthrous	Robison 1967
Dentaloscutellum hudsoni Chatterton 1971	Corynexochida, Styginidae	Early Devonian	Hypoprotomeric	Chatterton 1971
Scutellum calvum Chatterton 1971	Corynexochida, Styginidae	Early Devonian	Hypoprotomeric	Chatterton 1971
Dimeropyge speyeri Chatterton 1994	Proetida, Dimeropygidae	Middle Ordovician	Hypoprotomeric	Chatterton 1994
Chomatopyge canasi Chatterton, Edgecombe, Waisfeld and Vaccari 1998	Proetida, Toernquistiidae	Middle Ordovician	Hypoprotomeric	Chatterton et al. 1998
Paratoernquistia sanchezae Chatterton, Edgecombe, Waisfeld and Vaccari 1998	Proetida, Toernquistiidae	Late Ordovician	Hypoprotomeric	Chatterton et al. 1998
Lasarchopyge benedettoi Chatterton, Edgecombe, Waisfeld and Vaccari 1998	Proetida, Toernquistiidae	Late Ordovician	Hypoprotomeric	Chatterton et al. 1998
Telephina problematica Chatterton, Edgecombe, Vaccari and Waisfeld 1999	Proetida, Telephinidae	Late Ordovician	Hypoprotomeric	Chatterton et al. 1999

TABLE 1. Continued.

| Species name	Order/suborder and family	Age	Developmental mode	Reference
Aulacopleura konincki (Barrande 1846)	Proetida, Aulacopleuridae	Early Silurian	Synarthromeric	Fusco et al. 2004
Stenoblepharum astinii Edgecombe, Chatterton, Vaccari and Waisfeld 1997	Proetida, Tropidocoryphidae	Late Ordovician	Hypoprotomeric	Edgecombe et al. 1997
Osmolskabole prima (Osmólska 1962)	Proetida, Proetidae	Late Devonian	Synarthromeric	Lerosey-Aubril and Feist 2005b
Paladin eichwaldi shunnerensis (King 1914)	Proetida, Proetidae	Early Carboniferous	Protarthrous	Clarkson and Zhang 1991
Cryptolithus tesselatus Green 1832	Asaphida, Trinucleidae	Middle Ordovician	Protarthrous	Chatterton et al. 1994
Lonchodomas chaziensis Shaw 1968	Asaphida, Raphiophoridae	Middle Ordovician	Hypoprotomeric	Chatterton et al. 1994
Tesselacauda depressa Lee and Chatterton 1997	Phacopida, Pilekiidae	Early Ordovician	Hypoprotomeric	Lee and Chatterton 1997
Pseudocybele nasuta Ross 1951	Phacopida, Pliomeridae	Early Ordovician	Hypoprotomeric	Lee and Chatterton 1997
Hinzteia plicamarginis Simpson, Hughes, Kopaska-Merkel and Ludvigsen 2005	Phacopida, Pliomeridae	Early Ordovician	Hypoprotomeric	Simpson et al. 2005
Ceraurinella typa Cooper 1953	Phacopida, Cheiruridae	Middle Ordovician	Hypoprotomeric	Whittington and Evitt 1954
Ceraurinella chondra Whittington and Evitt, 1954	Phacopida, Cheiruridae	Middle Ordovician	Hypoprotomeric	Whittington and Evitt 1954
Cryphops? ensae (Richter and Richter 1926)	Phacopida, Phacopidae	Late Devonian	Protarthrous	Crônier et al. 1999
Trimerocephalus lelievrei Crônier and Feist 1997	Phacopida, Phacopidae	Late Devonian	Synarthromeric	Crônier et al. 1998
Hemiarges turneri rasettii Tripp and Evitt 1981	Lichida, Lichidae	Middle Ordovician	Hypoprotomeric	Tripp and Evitt 1981
Amphilichas spp.	Lichida, Lichidae	Middle Ordovician	Hypoprotomeric	Tripp and Evitt 1981
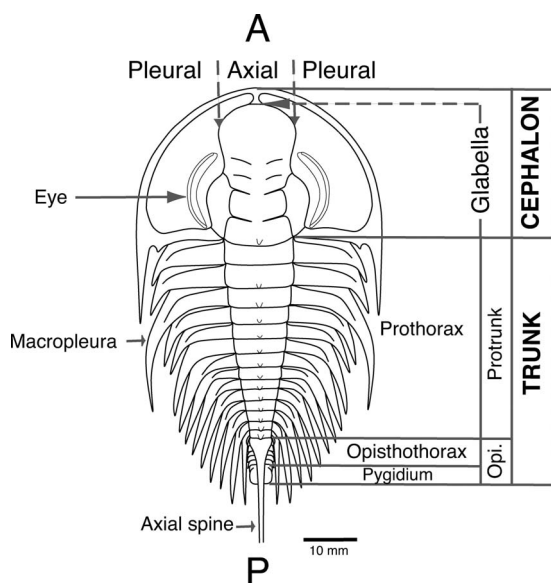
FIGURE 1. Major structures and regions of the mature trilobite dorsal exoskeleton. The figure depicts an Early Cambrian olenelloid trilobite with a macropleural segment and a marked division of the trunk into a protrunk (here a prothorax) and opisthotrunk (Opi.) (here an opisthothorax and a pygidium). A is anterior, P is posterior. Modified from Hughes (2003a: Fig. 3).

segments, and those that composed the trunk region (Hughes 2003b). In the mature trilobite, the trunk exoskeleton was divided into an anterior set of articulating segments called the thorax, and a posterior set of dorsally conjoined segments, called the pygidium, that formed a single dorsal terminal shield (Fig. 1). The dynamic segmental composition of thorax and pygidium (see below) questions their status as distinct tagmata per se (Minelli et al.

2003) although differences in segment morphology between the mature thorax and pygidium may justify this distinction in some cases (Hughes 2003a,b). During postembryonic development progressive changes in the number and articulation state of segments were confined to the trunk region.
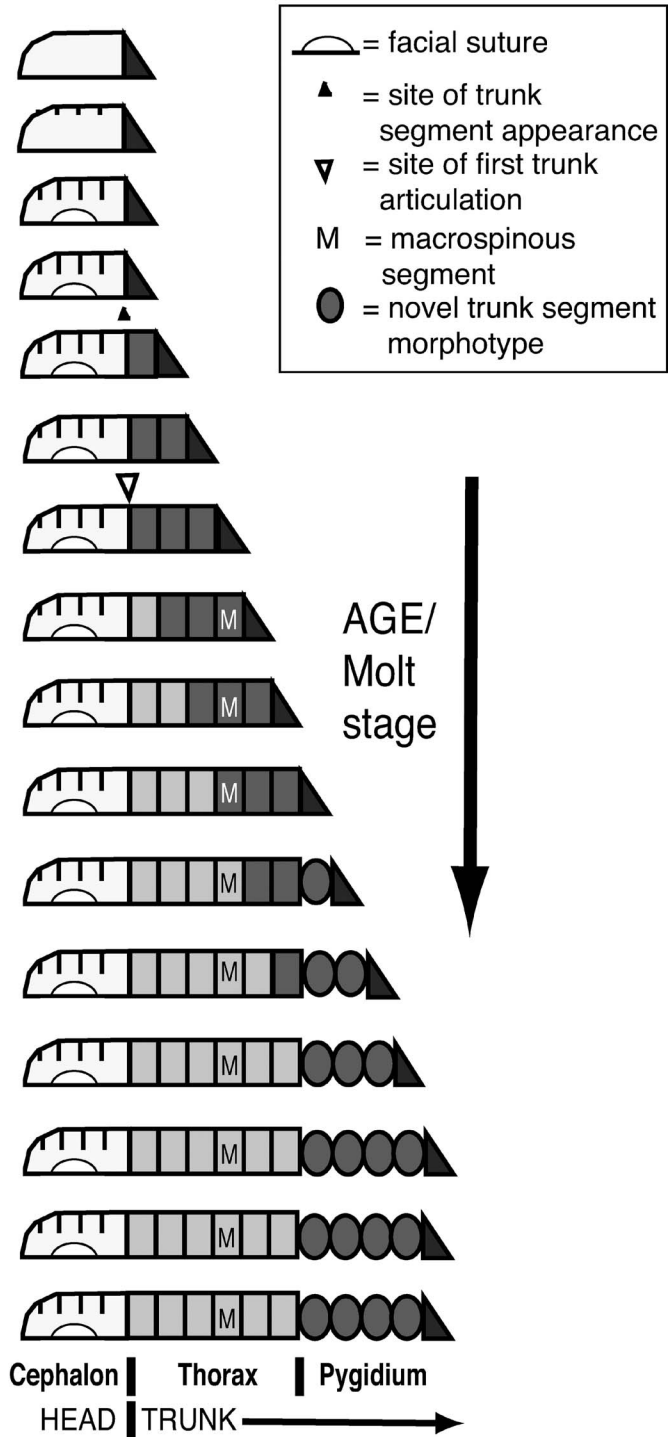
Trilobite Trunk Segment Generation, Articulation, and Differentiation

Phase transitions in the development of segment generation, articulation, and morphology each provide criteria for the recognition of ontogenetic phases (Fig. 2). Here we advocate that the diversity of trilobite segmental development can be best appreciated if ontogenetic phases are defined with respect to each aspect of development independently, and then the results of these different approaches compared and, where possible, combined. Most of the examples of trilobite ontogeny given below come from our growth increment database (Table 1). This database, while not fully representative of all known trilobites ontogenies, does focus on ontogenetic series best suited for the analysis of the development of segmentation, and includes representatives of most major clades.
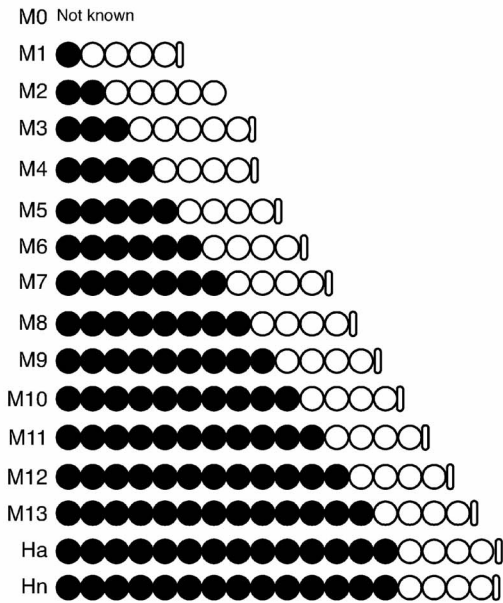
Segment Generation.—Arthropod postembryonic development is commonly classed with respect to the number of segments added after hatching. Those arthropods that possess the full complement of body segments at hatching exhibit ''epimorphic development,'' whereas those that add segments after hatch-

