Trilobite Tagmosis and Body Patterning from Morphological and Developmental Perspectives[1]

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SYNOPSIS.   The Trilobita were characterized by a cephalic region in which the biomineralized exoskeleton showed relatively high morphological differentiation among a taxonomically stable set of well defined segments, and an ontogenetically and taxonomically dynamic trunk region in which both exoskeletal segments and ventral appendages were similar in overall form. Ventral appendages were homonomous biramous limbs throughout both the cephalon and trunk, except for the most anterior appendage pair that was antenniform, preoral, and uniramous, and a posteriormost pair of antenniform cerci, known only in one species. In some clades trunk exoskeletal segments were divided into two batches. In some, but not all, of these clades the boundary between batches coincided with the boundary between the thorax and the adult pygidium. The repeated differentiation of the trunk into two batches of segments from the homonomous trunk condition indicates an evolutionary trend in aspects of body patterning regulation that was achieved independently in several trilobite clades. The phylogenetic placement of trilobites and congruence of broad patterns of tagmosis with those seen among extant arthropods suggest that the expression domains of trilobite cephalic Hox genes may have overlapped in a manner similar to that seen among extant arachnates. This, coupled with the fact that trilobites likely possessed ten Hox genes, presents one alternative to a recent model in which Hox gene distribution in trilobites was equated to eight putative divisions of the trilobite body plan.

INTRODUCTION

The form and numbers of segments in the trilobite body varied markedly, both during ontogeny and among taxa, and extreme differences among trilobite morphotypes commonly reflect marked differences in total numbers of body segments. While the number of segments in the cephalon was apparently almost invariant throughout the Trilobita, the number of trunk segments was flexible and is known to have varied among adults of individual species. This paradox of stability and lability, coupled with the difficulty of establishing reliable homologies of the cephalic segments with those of other arthropods, may have contributed to diminished interest in trilobite segmentation in recent years, despite new descriptions of ventral appendages in a number of species.

New insights into developmental mechanisms shared among extant arthropods have rekindled interest in trilobite segmentation (*e.g.,* Akam *et al.*, 1994). The opportunity now exists to consider the regulatory basis of the segmental morphology of trilobites based on correlations between shared patterns of regulatory genetics and their morphological expression among extant arthropods. Indeed, some such attempts have already been made (*e.g.,* Hughes and Chapman, 1995; McNamara, 1997; Sundberg, 2000; McMenamin and McMenamin, 2001). The aim of this paper is to further explore this area, firstly by reviewing some of the major features of trilobite segmentation and body construction, and secondly by relating some of these to aspects of developmental genetics that can be inferred on phylogenetic grounds to have been operative in tri-

lobites. The purpose of this paper is not to provide a comprehensive review of trilobite segmentation, but to highlight some features that may guide inferences into the developmental mechanisms by which the trilobite body plan was specified. The significance of this is not in the attempt to tie particular body regions to particular genes, but in exploring the ways in which trilobites may have used the developmental toolkit inherited from their ancestors among the basal Arthropoda.

WHY TRILOBITES?

Five aspects of the Trilobita make them particularly appropriate candidates for consideration in the light of developmental genetics. Firstly, trilobites belong within the Arthropoda, and evolutionary relationships within and among extinct and extant members of this phylum are relatively well understood. Secondly, segmentation is clearly expressed in the dorsal exoskeletons of all trilobites, and genetic mechanisms of segment specification and fate in arthropods are currently among the best known regulatory systems (see Carroll *et al.*, 2001 for a summary). Thirdly, trilobites were abundant both in numbers of individuals (Hughes, 2000) and taxa (Foote, 1991, 1992, 1997*a*), and were also rich in morphological characters. An estimate of the number of taxa that can be reliably diagnosed is about 2,000 genera and 10,000 species. This abundance contributes to the relative reliability of our understanding of aspects of the evolutionary history of the group (Foote, 1997*b*). Fourthly, information on morphological development is available for a substantial portion of the ontogeny of several tens of species. This is due to preservation of sequences of molted and dead instars that collectively represent much post-embryonic life history of the species to which they belonged. Fifthly, the Trilobita is by far the best-represented arthropod group within Paleozoic rocks, from

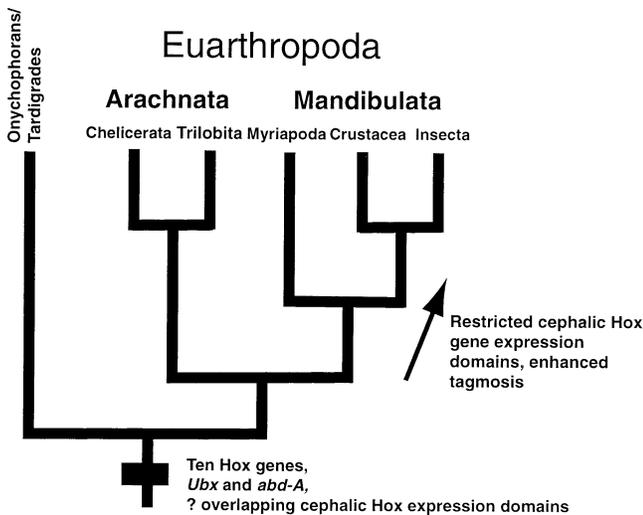---

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FIG. 1. A scheme of phylogenetic relationships among euarthropods adopted as a framework for this study. The scheme is consistent with some recent analyses of extant arthropods, and places Trilobita with Chelicerata in an arachnate clade, based on characters discussed in the text. Some attributes of Hox genes and tagmosis discussed in the paper are mapped as putative synapomorphies.

an important interval in the evolutionary history of the phylum Arthropoda. Thus the Trilobita offer a promising opportunity for examining the early evolution of segmentation patterns in the aftermath of the Precambrian/Cambrian radiation.

TRILOBITE PHYLOGENETIC RELATIONSHIPS

Details of the segmented, biomineralized trilobite exoskeleton and of appendage morphology confirm that trilobites belong within the Arthropoda, a clade whose relationships both internally and with other protostomes have recently been clarified (Aguinaldo *et al.*, 1997; Giribet *et al.*, 2001; Peterson and Eernisse, 2001). Most recent phylogenetic analyses place biomineralized trilobites as a clade within the Arachnata (Edgecombe and Ramsköld, 1999), a sister taxon to other euarthropods including crustaceans, insects, and, possibly, myriapods (Fig. 1). Synapomorphies placing trilobites with other arachnates include the ventral anus, trilobation (*i.e.,* differentiation into axial and pleural regions), pleural overlap of the trunk tergites (Briggs and Fortey, 1989, 1992; Wills *et al.*, 1994), and a gnathobasic feeding pattern with combined locomotion and feeding (Müller and Walossek, 1987). An alternative view, which rejects many of these putative arachnate synapomorphies, nevertheless also places Trilobita within the euarthropods, as member of a derived arthropod clade containing crown group Mandibulata and Chelicerata (Budd, 2002). Relationships between trilobites and the Myriapoda remain unclear, although recent evidence apparently suggests that myriapods are relatively basal within the mandibulates (Giribet *et al.*, 2001; Peterson and Eernisse, 2001), rather than being the sister taxon of insects (Fig. 1). The Trilobita itself is defined by characters includ-

ing a calcitic exoskeleton and lenses situated within dorsal eyes, and a circumocular suture (see Edgecombe and Ramsköld, 1999). Debate continues about whether the calcified Order Agnostida are members of the Trilobita or are allied with basal crustaceans, and about the relationships among trilobites and non-calcified Cambrian arachnates. Henceforth, this paper uses the term Trilobita to include the agnostids but to exclude non-calcified arachnates, but the questionable status of the agnostids is noted and the paper highlights several differences between agnostids and other trilobites with respect to body patterning.

Barring the question of the position of Agnostida there is current consensus that Trilobita were monophyletic (Fortey, 1997). Accordingly, they were not a stem group to any extant clade and cannot inform us directly about the early evolution of apomorphic body patterning innovations present among extant taxa. The phylogenetic position of the Trilobita nested within the euarthropods (some authors even consider trilobites to be among the most derived arthropods [Wills *et al.*, 1997]) is of importance because it permits inferences about trilobites based on developmental mechanisms shared among extant members of more inclusive arthropod clades to which the trilobites belonged. The outlines of a phylogenetic classification of major clades within the Trilobita is emerging (Fortey, 1990, 1997; Fortey and Owens, 1997), supplemented by ongoing work of various authors on the ontogenies of Cambrian trilobites.

ASPECTS OF TRILOBITE SEGMENTATION

Like many metazoans, the trilobite body displayed a series of segments that were modified in various ways along the anterior/posterior (A/P) axis. The group varied in both overall numbers of segments and in the modifications of particular segments, and some aspects of segment modification were apparently at least partially autonomous. The following discussion summarizes information on trilobite segmentation as expressed in the dorsal exoskeleton and among the ventral appendages of adult trilobites, and then considers dynamic aspects of trilobite segmentation through a discussion of ontogeny. The intention is to draw attention to those features of trilobite segmentation that appear general to the group as a whole, rather than specific patterns, such as unusual modifications of the axes or pleural tips of trunk segments, that may characterize individual clades. Similarly, a discussion of "merocyclism" (Raw, 1953; Sundberg, 1995; McMenamin and McMenamin, 2001), purported patterns of shape periodicity among segments, is deferred until elsewhere, as it is contentious.