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FIGURE 2. Generalized trilobite ontogeny showing the boundaries of ontogenetic stages based on three aspects of the development of segments: generation, articulation, and morphology. ''Gn'' refers to stages based on segment generation and 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. ''Art'' refers to developmental stages based on dorsal sclerite articulation pattern and includes the stages previously applied in studies of trilobite ontogeny. ''Form'' refers to the morphology of newly generated trunk segments that in some trilobites are divided into discrete batches of anterior (protrunk) and posterior (opisthotrunk) segments. Here we define the protaspid stage as beginning with the appearance of the facial suture, and distinguish it from the poorly known phaselus phase, considered by some to belong to trilobite ontogeny. Note that olenelloids and agnostinids (possibly trilobites) lacked both a facial suture and any known pre-meraspid phase. The site of the appearance of new trunk segments is shown for the first trunk segment only. Solid gray triangle is the terminal piece; darker gray segments are conjoined and part of the pygidium. Lighter gray segments are thoracic. 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 first appearance, indicating that the site of appearance of new segments was subterminal, and that the boundary between articulating and conjoined segments migrated posteriorly during the meraspid phase (Stubblefield 1926).
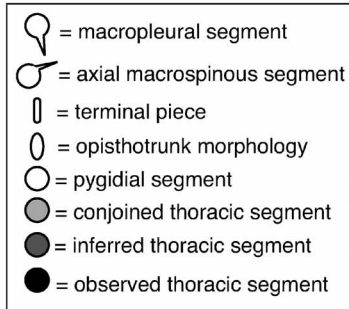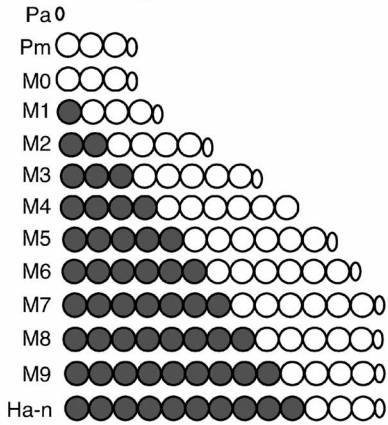
Gn | Art | Form

Constant? — Phaselus

Anamorphic — Protaspid — Protrunk

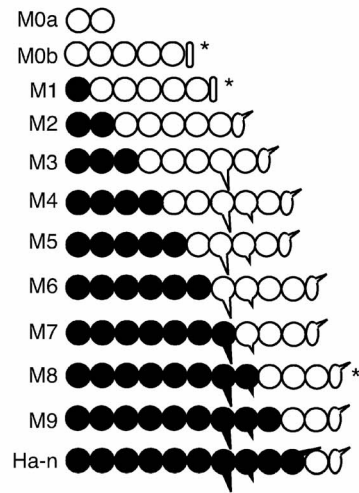Meraspid — Opistho-trunk

Epimorphic — Holaspid

= facial suture

▲ = site of trunk segment appearance

▽ = site of first trunk articulation

M = macrospinous segment

⬤ = novel trunk segment morphotype

AGE/ Molt stage

Cephalon | Thorax | Pygidium

HEAD | TRUNK →

A *Triarthrus eatoni*

B *Ctenopyge (Eoctenopyge) angusta*

C *Ctenopyge ceciliae*

D *Stenoblepharum astinii*

E *Dentaloscutellum hudsoni*

Legend:

= macropleural segment
= axial macrospinous segment
= terminal piece
= opisthotrunk morphology
= pygidial segment
= conjoined thoracic segment
= inferred thoracic segment
= observed thoracic segment
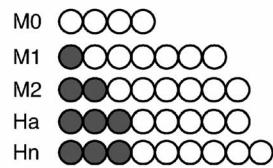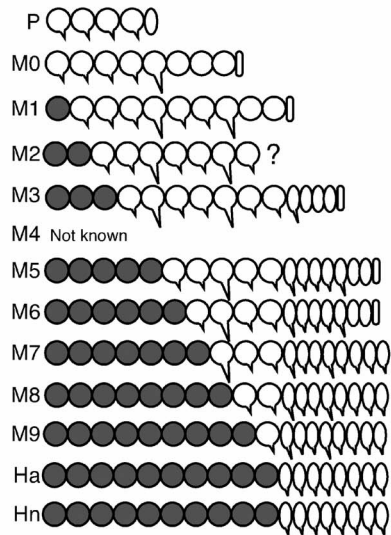
ing show ''anamorphic development'' (Haase 1880; Snodgrass 1956). Some anamorphic arthropods show a period during which segment number increases (anamorphic phase) followed by additional instars in which the number of segments remains constant (epimorphic phase: see Verhoeff 1905: pp. 206–207; Demange 1967: p. 157; Lewis 1981: p. 321; Enghoff et al. 1993: pp. 106–107). Such animals are said to show ''hemianamorphic development'' (Enghoff et al. 1993). This classification is distinct from those relating to the pattern of segment specification during embryogenesis.

Trilobite development was hemianamorphic (Fusco et al. 2004; Minelli et al. 2003), with the anamorphic addition of trunk segments during juvenile ontogeny, and a stable number during the mature phase. This pattern is evident wherever trilobite ontogeny is well known, including in agnostinids (the phylogenetic placement of which we consider equivocal [following Cotton and Fortey 2005; Stein et al. 2005; Walossek and Müller 1990]). The number of cephalic segments appears to have remained constant from the earliest stages of ontogeny onward (evidence for the addition of cephalic segments during the putative phaselus phase of trilobite ontogeny is weak; see below). Although in the calymenids *Flexicalymene senaria* and *Diacalymene gabrielsi*, and in

the cheirurid *Tessalacauda depressa* the posteriormost glabellar segment became clearly defined between molts (Chatterton et al. 1990; Lee and Chatterton 1997), a persistent marginal spine suggests that the last glabellar segment was present initially but poorly differentiated in the most juvenile instars known.

The location of the zone where new trunk segments emerged is evident from the ontogenies of segments with persistent unique structures such as individualized axial or pleural spines that first appeared at this site, situated near the extreme rear of the trunk (see Hughes 2003b). This is evident in the ontogenies of five species in our data set (e.g., Figs. 3B, 4A–C, 5B), and is also known in other species (e.g., Zhang and Pratt 1999).

The number of trunk exoskeletal segments at the onset of the epimorphic phase varied markedly within the group, from eight segments in eodiscids such as *Neocobboldia chinlinica* (Zhang 1989) and *Pagetia significans* (Jell 1975)—and even fewer in the agnostinids such as *Trinodus elspethi* (Hunt 1967)—to over 25 in *Paladin eichwaldi shunnerensis* (Clarkson and Zhang 1991) and in some *Aulacopleura konincki* (Fusco et al. 2004). Other species, such as members of the early Cambrian Emuellidae, developed over 100 trunk segments (Paterson and Edgecombe 2006; Pocock 1970) and it is possible that such species continued to add

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FIGURE 3. Trunk segmentation schedules for selected trilobite taxa. Note that the schedules shown are those inferred from the descriptions and illustrations given by the authors referenced. Commonly the exact number of segments present at each stage is uncertain, and the schedules are approximations. Cephalon (not shown) is to the left side in all panels. P designates protaspid instars, M designates meraspid with degrees and instars within degrees given by numbers and letters, and H designates holaspid instars. Open shapes represent segments in the pygidium. Closed shapes represent articulating segments: those in black are observed from articulated material, and those in gray are inferred to have been present. Individualized macrospinous segments are shown with position and relative size of spines stylized: absence of these symbols need not imply that segments lacked spines. * indicates that the meraspid pygidia of some individuals may have one extra axial ring in that degree. New trunk segments appeared at the anterior margin of the terminal piece, the posteriormost division of the trunk (see Hughes 2003b). Note that stages shown may have contained more than one instar, and this was certainly the case for holaspids in the epimorphic phase. A, *Triarthrus eatoni* based on descriptions of Whittington (1957) and Cisne (1973), excluding the protaspids assigned by Cisne (1973) to that species. Synarthromeric development. B, *Ctenopyge* (*Eoctenopyge*) *angusta* based on Clarkson et al. (2003). Hypoprotomeric development. Authors note that the transition between M0a and M0b may have involved additional, unsampled instars. The seventh and eighth trunk segments were macropleural, the onset of the epimorphic phase at M8 preceded onset of the holaspid phase, stages M4 and M5 apparently retained a constant number of segments, and the terminal segment showed the persistent presence of an axial spine. C, *Ctenopyge ceciliae* based on Clarkson and Ahlberg (2002). Protarthrous development. D, *Stenoblepharum astinii* based on Edgecombe et al. (1997). Hypoprotomeric development. E, *Dentaloscutellum hudsoni* based on Chatterton (1971). Axial spines not shown because of their marked variability. Hypoprotomeric development. Note the periodic development of macropleural spines in early trunk ontogeny and the later distinct morphology of opisthotrunk segments, the anterior boundary of which ultimately became the mature thoracic/pygidial boundary.
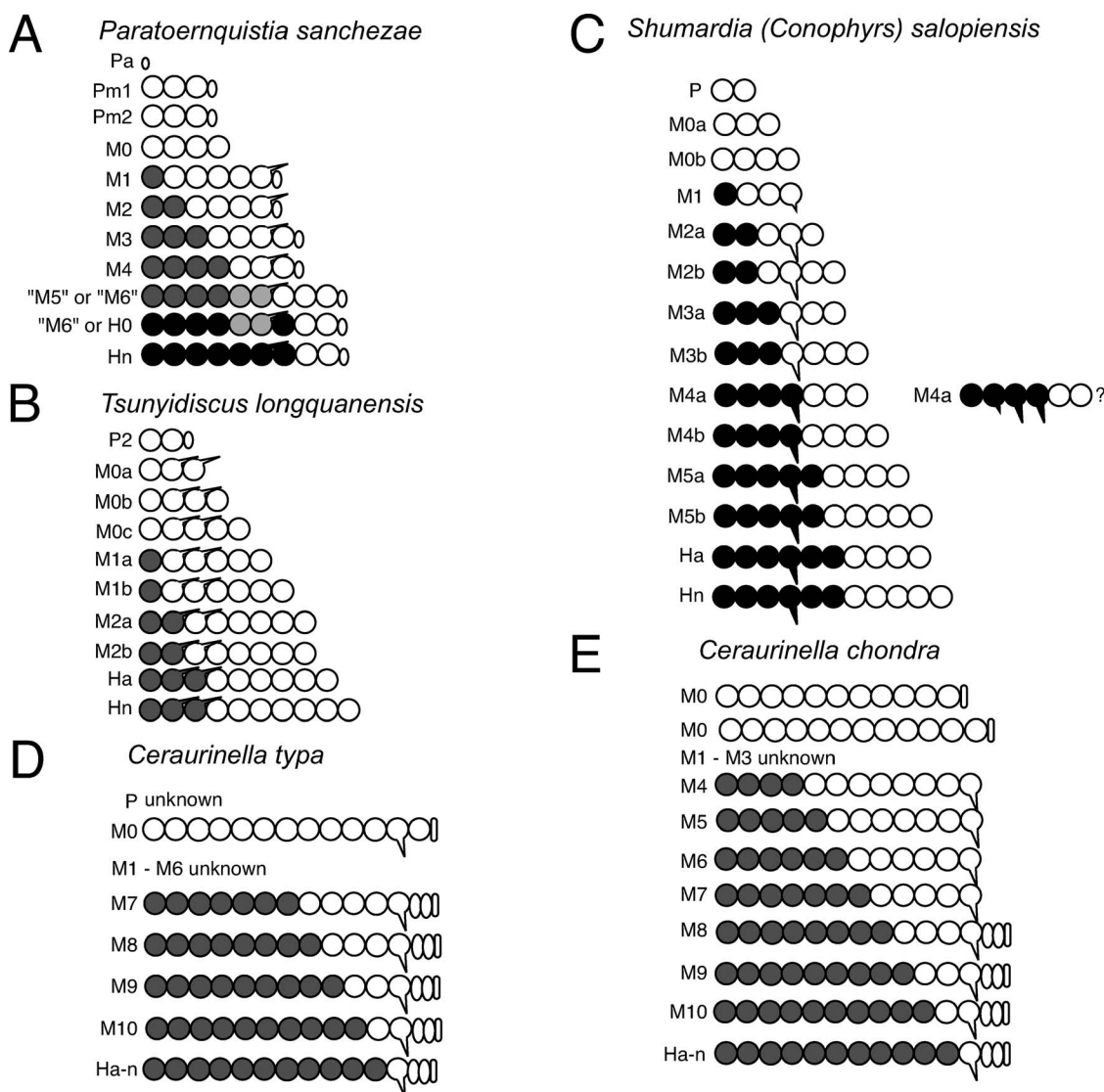
FIGURE 4.   Trunk segmentation schedules for selected trilobite taxa. Legend as for Figure 3. A, *Paratoernquistia sanchezae* after Chatterton et al. (1998). Segments in lightest gray remained fused together even after release into the thorax, but separated later to form normally articulated thoracic segments. The implications of this pattern for articulation-based life history stages are discussed in the text. Hypoprotomeric development. B, *Tsunyidiscus longquanensis* after Zhang and Clarkson (1993), showing multiple molts per meraspid degree. Protarthrous development. C, *Shumardia* (*Conophyrs*) *salopiensis* after Stubblefield (1926) and Fortey and Owens (1991), showing multiple molts per meraspid degree, alternate segment generation and articulation instars between meraspid degrees 2–4. The M4a instar might have been represented by two forms (Stubblefield 1926); both are represented here. Chatterton and Speyer (1997: p.175) disputed the presence of two segments in the protaspis. Protarthrous development. D, *Ceraurinella typa* after Whittington and Evitt (1954), showing that all protrunk segments were present in a degree 0 meraspid, and the subsequent appearance of posterior opisthotrunk segments. Hypoprotomeric development. E, *Ceraurinella chondra* after Whittington and Evitt (1954) showing broadly similar ontogeny to that of *C. typa* but with sequential appearance of posteriormost protrunk and opisthotrunk segments. Hypoprotomeric development.

trunk segments throughout life (Raw 1925), thus exhibiting the form of anamorphosis known in living millipedes as ''euanamorphosis'' (Enghoff et al. 1993). Unfortunately, specimens described to date do not permit resolution of the developmental mode. Distinctive aspects of trilobite development, such as the development of trunk segment articu-
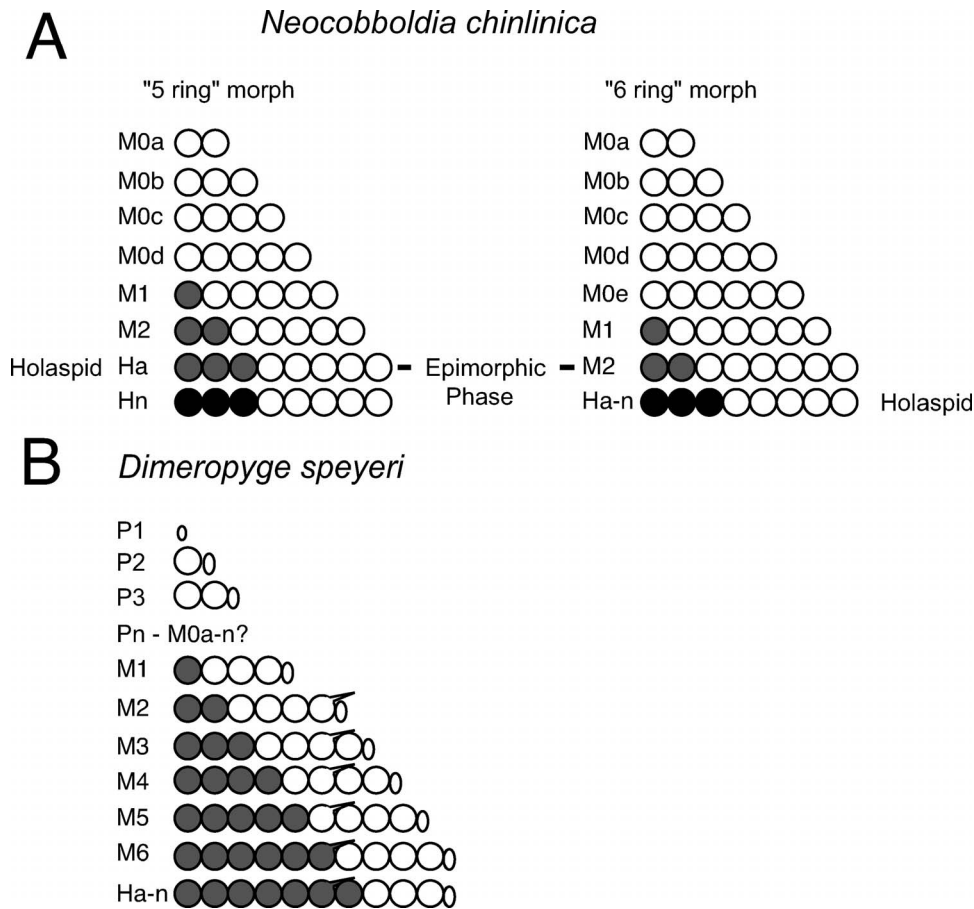
A　　　*Neocobboldia chinlinica*

FIGURE 5. A, Model of trunk segment accumulation history for *Neocobboldia chinlinica* based on Zhang's (1989) data. The presence of pygidia with five and six axial rings respectively at overlapping size range is explained by the presence of two cohorts with the same segment generation schedule, but one with an extra meraspid degree 0 instar and hence a delayed release of the first thoracic segments. The final, mature form is similar in both cohorts because, although the onset of the epimorphic phase is similar in both cohorts, the onset of the holaspid phase is delayed by one molt in the ''six ring'' cohort. If so, ''five ring'' cohort would be synarthromeric, whereas ''six ring'' cohort would be hypoprotomeric. B, *Dimeropyge speyeri* after Chatterton (1990). Hypoprotomeric development.

lation and segment morphology, are super-imposed upon the primary scaffold of hemi-anamorphic development.

The twofold division of postembryonic segment expression history proposed here serves as an adequate framework to describe the generation of new segments in most trilobites, but exceptions do occur. Most notable are apparent transient phases of constant trunk segment numbers intercalated within the anamorphic phase. Such a pattern is seen among articulated exoskeletons of the olenid *Ctenopyge* (*Eoctenopyge*) *angusta*, which apparently maintained the same number of segments for at least two consecutive instars (M4 and M5

with ten segments, and M6 and M7 with 11 segments) (Fig. 3B), and in *Shumardia* (*Conophrys*) *salopiensis* between the M2b and M3a and the M3b and M4a instars. A similar situation apparently also occurred in the corynexochids *Arthricocephalus chauveaui* (see McNamara et al. 2003) and *Duyunaspis duyunensis* (see McNamara et al. 2006). In *A. chauveaui* the first three molts after the appearance of the cephalic-trunk articulation were reportedly accompanied by the appearance of two segments, but the next four instars maintained a total of ten trunk segments, after which additional segments appeared at the rate of one segment per molt (McNamara et al. 2003). The

variable rate of appearance of segments per molt is also worthy of comment, with as many as three new segments appearing between the development of the first and second trunk articulations in the olenid *Ctenopyge ceciliae* (Fig. 3C) (Clarkson and Ahlberg 2002). This transition was apparently accomplished in a single molt and was followed by a somewhat irregular expression schedule thereafter. Likewise, two segments were added between apparently sequential protaspid molts in the lichid *Hemiarges turneri rasettii* (Tripp and Evitt 1981), and a similar situation occurred in other trilobites (see Chatterton et al. 1990). Interpretation of these patterns is hampered by the fact that segment boundaries were commonly obscure toward the posterior of the trunk, making accurate counts difficult. Nevertheless, departure from an idealized ''one new segment per molt'' schedule during the anamorphic phase appears to be firmly established in some cases and investigations of the growth rates of individual segments are needed to explore this issue further.