Distinct regions of the trilobite body, be they within the dorsal exoskeleton or among the ventral appendages, have commonly been equated with the boundaries between distinct tagmata—divisions of metameric body plans into distinct functional regions (Burmeister, 1846; Bergström, 1969). Assessment of functionality is inevitably indirect in trilobites, and it is
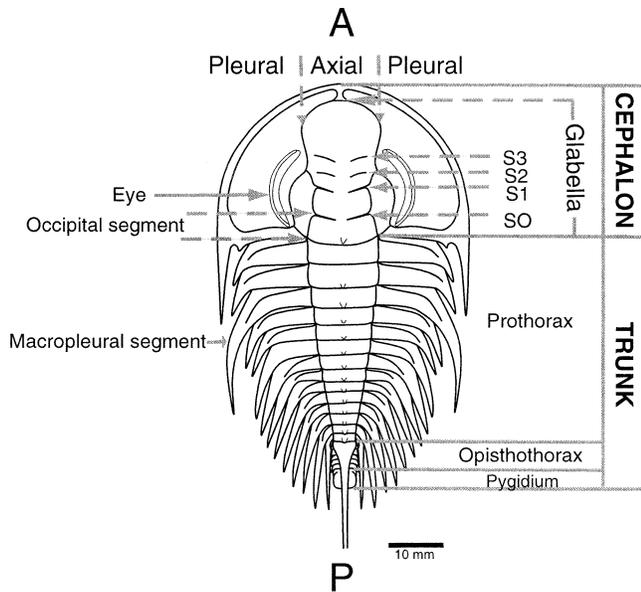
FIG. 2. Features of the trilobite dorsal exoskeleton discussed herein. The figure is a cartoonized version of a Lower Cambrian olenelloid trilobite showing the ''two batch'' trunk segment condition described in the text.
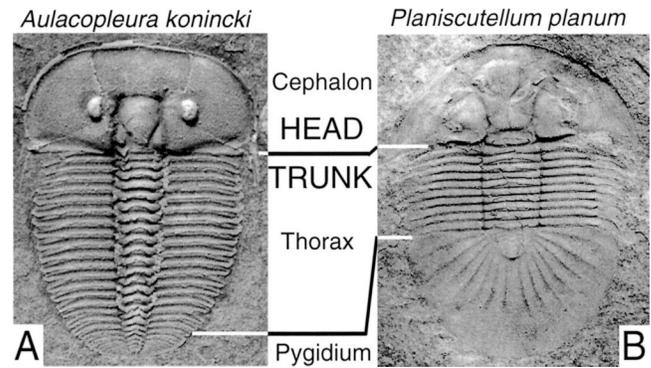

FIG. 3. Major divisions of the adult body of trilobites into cephalic and trunk regions. The trunk region is divided into the freely articulating segments of the thorax and the fused segments of the pygidium. In A, *Aulacopleura konincki*, the segments of the adult thorax and pygidium are similar in morphology (specimen is about 2 cm long), whereas in B, *Planiscutellum planum*, adult thoracic and pygidial segments bear strikingly different morphologies (specimen is about 2 cm long). Both specimens are from the Silurian rocks near Loděnice in the Czech Republic.

clear that the sharpest morphological differences between dorsal exoskeletal and ventral appendage aspects of trilobite segmentation are not coincident (Minelli *et al.*, 2003). Given this, a summary of patterns of tagmosis in trilobites is deferred until later in the paper.

Dorsal exoskeleton

Articulated dorsal exoskeletons of trilobites suggest that the adult exoskeleton was divided into three structural regions along the anterior/posterior (A/P) axis (Figs. 2, 3) (Burmeister, 1846). The anteriormost region was the cephalon and was constructed from segments that were commonly demarcated by lateral furrows in the glabella (the stomach capsule), but which were fused together. The boundaries of individual segments are generally unclear in the pleural regions (*i.e.,* those away from the axis) and anterior to the glabella, and the exact number of cephalic segments expressed in the exoskeleton and their boundaries have been debated for many years (*e.g.,* Beecher, 1896; Raw, 1927*a, b*; Raymond, 1920; Stubblefield, 1936; Størmer, 1942, 1951; Hupé, 1954; Palmer, 1957).

The trunk region of adult trilobites was divided into two sectors: the thorax and the pygidium. The thorax consisted of freely articulating segments, and its modular construction is obvious. The pygidium, like the cephalon, was a structure in which segments were fused together. In most trilobites, such as *Aulacopleura konincki* (Fig. 3A), segmentation was clearly expressed in the pygidium, but in various effaced taxa, such as certain illaenids, agnostids, and asaphids, little or no trace of segmentation was expressed dorsally. Among adult trilobites with clearly incised pygidial

segments some, such as *A. konincki*, show a basic uniformity of segment structure throughout the trunk region (Fig. 3A), while others, particularly scutelluids (Fig. 3B), some lichids, and deiphoninid cheirurids, show distinctly different segmental structure within these two regions of the trunk. Other trilobites displayed additional patterns—in many olenelloid and emuelloid species the thorax was divided into an anterior region, the prothorax, that differed from the posterior opisthothorax by a marked decrease in segment size, and the pygidium that, when preserved, was a tiny terminal plate containing no more than a couple of segments. Many trilobite species also possessed individual or small subsets of trunk segments that were characterized by unique features such as pronounced axial or pleural spines, or gross overall enlargement of the pleural (but not axial) regions. The latter are commonly referred to as macropleural segments (but see Palmer [1998, p. 657] for a more detailed terminology), and may occur in either thorax or pygidium.