It is difficult to accurately estimate the number of segments in the developing trunk among the earliest juvenile trilobite instars. As the number of cephalic segments was apparently constant between molts, it is possible that there was a juvenile phase of constant cephalic segmentation (Fig. 2) that preceded the development of the first trunk segments. In extant arthropods, the quasi-simultaneous (non-sequential) formation of a small set of anterior segments, even in those clades with marked sequential segmentation, suggests that these segments are generated by a different mechanism with respect to that that produces the more posterior ones. This could be an ancestral condition for arthropods (Minelli 2003; Peel et al. 2005).

Segment Articulation.—Trilobite ontogeny has been divided into four phases based on the development of articulation between neighboring exoskeletal segments (Beecher 1895; Chatterton et al. 1990; Raw 1925) (Fig. 2). The first of these, the phaselus phase, is contentious, as discussed below. During the earliest undisputed phase of trilobite ontogeny, the protaspid phase, all body segments formed a single dorsal shield. This period typ-

ically embraced a small number of instars. During the subsequent meraspid phase trunk segments at the anterior margin of the pygidium were sequentially released into the thorax via the development of an articulation along their posterior margins. The meraspid period was divided into a series of degrees, each defined by the number of freely articulating segments within the thoracic region. Meraspid degrees did not necessarily correspond to meraspid instars, as cases of the release of more than one segment per molt, and cases of intercalation of molts without segment release, are known (see below). Progressive release of trunk segments into the thorax continued until the individual entered the final, holaspid period, characterized by a stable number of thoracic segments despite continued growth and molting.

There is some debate about the authenticity and value of an initial postembryonic phase, called the phaselus phase (Chatterton et al. 1990; Fortey and Morris 1978). This is partly because it is not certain that the small specimens assigned to phaselus are actually trilobites (see Schram 1982), although they are quite commonly found along with trilobite protaspids (Chatterton and Speyer 1997; Fortey and Whittington 1989). Some of those accepting phaselus as trilobites have included them within the protaspid phase (e.g., Speyer and Chatterton 1989, 1990). Morphological characters were poorly differentiated within the phaselus, but the putative trilobite dorsal shield lacked articulation (or traces of segmentation) in any region (Chatterton and Speyer 1997; Fortey and Whittington 1989). Here we favor defining the onset of the protaspid phase with the appearance of a dorsal facial suture, and note that those trilobites that lacked the protaspid phase, including olenelloids and agnostinids (if trilobites), also lacked dorsal facial sutures. If so, this articulation-based criterion is consistent with other phase boundaries of the protaspid, meraspid, holaspid phase series. This solution may also ameliorate the difficulty identified by Ramsköld and Edgecombe (1991: p. 227) in separating the character ''presence of a protaspid'' from the character ''presence of calcification.'' If phaselus prove not to have been trilobites

this stage can be abandoned without requiring modification of the definitions of the articulation-based phases of trilobite ontogeny. The relationship between the trilobite facial suture and the boundaries of cephalic segments remains obscure, even though many protaspids show clear cephalic segmentation in the axial region. During the protaspid phase segments of the cephalic and trunk regions remained dorsally conjoined (Beecher 1895: p. 169) and the meraspid phase began at the appearance of an articulating joint that separated the head from the developing trunk (Raw 1925: p. 226). At the onset of the meraspid phase the dorsal exoskeleton was thus divided into two sclerites: the cephalic shield referable to a set of anterior segments, those of the head, and the pygidial shield referable to a set of posterior segments, those of the pygidium. The meraspid period encompassed the interval in which segments were released from the anterior of the pygidium to become freely articulating thoracic segments (Fig. 2). The final articulation-based ontogenetic stage, the holaspid phase, began when the thorax achieved the complete complement of thoracic segments (Raw 1925: p. 226).

Although early workers used a variety of terms, such as post-abdomen (Brongniart 1822), abdominal or caudal shield (Burmeister 1846), and tail (Salter 1864), the name ''pygidium'' has long been applied to the set of dorsally conjoined segments at the posterior of the trilobite trunk (e.g., Hawle and Corda 1847). Richter (1925: pp. 104–105) pointed out that the trilobite pygidium, unlike that of annelids, corresponded to multiple segments rather than a single terminal trunk unit, and advocated use of the term ''cauda'' or ''prepygidium'' instead. However, ''pygidium'' remains firmly entrenched in the trilobite literature, although the precise definition of the structure remains poorly resolved. Barrande (1852), who was the first to recognize the dynamic pattern of segment articulation during meraspid ontogeny, applied the term to all conjoined trunk segments, regardless of ontogenetic stage. Segments that would ultimately become the mature pygidium were termed the ''pygidium définitif'' (Barrande 1852: p. 264) (i.e., the ''true pygidium'' of

Stubblefield [1926] and Whittington and Evitt [1954]) and those that would become thoracic, Barrande (1852: p. 264) termed the ''pygidium transitoire.'' More recent definitions of the pygidium have stressed articulation between the posterior exoskeleton and the thorax (Harrington et al. 1959; Whittington and Kelly 1997). According to all these definitions, the term pygidium refers to the set of conjoined segments posterior to the last trunk articulation, regardless of ontogenetic stage, specific identity or ultimate fate. Here we accept this view and define the pygidium as the set of conjoined segments posterior to the last trunk articulation. This maintains an articulation-based definition, and can be applied to all meraspid and holaspid instars. Harrington et al.'s (1959) and Whittington and Kelly's (1997) definitions left the status of the set of posterior conjoined segments in the meraspid degree 0 unclear, because the thorax did not exist until meraspid degree 1.

Because the meraspid and holaspid phases related explicitly to articulation state we use ''meraspid pygidium'' and ''holaspid pygidium'' to distinguish between pygidia before and after the completion of the thorax. The term ''transitory pygidium'' is commonly applied to the entire pygidium in the meraspid stage, but Barrande's (1852) original concept of ''pygidium transitoire'' applied only to those segments that would ultimately become thoracic. Given the inconsistent usage, and the fact that many holaspid pygidia continued to accrue segments posteriorly during the holaspid phase (see below), the term ''transitory pygidium'' is, at best, confusing. ''Protopygidium'' and ''neopygidium'' have also been used in different ways by different authors. As originally defined (Matthew 1896) these terms applied respectively to anterior and posterior portions of the holaspid pygidia of certain miomerid trilobites that showed a distinctive change in segment morphology along the a-p axis. Currently ''protopygidium'' is applied either to the entire trunk region in the protaspid stage (Chatterton and Speyer 1997: p. 183) or to that portion of the meraspid pygidium that would ultimately become the holaspid pygidium (Chatterton and Speyer 1997: p. 194). These differences result from inconsis-

tent usages of segment articulation and segment identity in the definition of these different types of ''pygidia'' and can be overcome by relating definitions of trilobite pygidia to articulation-state only. Accordingly, we suggest simply using ''trunk'' to describe the protaspid postcephalic region.

Many authors (e.g., Simpson et al. 2005) have used the term ''pygidium'' as a synonym for the holaspid pygidium, preferring alternatives such as ''caudal plate'' or ''caudal shield'' for the posterior set of conjoined segments at any point of meraspid or holaspid ontogeny. If the scheme advocated herein is adopted, use of ''caudal plate'' etc. is unnecessary. As the term ''pygidium'' refers to the body region posterior to the last articulation we recommend the use of ''pygidial shield'' when specifically referring to the single dorsal pygidial sclerite, independently of developmental phase.

In most cases recognition of trilobite articulation-based ontogenetic phases is straightforward because articulation developed in a progressive, sequential manner from the anterior of the trunk backward. An interesting exception is the bathyuroid *Paratoernquistia sanchezae*, a form that ultimately achieved seven articulating thoracic segments but apparently did so in an unconventional manner (Chatterton et al. 1998) (Fig. 4A). In this species trunk segments 5 and 6, which bore a distinctive large axial spine, remained conjoined during meraspid ontogeny and were together released into the thoracic region when an articulation developed at the back of the sixth trunk segment. The fifth and sixth segments later separated, forming an articulation between them, but apparently only after the seventh trunk segment was released into the thorax. In terms of segment numbers, the thorax was complete, and thus the holaspid phase commenced, when the seventh, posteriormost, trunk segment was released (Chatterton et al. 1998), but in terms of overall articulation the thorax remained incomplete until an articulation was formed between the fifth and sixth trunk segments at the following molt. As meraspid ''degrees'' have been defined by the number of ''free'' thoracic segments (Barrande 1852; Stubblefield 1926: p. 351), the evaluation

of the conjoined fifth and sixth segments in this case is disputable, as is the onset of the holaspid phase. We advocate definition of the onset of the holaspid phase at the development of the articulation between the last thoracic segment and the pygidial shield, but stress that the variability of trilobite segmental development can frustrate definitive boundary criteria that are applicable in all cases. The pattern seen in *P. sanchezae* is apparently mimicked in *Telephina chingola*, *T. calandria*, and *T. problematica*, each of which also had a long axial spine on the sixth segment (see Chatterton et al. 1999).

The majority of trilobite meraspid ontogenetic series show that articulation developed at a rate equal to or less than one new articulation per instar. Cases of ''missing'' degrees are reported, such as the absent meraspid degree 4 in the ontogeny of *Dentaloscutellum hudsoni* (Fig. 3E). Chatterton and Speyer (1997: p. 189) suggested that this species repeatedly released segments in increments of 2, but in the original description of this ontogeny (Chatterton 1971) it was suggested that degree 4 meraspis may have existed but had not been recovered to date. It is possible that *Ceraurinella typa* and *C. chondra* may have released more than a single segment subsequent to the last meraspid degree 0 instar, but in later phases of their ontogeny segments were apparently released sequentially, one per molt (Fig. 3D,E). Hence there are no cases in our data set in which we can be confident that multiple articulations developed at a single molt. On the other hand, there are several cases in which more than one molt apparently occurred within a meraspid degree, an example of which is the ontogeny of *Neocobboldia chinlinica*, which apparently had at least six meraspid instars but only three meraspid degrees (Fig. 5A). Other possible examples are given in Figures 3B, 4B, and 4C.

Morphological Differentiation.—In some trilobites segments within the trunk region showed marked differentiation in shape (Hughes 2005). Such differences ranged from uniquely shaped individual segments to heteronomous trunks, divided into sets or ''batches'' of similar segments distinguished from one another by such features as shape,

size, and rate of appearance per molt (e.g., in the scutelluids *Dentaloscutellum hudsoni* and *Scutellum calvum* [Chatterton 1971], and perhaps also the cheirurid *Ceraurinella* (Whittington and Evitt 1954) and the odontopleurid *Diacanthaspis cooperi* [Whittington 1956]). In the taxa listed above major differences in segment morphology were evident at or shortly after the earliest appearance of such segments near the subterminal growth zone (e.g., Feist 1970; Chatterton 1971; Kácha and Šaric 1991). Hence, in these trilobites an ontogenetic phase boundary can be recognized at the point of morphological differentiation of the anterior trunk (protrunk) and posterior trunk (opisthotrunk) segments (Figs. 1, 2). Such a distinction necessarily occurred within the anamorphic phase of development. In some olenelloid and emuellid trilobites the boundary between trunk segment morphotypes occurred within the mature thorax, which was divided into the ''prothorax'' and ''opisthothorax'' (Harrington et al. 1959). Use of the terms ''protrunk'' and ''opisthotrunk'' draws attention to similarly sharp transitions in segment morphology but notes that these are not restricted to a location within the thorax, but commonly occur at the divide between the mature thorax and pygidium, or even within the pygidium (see Matthew 1896).

Division of the trunk into two batches of similar segments apparently occurred independently in several trilobite clades (Hughes 2003a,b). Batches of segments interface sharply in some cases, but in some olenelloids the transition between distinct protrunk and opisthotrunk segment morphotypes took place over a graded series of intermediate segments. In some other trilobites, such as the encrinurids, morphological expression of distinct differences between the segments of the mature thorax and pygidium developed toward the posterior of the holaspid pygidium with the offset between pleural and axial aspects of segmentation increasing progressively toward the rear (as in *Wallacia laevis* [see Ramsköld and Edgecombe 1994: Fig. 3]). Exploration of the comparative development of the heteronomous trunk condition in different phylogenetic lineages will provide a basis for assessing commonalities underlying the development of trilobite trunk heteronomy.

Matches and Mismatches between Different Aspects of Trunk Segmentation

Transitions among ontogenetic phases defined using segment generation, articulation, and form were commonly coincident. In the scutelluid *Dentalosctuellum hudsoni* the boundary between the thorax and the holaspid pygidium was also coincident with the boundary between protrunk and opisthotrunk segments (Chatterton 1971) (Fig. 3E).

Coincidence in the onset of the holaspid and epimorphic phases occurred in the olenid *Triarthrus eatoni* (Cisne 1973; Whittington 1957) (Fig. 3A), the aulacopleurid *Aulacopleura konincki* (Fusco et al. 2004), and apparently also in the phacopid *Cryphops*? *ensae* (Crônier et al. 1999). The onsets of the epimorphic phase and the holaspid phase were decoupled in many other trilobites. The start of the holaspid phase preceded onset of the epimorphic phase in such species as the corynexochid *Bathyriscus fimbriatus* (Robison 1967), the proetid *Paladin eichwaldi shunnerensis* (Clarkson and Zhang 1991), the eodiscid *Tsynidiscus longquanensis* (Zhang and Clarkson 1993) (Fig. 4B), the olenid *Ctenopyge ceciliae* (Clarkson and Ahlberg 2002) (Fig. 3C), in the classic case of *Shumardia* (*Conophrys*) *salopiensis* (see Stubblefield 1926; Fortey and Owens 1991) (Fig. 4C), and in the common ''ptychopariid'' *Elrathia kingii* (Hughes and Chapman 1995). In these cases the number of pygidial segments increased after completion of the thorax.

The opposite situation, in which the onset of the epimorphic phase preceded the start of the holaspid phase, was also common in trilobites. Examples from our data set include the olenid *Ctenopyge* (*Eoctenopyge*) *angusta* (Clarkson et al. 2003) (Fig. 3B), the proetids *Dimeropyge speyeri* (Chatterton 1994) (Fig. 5B) and *Stenoblepharum astinii* (Edgecombe et al. 1997) (Fig. 3D), the lichid *Hemiarges turneri rasettii* (Tripp and Evitt 1981), and the scutelluid *Dentaloscutellum hudsoni* (Chatterton 1971) (Fig. 3E). In such cases during the later part of the meraspid phase the pygidium underwent a ''depletion phase'' (Kopaska-Merkel 1987; McNamara et al. 2003; Simpson et al. 2005) in which

segment release from the anterior border of the pygidium continued after the generation of new segments had ceased. Striking cases of this kind were the cheirurids *Ceraurinella typa* and *C. chondra* in which all, or nearly all, of the trunk segments were expressed prior to the release of any thoracic segments (Chatterton 1980; Whittington and Evitt 1954) (Fig. 4D,E). Did this situation arise because segment accretion was unusual in these species, possibly akin to hatching at or near the onset of the epimorphic phase? Unfortunately, protaspid specimens of these species are unknown. Nevertheless, the size of the anteriormost opisthotrunk segments in the available meraspid degree 0 specimens of *Ceraurinella typa* are larger than their equivalents in what we interpret to be the meraspid degree 7 of the related *Ceraurinella nahanniensis* (Chatterton 1980). The later species apparently developed according to a normal schedule, beginning to release thoracic segments shortly after the meraspid phase commenced. Assuming that *Ceraurinella* trunk segments grew at a broadly comparable rate, the larger size of opisthotrunk segments in the M0 degree of *C. typa* may suggest that the development of articulation was delayed in that species compared to *C. nahanniensis* (a conclusion shared by Chatterton [1980]). If this growth rate assumption is correct there may have been an extended series of protaspid or degree M0 instars in *C. typa* and *C. chondra* during which trunk segments appeared progressively. An even more curious pattern is that illustrated by the burlingiid trilobite *Schmalenseeia fusilis*. According to Peng et al. (2005) the cephalon and trunk remained fused during both the anamorphic and epimorphic phases. All known specimens of this trilobite possessed a functional facial suture, and hence the species apparently never progressed beyond the protaspid phase.

Chatterton and Speyer (1997: p. 194) suggested that ''most if not all trilobites'' had a depletion phase. Such a phase was necessarily present in trilobites in which the onset of the epimorphic phase preceded the onset of the holaspid phase, but need not have been present in forms in which onset was coincident, or in which the epimorphic phase began after onset of the holaspid phase. Thus the ontog-

enies of *Triarthrus eatoni* (Fig. 3A) and *Tsunuidiscus longquanensis* (Fig. 4B), among others, apparently lacked a depletion phase. Furthermore, as McNamara et al. (2003, 2006) point out, the balance between segment generation and articulation varied markedly during the ontogenies of some trilobites and there may have been multiple depletion phases separated by periods of stable numbers of segments (''equilibrium phase'' of Simpson et al. [2005]) in the corynexochid *Arthricocephalus chauveaui*.

The diagrams of segmentation schedules illustrate sequential changes in morphology but it is possible that more than one instar could occupy any of these morphological steps (as was certainly the case in the holaspid phase). In some cases abrupt changes in morphology might imply incomplete recovery of instars (as was likely the case in *Ceraurinella typa*, Fig. 4D). Understanding of intraspecific variation among different aspects of segmental development, including in the rate of growth of individual segments, remains rudimentary. This will affect the generality of the segmentation schedules shown in Figures 3–5 because it is possible that some putative instars instead represent intra-instar variants, or that there was more than a single instar in some of the phases shown. Analyses of large numbers of specimens from taxa with individualized marker segments will be necessary to assess this further, and there may be more variation than commonly appreciated. Multiple instars have been invoked when a single morphotype displayed a broad size range (e.g., Whittington and Evitt 1954), but these arguments await evaluation through ongoing analysis of trilobite growth rates. In addition, future studies must also pay attention to preservation-induced variation.

Apparent irregularity in segment generation schedules during the anamorphic phase might also reflect intraspecific variation. An interesting case is provided by the eodiscid *Neocobboldia chinlinica* (Zhang 1989) in which the number of segments in the pygidium during the meraspid period rose steadily from two to five segments. After this point some specimens had six segments in the pygidium whereas others of the same size retained only five, but above a certain size threshold all py-

gidia possessed only five segments. An estimate of the growth increment in earlier instars led Zhang (1989: p. 15) to propose that the morph with six axial rings would have occupied three instars, but he did not interpret the pattern in detail. One possible explanation of this pattern is intraspecific variation in the instar at which articulated thoracic segments first appeared, superimposed upon a common schedule of segment generation (Fig. 5A). We are currently conducting modeling of the size-frequency distributions of the various axial-ring morphotypes to test this hypothesis and other alternatives, but more specimens are likely needed to resolve among these. Another case of intraspecific variation in segmentation schedule, in which there was apparently coordinated variation in the onset of both the epimorphic phase and the holaspid phase, was provided by the aulacopleurid *Aulacopleura konincki* (Fusco et al. 2004).

Degrees 2–5 of the ontogeny of *Shumardia* (*Conophrys*) *salopiensis* apparently encompassed two instars each (Fig. 4C), while molts from meraspid degrees 2 to 3, 3 to 4, and 5-holaspid (sensu Raw 1925) did not increase the numbers of trunk segments. This ontogeny apparently alternated between molts in which new segments were produced, and those in which new articulations were formed. This is the simplest explanation of these data, but other alternatives may exist. For example, in the degrees 2–4 there could have been two parallel ontogenies represented by polymorphs with three and four segments in the pygidium respectively. Stubblefield (1926) also noted an unusual but apparently related alternative meraspid degree 4 morph within the sample (see Fig. 4C), raising the possibility of further deviation from a stereotyped ontogenetic series. We do not claim that the polymorphism explanation is preferable for *Shumardia* (*Conophrys*) *salopiensis*, but intend it to illustrate that the ontogeny of trilobite segmentation may be interpreted in different ways unless additional evidence, such as growth data, is available.