Although the expression of individual segments is least clear in the cephalon, this region was apparently stable in the number of segments, at least as can be inferred based on glabellar furrows (following the argument of ''serial similarity'' [Bergström, 1973*a*, p. 9]). Many trilobites showed three or four clearly incised furrows on the glabella (termed SO to S3 from the posterior to the anterior of the glabella). Traces of a fifth pair, S4, are known in some species, and a sixth pair has been reported in rare cases. The serial homology of the posterior segments is generally accepted on the grounds of similarity, but that of S4 is less secure: where present this furrow is short, weakly incised, and is commonly spaced and oriented differently from those furrows succeeding it. Thus, most trilobites apparently expressed at least four glabellar segments (including the occipital segment, located at the posterior of the glabella) in addition to the anterior glabellar

TABLE 1. *Distribution of dorsal and ventral aspects of trilobite segmentation in those taxa with limb anatomy preserved.*

Taxon	Preservation	Age	Cephalon		
			Glabellar furrows	Glabellar segments	Ventral appendages
Eoredlichia intermedica	Burgess	Early Cambrian	4	4+ anterior	?4
Yunnanocephalus yunnanensis	Burgess	Early Cambrian	?4	?4+ anterior	?5
Olenellus getzi	Burgess	Early Cambrian	4	4+ anterior	N/A
Olenoides serratus	Burgess	Middle Cambrian	3	3+ anterior	4
Kootenia burgessensis	Burgess	Middle Cambrian	?4	?4+ anterior	N/A
Elrathina cordillerae	Burgess	Middle Cambrian	4	4+ anterior	N/A
Elrathia permulta	Burgess	Middle Cambrian	4	4+ anterior	N/A
Agnostus pisiformis	Phosphatic	Late Cambrian	2	3	4
Placoparia (Placoparia) cambriensis	Mudstone mold	Middle Ordovician	4	4+ anterior	4/4.5
Isotelus latus	Mudstone impression	Late Ordovician	Indistinct	Indistinct	>2
Isotelus maximus	Mudstone impression	Late Ordovician	Indistinct	Indistinct	N/A
Triarthrus eatoni	Pyritic	Late Ordovician	4	4+ anterior	4/4.5
Cryptolithus tessellatus	Pyritic, Calcitic	Middle and Late Ordovician	Indistinct	Indistinct	N/A
Primaspis trentonensis	Pyritic, ?Calcitic	Middle and Late Ordovician	3	3+ anterior	N/A
Primaspis sp. X	Silicified	Late Ordovician	3	3+ anterior	N/A
Ceraurus pleurexanthemus	Calcitic	Late Ordovician	4	4+ anterior	5
Flexicalymene senaria	Calcitic	Late Ordovician	4	4+ anterior	N/A
Phacops (Chotecops) ferdinandi	Pyritic	Early Devonian	2	2+ anterior	4
Asteropyge sp.	Pyritic	Early Devonian	4	4+ anterior	4
Rhenops cf. *R. anserinus*	Pyritic	Early Devonian	4	4+ anterior	4/4.5

region, but segmentation within the anterior region remains difficult to interpret (Hupé, 1954; Palmer, 1957). Many trilobites also possessed an extended frontal area anterior of the glabella, but expression of segmentation within this region was also unclear.

The number of dorsal exoskeletal segments in the trunk region was considerably more variable, and ranged from over 45 in some olenelloids (Minelli *et al.*, 2003), to about 5 in some agnostids (and probably only a few more in some eodiscinids [Jell, 1975]). The numbers of trunk segments allocated to the thorax and the pygidium respectively varied widely across the clade, although there apparently was a general tendency for the number of segments in the pygidium to increase at the expense of those in the thorax through the temporal history of the clade—a trend termed "caudalization" (Raymond, 1920, p. 73, 128–132; Hupé, 1954; Stubblefield, 1959, p. 152). A consequence of this was that the relative size of the pygidium tended to increase during the history of the group (Fortey and Owens, 1997, fig. 191). In some groups the numbers of adult segments within the different trunk regions were stable at high taxonomic levels, in others it varied markedly among species, or even intraspecifically (McNamara, 1983; Hughes and Chapman, 1995; Hughes *et al.*, 1999).

Differentiation of the trunk region into two "batches" of similar exoskeletal segments was seen in some clades—examples being the prothorax and opisthothorax of olenelloid trilobites, which can be distinguished principally by a decrease in the relative proportions of the posterior thorax (Fig. 2), and the sharp distinction between segments of the thorax and the adult pygidium, particularly obvious in scutelluid (Fig. 3B) and some lichid trilobites. A more common condition, seen in many libristomate trilobites, is for all dorsal trunk segments conform to a single morphotype forming one "batch" of homonomous segments (Fig. 3A).

Ventral appendages

Details of trilobite ventral appendages are known only from cases of exceptional preservation (Table 1). Fortunately, these examples span a diverse range of stratigraphic intervals, preservational styles, and trilobite clades, although most of the species with appendages preserved display morphotypes that were apparently suited to epibenthic particulate feeding lifestyles. (An exception may be the agnostid *Agnostus pisiformis*.) It is important to appreciate that the quantity and quality of preservation varies markedly among these cases and that this limits the ability to generalize about some aspects of trilobite ventral appendages and their relationships to dorsal segments. That said, several aspects of appendage arrangement appear to have been consistent wherever preservation permits evaluation, and this has led to the notion that many characteristics are widely conserved throughout the group.