Integrated Ontogenetic Scheme for Trunk Segment Generation and Articulation

A more comprehensive description of trunk segmentation can be achieved if ontogenetic schemes based on segment articulation and segment generation are combined. Such a factorial approach to the periodization of arthropod development has been recently proposed (Minelli et al. 2006). Here we have taken a ''coarse grained'' approach, focusing on the definitive transitions from the anamorphic phase to the epimorphic phase, and from the meraspid phase to the holaspid phase. We ignore instars of stable segment numbers intercalated within the anamorphic phase, or punctuated patterns of segment release during the meraspid phase. Such periods of stasis (see Figs. 3–5) are apparently rare, and we consider them to be trivial compared to the definitive transitions that mark the onsets of the epimorphic and holaspid phases. By using this approach we focus on the major transitions between stages of trunk segmentation, rather than on the condition of the instar immediately succeeding.

This approach yields a finite set of six, non-repeatable ''segmental conditions'' that may endure for one or more instars each. The six are analogous to phases of postembryonic development in extant arthropods. These conditions combine the two phases of trunk segmentation (anamorphic, epimorphic) with the three classical periods for the development of trunk segment articulations (protaspid, meraspid, holaspid). They are

1. anamorphic protaspid (a-p)
2. epimorphic protaspid (e-p)
3. anamorphic meraspid (a-m)
4. epimorphic meraspid (e-m)
5. anamorphic holaspid (a-h)
6. epimorphic holaspid (e-h).

Combining these six conditions yields five modes of trunk segment development that are potentially evident among trilobite ontogenies, each characterized by a distinctive sequence of three or four of the six conditions (Fig. 6). Development in which onset of the holaspid phase preceded onset of the epimorphic phase is here termed *protarthrous* (Fig. 6A). *Protomeric* describes development in which onset of the epimorphic phase preceded onset of the holaspid phase (Fig. 6C–E), and *synarthromeric* that development with the coincident onset of both phases (Fig. 6B). There are
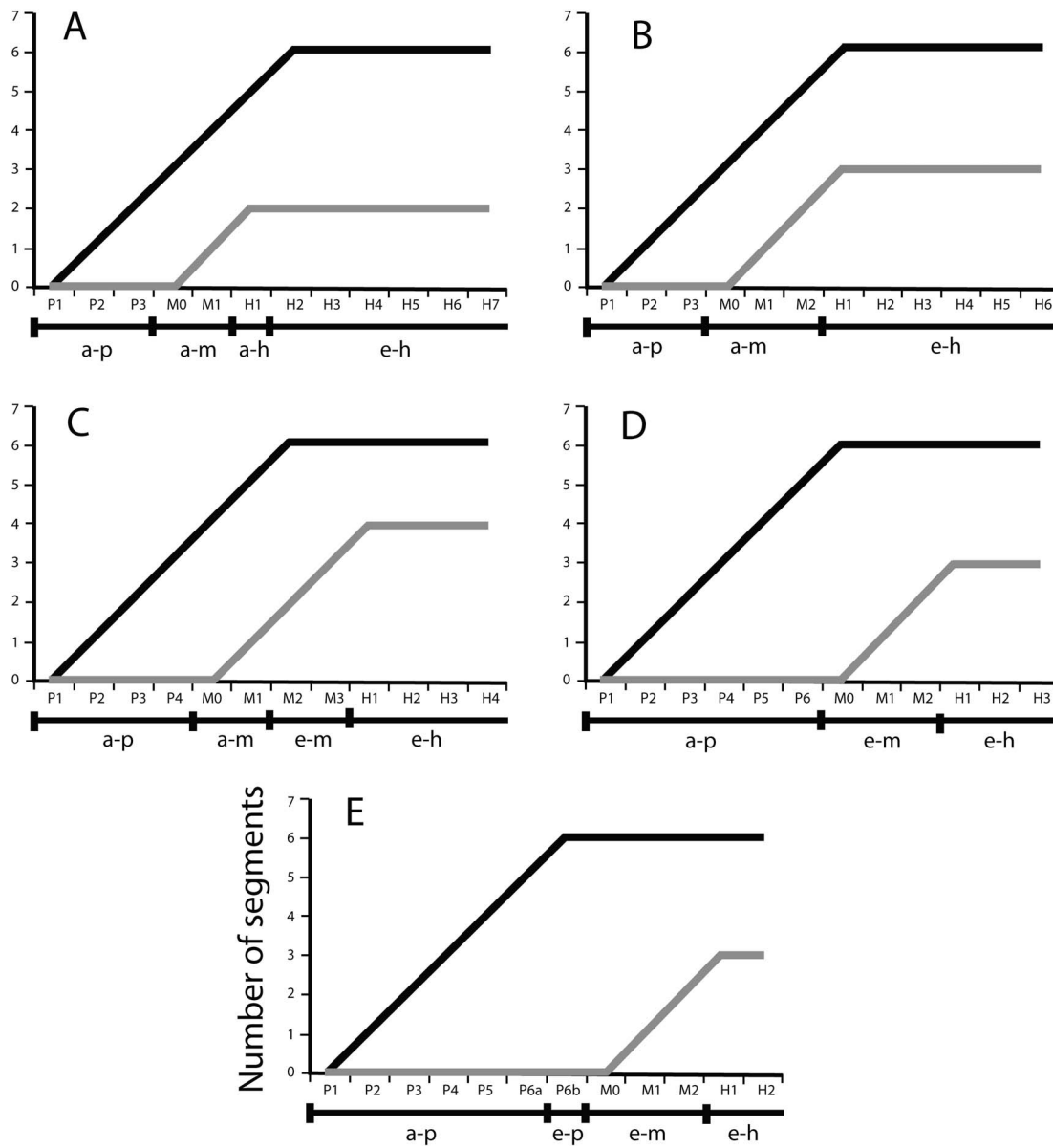
FIGURE 6. Modes of segmental development of the trilobite trunk. The y-axis is the number of segments. Instars within the articulation-based stages protaspid (P), meraspid (M), and holaspid (H) are displayed in ontogenetic order along the x-axis. For simplicity, here meraspid instars equate directly to meraspid degrees and are labeled as such. Black line represents the total number of trunk segments, and a gray line represents the number of thoracic segments. The six conditions of trunk development are anamorphic protaspid (a-p), epimorphic protaspid (e-p), anamorphic meraspid (a-m), epimorphic meraspid (e-m), anamorphic holaspid (a-h), and epimorphic holaspid (e-h). A, Protarthrous development in which onset of the holaspid phase preceded onset of the epimorphic phase. B, Synarthromeric development in which onset of the epimorphic and holaspid phases occurred in the same instar. C–E, Three modes of protomeric development in which onset of the epimorphic phase preceded onset of the holaspid phase. C, Hypoprotomeric mode: epimorphic phase begins within the meraspid phase. D, Euprotomeric mode: epimorphic phase begins at the onset of the meraspid phase. E, Hyperprotomeric mode: epimorphic phase begins within the protaspid phase.
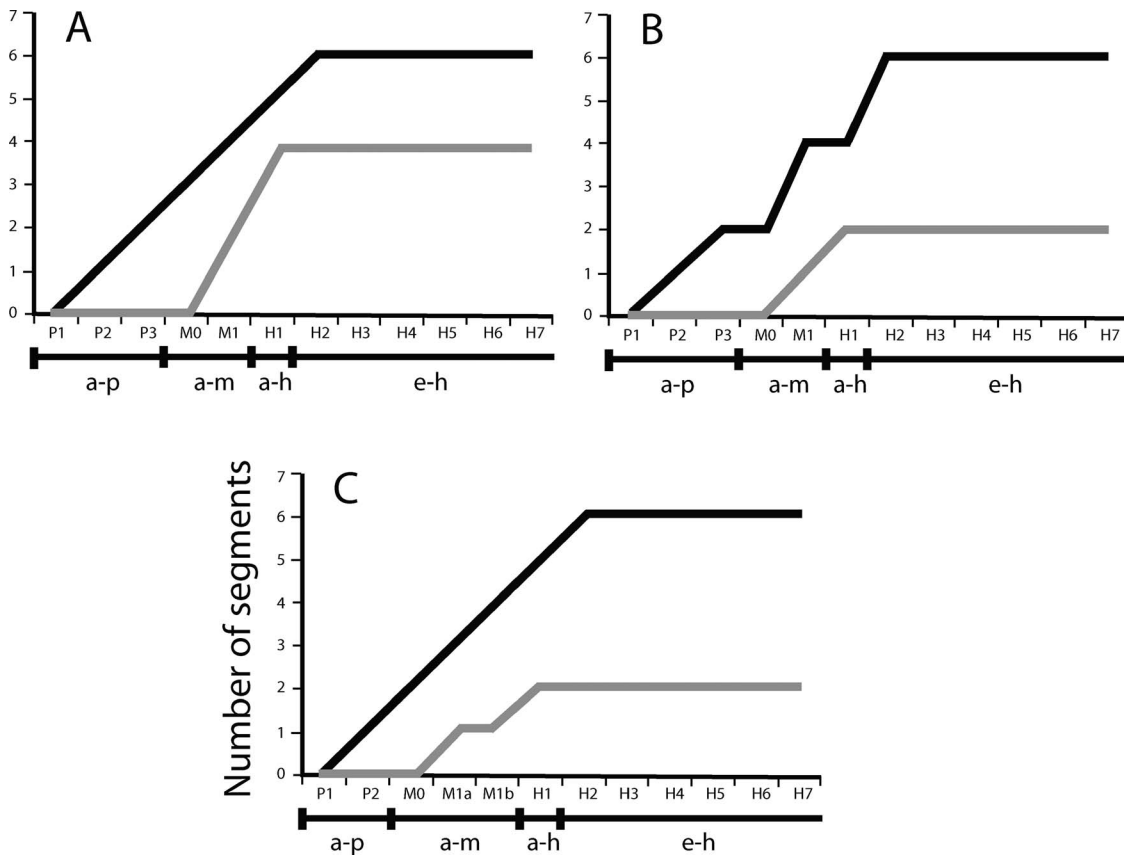
FIGURE 7. Hypothetical variation in segmentation schedule within the same developmental mode. Legend and axes as in Figure 6; in all cases development is protarthrous. A, Meraspid pygidium experienced progressive depletion in the numbers of segments because the rate at which trunk articulations developed exceeded the rate of segment production. Meraspid instars are labeled as meraspid degrees. B, Periodic production of new segments, resulting in complex variation in the numbers of segments in the pygidium with both an accumulation and a depletion phase (Simpson et al. 2005). C, Meraspid pygidium experienced changes in the number of segments because although the rate of segment production was constant, the rate of release of segments was stepped.

three possible modes of protomeric development: *euprotomeric*, in which the onset of articulation coincided with onset of the epimorphic phase (Fig. 6D); *hypoprotomeric*, in which the onset of articulation preceded onset of the epimorphic phase (Fig. 6C); and *hyperprotomeric*, in which the onset of articulation followed onset of the epimorphic phase (Fig. 6E).

As different modes are insensitive to the relative speed of segment production and formation of articulation, to intercalary steady states, and to the overall number and ultimate distribution of trunk segments, several alternative segmentation schedules can be assigned to the same mode (Fig. 7).

Similar graphs for the ontogenies of actual species may illustrate several kinds of information: number of segments in the trunk and their allocation to thorax or pygidium, intraspecific variation in ontogenetic schedule, missing data, alternative data interpretation, etc. (Fig. 8).

These five modes describe a ''space of segmentation schedules'' for trilobite trunk development, and a review of trilobite ontogenies will reveal the structure of realized space occupation. Our sample (Table 1) is based on those cases in which putative instars have been recorded (regardless of the quality of support for the recognition of instars), and is a haphazard representation of the entire clade. However, the sample spans much of the tax-
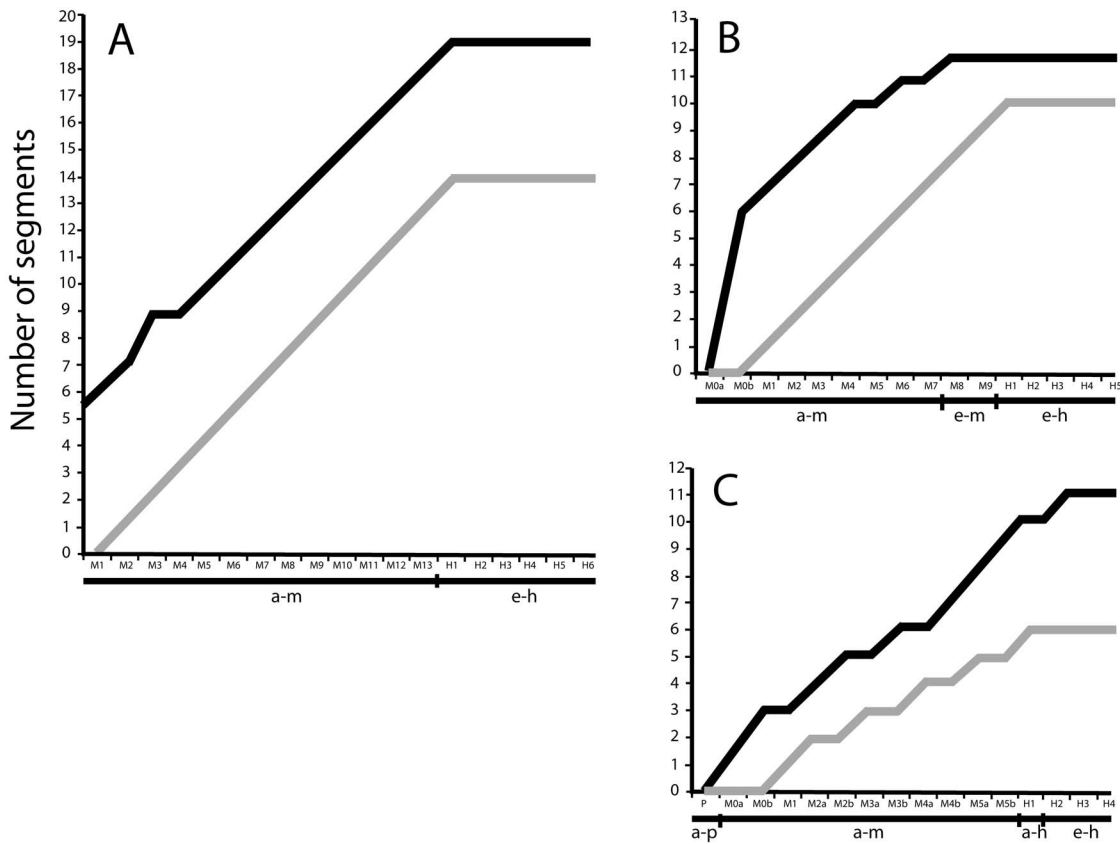
FIGURE 8.   A–C, Three examples of trilobite ontogenies known from articulated material with thoracic segment numbers directly observed. A, *Triarthrus eatoni* showing synarthromeric development. B, *Ctenopyge* (*Eoctenopyge*) *angusta* showing hypoprotomeric development. C, *Shumardia* (*Conophyrs*) *salopiensis* showing protarthrous development. Details of these taxa and their ontogenies are given in Figures 3 and 4.

onomic and temporal diversity of the group, and includes several groups of closely related taxa. The most striking result is that developmental mode varies widely across the clade Trilobita, commonly at low taxonomic levels. Congeners *Ctenopyge* (*Eoctenopyge*) *angusta* and *C. ceciliae* have hypoprotomeric and protarthrous modes respectively (Fig. 3B,C). Furthermore, cohorts of *Neocobboldia chinlinica* from the same locality appear to show either hypoprotomeric or synarthromeric modes (Fig. 5A). No cases of hyperprotomeric or euprotomeric development are recorded in this data set, though these modes may have occurred among Trilobita. The most common mode is hypoprotomeric, with 21 cases in our data set. There are seven cases of protarthrous development and four of synarthromeric development. The synarthromeric mode may be rare because it requires a syn-

chronous transition to maturity in segment generation and segment articulation, whereas the offset in transition to maturity in both the protomeric and protarthrous modes was free to vary over a wider number of instars. It is possible that certain clades were characterized by particular conditions (an example might be the Cheirurina by the hypoprotomeric mode), but this sample is too small to confirm that.

The first three modes are represented by multiple examples in our database, with the hypoprotomeric mode as the most common style. *Ceraurinella typa* might represent the euprotomeric mode, but in the absence of information on the protaspid stage of that species this cannot be confirmed. The hyperprotomeric mode has not been described in any trilobite ontogeny known to us, although the permanently protaspid *Schmalenseeia fusilis*

(see Peng et al. 2005) represents an extreme example of this kind of development in which thoracic segments never developed.

Comparison with Other Arthropods

The need for a new comparative framework for trilobite ontogeny is demonstrated by the misunderstandings propagated in several leading biology texts. For example, the latest edition of Brusca and Brusca's (2003: p. 499) textbook *Invertebrates* suggests that the classical protaspid, meraspid, and holaspid stages of trilobite life history all encompassed larval development and that segments were added in all these stages. As shown above, both these claims are either false or seriously misleading and apparently result from the fact that these articulation-based trilobite life stages, which use a pattern of development unique to trilobites, are not readily comparable to the life stages of living arthropods.

In fact, the two-phase pattern of trunk exoskeletal segment generation in trilobites shares parallels with that seen in a variety of other arthropods (Fusco 2005). The early Cambrian ''great appendage'' bearing arthropod *Leanchoilia illecebrosus* apparently showed an anamorphic phase (Waloszek and Maas 2005: Fig. 11). The small ''trilobitomorph'' arthropod *Primicaris larvaformis* has been compared to a trilobite protaspid (Hou and Bergström 1997: p. 52; Zhang et al. 2003) but does not appear to show an anamorphic phase of segment addition. The size range represented (Zhang et al. 2003: Text-fig. 4) might reflect specimens in the epimorphic phase.

Anamorphic addition of a small number of segments likely occurred in fossil, as in living, pycnogonids (Müller and Walossek 1986; Waloszek and Dunlop 2002), a group whose taxonomic placement as basal arthropods or basal chelicerates is currently debated (Dunlop and Arango 2005; Maxmen et al. 2005). Similarly, the postembryonic ontogenies of the Silurian eurypterids described as *Stylonurus myops* and *Hughmilleria shawangunk* reportedly (Clarke and Ruedemann 1912: Plates 51, 64) show an early anamorphic phase. Living chelicerates hatch with the full complement of segments.

The strongest parallels with the pattern of exoskeletal segmentation seen in trilobites are within the myriapods and crustaceans. Within myriapods, hemianamorphic segment development is present in the millipedes (Diplopoda) and was apparently phylogenetically basal within the group (Enghoff et al. 1993: Fig. 27). This developmental mode has been modified in derived clades, although all maintain the anamorphic appearance of additional segments in some portion of postembryonic ontogeny (Fusco 2005). Millipede evolution has apparently also been characterized by an increase in the number of segments that appeared between subsequent anamorphic molts, with basal members developing one or two new segments per molt but many derived members expressing five or more (see Fusco 2005). In millipedes, the number of segments added at each molt varies considerably between molts but also, during the same molt, among individuals of the same population and sex (Enghoff et al. 1993).

The other major myriapod clade, the centipedes (Chilopoda) also shows hemianamorphic development as a basal condition (Edgecombe et al. 1999; Fusco 2005; Minelli et al. 2000). In more basal groups such as the Lithobiomorpha the increment of legs is one to three leg pairs per molt (e.g., Andersson 1976). A derived clade that groups Scolopendromorpha and Geophilomorpha is epimorphic. Hence among myriapods the number of trunk segments expressed at hatching, and the number and rate of appearance of trunk segments during the anamorphic phase, is apparently somewhat more variable than in trilobites.

Crustaceans also commonly show hemianamorphic segment development. Examples include some members of the Bathynellacea, Cephalocarida, Anostraca, Mystacocarida, Branchiura, and some euphausiid malacostracans (Hartnoll 1982; Schram 1986; Walossek 1993; Walossek and Müller 1998; Waloszek and Maas 2005). Like Myriapoda, Crustacea are markedly varied in their modes of development, and it is not certain that hemianamorphosis was the ancestral crustacean developmental mode, although some form of anamorphosis appears highly likely to have been basal (Waloszek and Maas 2005).