A single pair of uniramous antennae, which form the anteriormost, preoral appendage pair, are known in fourteen taxa (Table 1). In twelve of these cases the antennae were elongated annulate structures, where well preserved, and apparently equaled or exceeded the length of the cephalon, and likely served a sensory function. In *Agnostus pisiformis* the antennae were shorter structures, and may have functioned as feeding appendages (Müller and Walossek, 1987, p. 47). "Mitten shaped" antennae were suggested to occur in *Primaspis* sp. X (Ross, 1979) but in this case the coarse

TABLE 1. *Extended.*

| Cephalon | | Thorax | | Pygidium | | | Rami preserved | Exopod podomeres |
Antennae	Biramous	Dorsal	Ventral	Dorsal (axial)	Ventral biramous	Cerci		
1	3?	15	N/A	3 + terminal piece	N/A	?Absent	End + Ex	?7
1	4?	14	N/A	2 + 2 faint terminal rings	N/A	?Absent	?End + ?Ex	N/A
?1	N/A	14 prothoracic	N/A	?2	N/A	?Absent	N/A	N/A
1	3	7	7	5 + terminal piece	≤6	1	End + Ex	6
N/A	N/A	7	N/A	5 + terminal piece	N/A	N/A	End + Ex	N/A
?1	N/A	?20	N/A	2? + terminal piece	N/A	N/A	Ex	N/A
1	N/A	14	N/A	3? + terminal piece	N/A	?Absent	N/A	N/A
1	3	2	2	3? + terminal piece	3	Absent	End + Ex	7
1	3/3.5	12	N/A	3? + terminal piece	N/A	N/A	N/A	N/A
N/A	N/A	8	?8	>8	N/A	N/A	End	N/A
N/A	N/A	8	?8	>10	?16	N/A	End	N/A
1	3/3.5	14	14	4 + terminal piece	10+	Absent	End + Ex	6
1	N/A	5	?5	>10	>10	Absent	End + Ex	?7
N/A	N/A	10	?10	2 + terminal piece	N/A	N/A	End	N/A
?1	N/A	10	>8	2 + terminal piece	N/A	N/A	End	N/A
1	4	11	?11	3 + terminal piece	3	?Absent	End + Ex	N/A
1	N/A	13	?13	4–8 + terminal piece	>2	?Absent	End + Ex	N/A
1	3	11	11	?9+	>12	Absent	End + Ex	6
1	3	10–12	?11	>10	>?4	?Absent	End	N/A
1	3/3.5	11	11	?12	>6	Absent	End + ?Ex	7

preservation in silica of the thoracic endopods, without traces of the exopods which likely accompanied them, suggests that the significance of the shape of any anterior appendages may be limited in this case. Antennae were apparently braced to the dorsal exoskeleton near the anterior lateral corners of the glabella (the stomach capsule).

Ten taxa show that the anterior antennae were directly succeeded by a series of biramous appendages (Fig. 4). These appendages comprised an outer blade-like branch (exopod), and an inner leg-like branch (endopod) that consisted of about seven podomeres, where well known (Fig. 4A). The broadly homonomous structure of these appendages throughout the cephalon and trunk is striking, for it contrasts markedly with the specialized feeding appendages seen in many other euarthropods. The detailed structure of both exopods and endopods varied, both along the trunk of individual trilobites, and among different taxa. For example, the relative proportions and detailed structure of exopods and endopods varied so considerably between adjacent cephalic appendages in *Agnostus pisiformis* (see Müller and Walossek, 1987) that Wills *et al.* (1997) considered them fundamentally different appendage types, worthy of allocation to distinct functional units (tagmata). However, others (Budd, 2000) saw these morphological differences as minor variations among structures fundamentally similar in anatomy and function. The extraordinary fidelity of the phosphatic preservation of *Agnostus pisiformis* allows the confident recognition of differences between adjacent appendages, but these were apparently relatively minor, at least compared to some of the distinct differences among appendages evident in other arthro-

pods with lower fidelity of preservation in the Burgess Shale or Chengjiang faunas.

In all other cases in which trilobite biramous appendages have been reported variations among serial biramous appendages are generally viewed to be minor and unworthy of designation as distinct tagma. An example of this kind of serial variation is the variable pattern of endite spinosity on the podomeres of the endopods. In *Triarthrus* and *Phacops* the spinosity increased on posterior trunk endopods (Fig. 4B1, B2). Such a pattern is consistent with the presence of ''protuberances'' on the pygidial podomeres of a single specimen of *Rhenops* that were not observed on the thoracic podomeres. This may call into question the argument (Bergström and Brassel, 1984) that these features, along with a marked decrease in appendage size, indicate in this species separate thoracic and pygidial tagmata in terms of appendages. The size-based distinction in thoracic and pygidial appendages was also questioned by Bartels and others (1998, p. 144, fig. 122) who illustrated an additional, less deformed specimen in which the sizes of thoracic and pygidial limbs were comparable. Other species showed additional patterns of variation in appendage structure. In *Olenoides serratus* the anterior trunk podomeres were more spinose, but in *Agnostus pisiformis* the morphology of endopods and exopods appears to have remained constant throughout all the appendages of the last cephalic segment and the trunk segments, and differ only in proportion (see Wills *et al.* [1997] for a different view). In *Eoredlichia intermedia* a transition in exopod structure, coincident with the ninth, axial-spine bearing thoracic segment, was reported by Shu *et al.* (1995), but insufficient evidence was presented