The ontogenies of several fossil crustaceans have been described from the spectacularly well preserved Late Cambrian Orsten beds of Sweden. Some of these development sequences have been compared to those of extant crustaceans (Walossek 1993; Walossek and Müller 1998; Waloszek and Maas 2005). In particular, the ontogeny of the branchiopod *Rehbachiella kinnekullensis* has been used to calibrate aspects of the development of other arthropods, based on the hypothesis that *Rehbachiella*'s apparently extremely regular pattern and rate of segment increment between instars equates to the basal condition for Crustacea. Numerous derived groups apparently add multiple exoskeletal segments simultaneously between particular instars, often associated with enhanced transitions in other aspects of development, commonly defined as metamorphoses. The development of trilobites is consistent with Waloszek's view that the basal crustacean condition was one of an extended series of anamorphic molts with limited morphological transition between molts.

A contrast between the strategies of segment generation seen among mandibulate arthropods and trilobites is the flexibility that myriapods and crustaceans display in their ontogenetic schedules compared to the relative consistency recorded in trilobites (also see Hughes and Chapman 1995). Crustaceans have been able to vary the manner, timing, and sequence of segment expression in ways that permit extremes ranging from the anamorphic addition of segments throughout ontogeny to segment invariance from hatching onward, with hatchlings differing from adults only in size and sexual immaturity (Williamson 1982). Waloszek has illustrated and discussed comparative segmentation schedules in crustaceans that demonstrate increasingly irregular and profound morphological ''jumps'' among derived anamorphic Crustacea (Walossek 1993; Waloszek and Maas 2005). Myriapods also display similar flexibility in the repeated and independent modification of a basal hemianamorphic condition. In both trilobites and myriapods the anamorphic appearance of segments and appendages is ordered such that anterior segments develop before posterior ones, although

slight departures from this order in the generation of trunk segments may have occurred near the anterior of the pygidium in both agnostoid (Hunt 1967) and eodiscid (Zhang and Clarkson 1993) trilobites. Departures from strict anterior-backwards developmental progression are more common among crustaceans. Development of both posterior cephalic limbs (e.g., Schram 1986: Fig. 34–5A,B) and posterior thoracic tergites (e.g., Williamson 1982: p. 56; Minelli and Peruffo 1991: p. 56; Walossek 1993: p. 91; Waloszek and Maas 2005) are commonly delayed compared to their more posterior equivalents. Particularly notable is the situation in cephalocarids, in which differentiation of thoracic and abdominal segments may have occurred synchronously during later juvenile ontogeny, according to Waloszek and Maas (2005: p. 521). Within the crustacean anamorphic phase the regular, stepwise appearance of segments and appendages can be punctuated by the simultaneous appearance of multiple segments between instars, such as in the transition between the nauplius and copepodite phases in copepods, and such changes are often correlated with significant transitions in body form described as crustacean metamorphoses (Snodgrass 1956). Although trilobites also showed some departures from a constant rate of segment generation during the anamorphic phase, it is the overall regularity of trilobite anamorphic development, rather than its variability, that is most notable in comparison to the condition in crustaceans. Walossek (1993: p. 88) also showed that the rate and manner of appendage development varies enormously with respect to the generation schedule of exoskeletal units among Crustacea and many mature mandibulate arthropods have apodous segments toward the posterior of the trunk. This is not characteristic of Trilobita. Indeed, in some trilobites with appendages preserved the number of pairs of appendages in the mature pygidium exceeded the number of tergites expressed in the exoskeleton (Hughes 2003b).

The subterminal appearance of new segments coupled with the delayed development of segment articulation was likely the developmental mode of several basal euarthropods other than trilobites, and a trilobite-like py-

gidium is considered synapomorphic for the clade Trilobitomorpha (Cotton and Braddy 2004). Several non-biomineralized Cambrian arthropods had a mature thorax and segment-rich posterior plate that appear morphologically similar to those of most Trilobita (Edgecombe and Ramsköld 1999; Hou and Bergström 1997), and these may have developed in a similar fashion. If so, this developmental mode apparently predated the evolution of Trilobita (Ramsköld and Edgecombe 1991).

Other Ontogenetic Transitions in Trilobites

Two other important ontogenetic transitions in trilobites require consideration. These are the changes in overall body plan in the ontogenies of some trilobites that are interpreted as metamorphoses, and the onset of maturity.

Metamorphosis and Larvae.—In some trilobite species particular molts were accompanied by elevated degrees of morphological change and these transitions are referred to as metamorphoses (Evitt 1961; Speyer and Chatterton 1989), sometimes termed ''radical metamorphosis'' (Chatterton and Speyer 1990). These marked changes likely corresponded to an important behavioral/ecological transition (Speyer and Chatterton 1989) and do not appear to be akin to the fundamental reorganization of body tissues seen in the metamorphosis of holometabolous insects, for example. We concur with Raw (1927: p. 141) that in trilobites ''true metamorphoses, in this restricted sense, are absent.'' Trilobite metamorphoses have been described among several groups (Chatterton and Speyer 1997; Lerosey-Aubril and Feist 2005a). Although generally occurring relatively early in postembryonic ontogeny, these changes do not appear to correlate with a specific point in either segment production or segment articulation history. The protaspids and meraspids of trilobites are commonly described as larvae (e.g., Beecher 1895; Chatterton and Speyer 1997). Many zoologists use the term ''larvae'' to imply early ontogenetic stages that differ markedly from the mature form, often having unique characters lost in later developmental stages and separated from them by a metamorphosis (e.g., Minelli 2003). Given that morphological change during early trilobite ontogeny is usu-ally incremental, we advocate use of the term ''juvenile'' as opposed to ''larva'' in cases of stepwise, progressive morphological change between instars (see Minelli 2003). The transition from larval to juvenile form was associated with the change from the ''nonadult-like'' to ''adult-like'' morphologies (Chatterton and Speyer 1989; Speyer and Chatterton 1990).

Maturity in Trilobites.—Each of the three aspects of segmentation discussed achieved a terminal phase. Where transitions among different aspects of segmentation were coincident and coupled with transitions in other characters, such as changes in cephalic allometric trajectory (e.g., Kim et al. 2002), there may have been an integrated transition to a terminal growth phase mature in multiple aspects of development. However, in many trilobites the transition to the terminal condition was achieved in different characters at different instars. Although the degree of allometry between instars generally declined during the holaspid phase, changes of proportion and other characters such as ornament are known during holaspid development (Hughes 1994). Such variations hinder recognition of a form that is mature in all skeletal characters.

Some studies have equated the onset of the holaspid phase with the advent of sexual maturity in trilobites (but see Cisne 1973), but no strong reasons for such a correlation have been advanced. There is no simple relationship between the transition to a stable number of trunk segments and sexual maturity in living hemianamorphic arthropods (see Enghoff et al. 1993), many of which become sexually mature instars after the onset of the epimorphic phase (Minelli 1992). Molting after the onset of sexual maturity is common among crustaceans (Schram 1986) and also occurs in collembolans, bristletails, silverfish, and mayflies (subimago to imago) (e.g., Dathe 2003). In trilobites such as *Aulacopleura konincki* there is no evidence of any ''final'' morphological stage, and the numbers of individuals near the maximum size would have been too small to act as a reproductive population (see Fusco et al. 2004). Thus it is likely that the transition to sexual maturity occurred earlier in ontogeny, but when is unknown. The fact that the onset of sexual maturity cannot be

equated to specific developmental transitions recorded in the exoskeleton complicates the application in trilobites of those heterochronic models that require recognition of the onset of sexual maturity (e.g., Gould 1977).

Conclusions

Trunk segments appeared sequentially during the postembryonic ontogeny of all trilobites. Ontogenetic series, where well known, indicate that trilobite development was hemianamorphic, with a mature phase during which growth and molting continued but in which the number of trunk segments remained constant. The development of trunk segment articulation also displayed a stable terminal state during which the number of segments allocated to the thorax remained constant. The transition to the mature phases of segment generation and segment articulation occurred at the same molt in some trilobites (synarthromeric), but were decoupled in others, with the onset of stable articulation either preceding (protarthrous) or succeeding (protomeric) the onset of a constant number of trunk segments. There is no evidence that either of these transitions correlated with the onset of sexual maturity. In some trilobites the trunk was regionalized into two or more batches of similarly shaped segments. In such cases the first appearance of the distinctive morphology of the posterior batch may serve as another ontogenetic boundary.

Examples above document a diversity of paths by which trunk segmentation developed in Trilobita. It is striking that the three modes outlined in Figure 6 have representatives spanning a wide array of clades. Figure 3A–C illustrates that these three conditions occurred among three closely related species belonging to the family Olenidae, implying that in this case that transition between schedules may have been achieved at little cost to fitness. Variability in the relationship between onset of stable articulation and stable segment numbers at low taxonomic levels offers the potential to explore microevolutionary changes in trunk segmentation. These changes are important because it appears that some major innovations in trilobite evolution, such as the holaspid pygidium in mature scutelluids, re-

quired specific and invariant relationships between segment appearance, articulation, and form (see Hughes 2003a,b). Thus, the different facets of the trilobite trunk may offer a route by which to examine the developmental compatibility and the evolutionary trade-offs between different aspects of segmentation.

In trilobites morphological transitions between instars were generally progressive and gradual. Although certain molts have been termed metamorphoses, no trilobite ontogeny is known to contain more than one such transition, and morphological changes at these molts are radical only in comparison to transitions between other instars of the same ontogeny.

Viewed in the context of the diversity of body form seen among Arthropoda, the diversity of trilobite trunk segmentation development, just as that of trilobite tagmosis (Hughes 2003a), appears to have been quite limited. Cephalic segmentation, at least in relation to appendage number, was apparently consistent in the group (Hughes 2003b), conforming to the basal ''head larvae'' pattern in Crustacea (Walossek 1993). Hemianamorphic development was apparently maintained throughout Trilobita. Although this condition was apparently basal in both myriapods (Fusco 2005) and crustaceans (Waloszek and Maas 2005) it was repeatedly modified in derived members of those mandibulate groups, though commonly in different ways. Trilobite trunk development was consistent with the model of gradual anamorphic development for early crustaceans presented by Walossek (1993). Hence hemianamorphic development with gradual morphological changes over an extended series of free-living instars characterizes what is known of the fossil record of development of early arthropods. As gradual changes with absent or modest ''metamorphoses'' also characterize Chelicerata, a group whose predominantly epimorphic development may be derived, hemianamorphosis could have been the basal style of development in Euarthropoda.

Acknowledgments

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