TABLE 1. *Extended.*

| Taxon	Endite spinosity strongest	Major reference
Eoredlichia intermedica	N/A	Shu et al., 1995; Ramsköld and Edgecombe, 1996
Yunnanocephalus yunnanensis	N/A	Shu et al., 1995
Olenellus getzi	N/A	Dunbar, 1925
Olenoides serratus	Anterior trunk	Whittington, 1975; 1980
Kootenia burgessensis	N/A	Walcott, 1918; Raymond, 1920
Elrathina cordillerae	N/A	Walcott, 1912; 1918; Raymond, 1920
Elrathia permulta	N/A	Walcott, 1918; Raymond, 1920
Agnostus pisiformis	Constant	Müller and Walossek, 1987
Placoparia (*Placoparia*) *cambriensis*	N/A	Whittington, 1993; Edgecombe and Ramsköld 1999
Isotelus latus	N/A	Raymond, 1920
Isotelus maximus	N/A	Raymond, 1920
Triarthrus eatoni	Posterior trunk	Raymond, 1920; Cisne, 1981; Whittington and Almond, 1987; Edgecombe and Ramsköld 1999
Cryptolithus tessellatus	N/A	Raymond, 1920; Størmer, 1939
Primaspis trentonensis	N/A	Raymond, 1920; Ross, 1979
Primaspis sp. X	N/A	Ross, 1979
Ceraurus pleurexanthemus	?Absent	Walcott, 1918; Raymond, 1920; Walcott, 1921; Størmer, 1939; 1951
Flexicalymene senaria	N/A	Walcott, 1918; 1921; Raymond, 1920
Phacops (*Chotecops*) *ferdinandi*	Posterior trunk	Stürmer and Bergström, 1973; Bruton and Haas, 1999
Asteropyge sp.	N/A	Stürmer and Bergström, 1973
Rhenops cf. *R. anserinus*	?Posterior trunk	Bergström and Brassel, 1984; Bartels et al., 1998; Edgecombe and Ramsköld, 1999
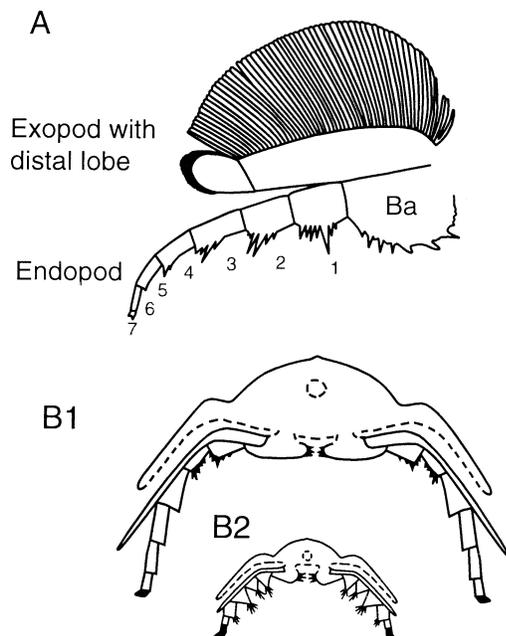
FIG. 4. A. The biramous limb in *Olenoides serratus* (after Ramsköld and Edgecombe, 1996, fig. 1), with lamellate exopod and endopod with seven podomeres attached to basis (Ba). B1, B2. Two transverse sections through the exoskeleton of adult *Triarthrus eatoni* showing the increased endopod podomere spinosity in the smaller, more posterior segments. B1 is near the anterior of the thorax, B2 is near the posterior of the thorax. Modified from Whittington and Almond (1987, fig. 39).

to fully document this interpretation. Thus, although trilobites varied in details of the structure of biramous appendages along the trunk, these changes were apparently sequential and, where well known, gradational. They do not appear to be directly comparable to those generally accepted to differentiate tagmata among extant and fossil crustaceans, in which appendages are organized into discrete batches of similar segments. Unfortunately, no trunk appendages are currently known from any species bearing macropleural trunk segments.

The presence of a single pair of preoral antennae followed by three pairs of postoral cephalic biramous appendages invites comparisons with the condition in mandibulates, which differ in having two pairs of preoral antennae subsequent to an anteriormost ocular segment. Unfortunately, knowledge of the preantennal segments of trilobites is so limited that it is presently hard to justify statements of homology between individual cephalic segments in trilobites with those of other arthropods.

Structural details of the biramous appendages differed more among trilobite taxa than they did along the bodies of individuals. Examples of distinctly different types are found in among the blade-like, lamellate exopodites in *Olenoides serratus*, *Triarthrus eatoni*, and *Phacops* (*Chotecops*) *ferdinandi*, and all these differed markedly from the spiny exopodites of *Agnostus pisiformis* (see Størmer, 1939, fig. 27; Müller and Walossek, 1987, fig. 27; Shu *et al.*, 1995, fig. 21) and may indicate functional (and, possibly, phylogenetic) differences among these taxa (Müller and Walossek, 1987). Nevertheless, in spite of these differences the basic biramous division of the limb into exo-

podite and endopodite was consistently maintained throughout the group, as were particular details of the bases and endopodite structure (Müller and Walossek, 1987, p. 47). Where adequately documented, with the possible exception of the cephalon of *Agnostus pisiformis*, differences among the serial biramous appendages appear to have been minor compared to the difference between the antennae and the biramous appendages, or between appendages assigned to different tagmata in crustaceans, for example (see Cisne, 1974; Schram, 1986).

Of the nine taxa that preserved pygidial appendages, (Table 1) six showed a pattern of numerous biramous appendages that decreased markedly in size posteriorly. Such a pattern was shown in the nearly isopygous (those in which the adult pygidium was of equivalent size to the cephalon) taxa *Rhenops* sp., *Isotelus maximus*, *Cryptolithus tessellatus*, *Asteropyge* sp., and *Phacops* (*Chotecops*) *ferdinandi*, but is best documented in the micropygous *Triarthrus eatoni*, in which the posteriormost region of the preserved softparts was made up of numerous tiny segments each apparently bearing a pair of biramous appendages (Walcott, 1921; Whittington and Almond, 1987). A strikingly different pattern is seen only in the posteriormost appendage pair of the Middle Cambrian corynexochide *Olenoides serratus*. This species bears a single pair of long, annulated, posteriorly directed, uniramous, antenniform cerci with small spines at each articulation, that were interpreted to be associated with the terminal piece of the rachis on the dorsal exoskeleton (Whittington, 1975).

Relationship between segmentation of the dorsal exoskeleton and ventral appendages

Eighteen species, known from a total of several hundred individuals, indicate that there was a correlation between the sagittal lengths of segments expressed on the dorsal exoskeleton and the size of the biramous appendage pairs (Table 1). This correlation suggests that, at least in the thoracic region of adult trilobites, there was a direct, one-to-one relationship between exoskeletal and ventral segments, although the boundaries of these segments may not have been exactly coincident (Hessler, 1962; Bergström, 1973b; Edgecombe and Ramsköld, 1999). The specific relationship between dorsal segments and individual ventral appendages has been ascertained in *Agnostus pisiformis* due to the extraordinary preservation and preparation of specimens of this species, but is less certain in all other taxa. Even in species represented by multiple specimens, such as *Olenoides serratus* and *Triarthrus eatoni*, it is evident that in most specimens many or all of the ventral appendages have been displaced from their original position with respect to the dorsal exoskeleton. This, coupled with the general similarity of biramous appendages along the body axis, makes it difficult to link individual appendages to specific dorsal segments. This problem is reflected in the ongoing uncertainty about the number of biramous appendages

in the trilobite cephalon (Whittington, 1997a; Edgecombe and Ramsköld, 1999). It is clear that the best specimens of the best-known taxon *Agnostus pisiformis* had three pairs of biramous appendages in the cephalon, and a similar situation has been reported in *Olenoides serratus* and *Triarthrus eatoni*. The cases in which four pairs of cephalic biramous appendages have been reported, as in *Rhenops* sp. and *Ceraurus pleurexanthemus*, are less securely documented. In the case of *Rhenops* the number reported has been revised to three pairs (Bartels *et al.*, 1998, p. 144). Reinterpretation of a single specimen of *Placoparia* (*Placoparia*) *cambriensis* in the context of a broader analysis of Cambrian arachnates (Edgecombe and Ramsköld, 1999) suggests that one biramous appendage may have overlapped the cephalic/trunk boundary, making the number of cephalic biramous appendages equate to three and one half dorsal segments as defined using glabellar furrows. The argument here is not that dorsal and ventral aspects of segmentation were decoupled, but simply that the furrows and sutures may occur within individual segments rather than between them (Hessler, 1962). Reliable testing of these ideas requires recovery of non-agnostid trilobites preserved in a manner comparable to that of the Orsten *Agnostus pisiformis*.

In summary, trilobite cephala were characterized relatively stable numbers of segments throughout the group, generally with four or five serially homologous segments expressed in the dorsal axis, and four, or possibly four and one half, appendage pairs. The anteriormost appendage pair was uniramous, preoral and antenniform, the other appendages were postoral, biramous and not markedly specialized for feeding in comparison to the head appendages of mandibulate arthropods. The number of preantennal segments is poorly constrained.

Within the pygidium the number of segments expressed dorsally was commonly at variance with the number of apparent ventral appendages (Table 1). In several cases, such as in *Flexicalymene senaria* and *Cryptolithus tessellatus*, this may have been due to preservational constraints. In *F. senaria* appendages in the pygidium described to date were indistinct and confined to the anterior portion, but the pygidial dorsal exoskeleton of this species is known to have contained from 4 to 8 segments defined in the axial region (Cisne *et al.*, 1980). Conversely, in *C. tessellatus* segmentation in the axial region of the pygidium became progressively effaced in the posterior region of the axis, with the result that the number of ventral appendages preserved greatly exceeded that recorded in the dorsal segments. It is also important to appreciate that the numbers of segments expressed on the internal (visceral) surface of the exoskeleton could differ markedly from that expressed on the outer side (Whittington, 1997b, figs. 51, 60).

Other mismatches in dorsal and ventral segment numbers are less easily explained as preservational artifacts. The mismatches in the pygidium discussed be-

low apparently related to differences in the degree or rate of segment expression on one surface when compared to the other, rather than fusion of segments or decoupling of dorsal and ventral aspects of segmentation. In *Triarthrus eatoni* the number of ventral appendages was approximately twice that expressed on the dorsal exoskeleton. Five axial rings were defined in adults of this species and it appears likely that each ring corresponded to a single ventral appendage pair. Behind this was a crowded zone of progressively smaller appendage pairs at the posterior of the trunk.

A different situation pertained in *Olenoides serratus*. In this species adult specimens apparently possessed either five or six axial rings plus a terminal piece (H.B. Whittington, personal communication), but the number of biramous appendage pairs in the pygidium apparently increased from four to six among progressively larger specimens (Whittington, 1975). Thus in this case there was an apparent mismatch between a relatively consistent number of segments expressed in the dorsal exoskeleton, and a variable number of appendages. Because the smaller adult specimens, with four biramous appendage pairs apparent in the pygidium, also possessed cerci as the posteriormost appendage pair, these cerci could have been specified prior to the complete specification of biramous appendage pairs. If so, this has implications for the position in which new biramous appendages were expressed and indicates that dorsal segments may have been specified prior to the complete development of ventral biramous appendages. An alternative explanation, favored by Prof. Whittington (personal communication) is that all adult *O. serratus* may have possessed a full complement of pygidial biramous appendages, but in smaller adults the fifth and sixth pairs were of smaller proportions and were not evident as extending beyond the pleurae. Preservational constraints preclude resolution of this issue, and no preholaspid specimens of this taxon have yet been described. It would be instructive to determine whether cerci were already present during those early ontogenetic phases in which additional biramous appendages were being expressed.

The sharp distinction in the morphology of dorsal segments in the adult thorax and pygidium, evident in "two batch" trilobites, is not clearly mimicked by a sharp transition in biramous appendage morphology in any case known to date. However, no cases of ventral appendages are currently known among those trilobites in which adult thoracic and pygidial segments are most distinct.

TRILOBITE ONTOGENY

One of the striking patterns of variation seen among characters that define the trilobite body plan is that of cephalic stability and trunk variability with respect to segment numbers. This taxic variability correlates with the pattern of segment development seen during the ontogeny of trilobites. Trilobites calcified their dorsal surfaces relatively early in ontogeny, and their molting
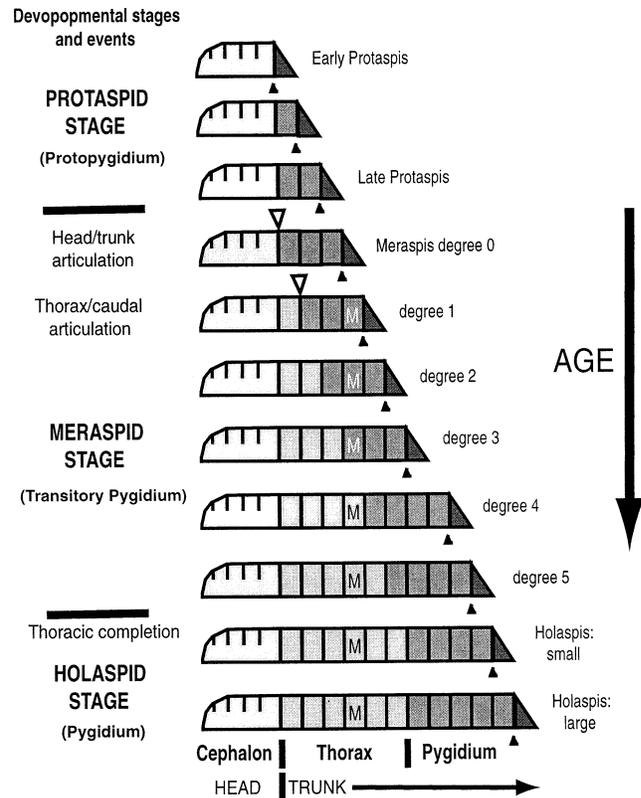

FIG. 5. Stylized representation of the ontogeny of the dorsal exoskeleton of trilobites based on the growth schedule of *Shumardia (Conophrys) salopiensis* (Stubblefield, 1926). Small solid triangle marks the place where additional segments are first expressed, larger open triangle marks points where articulations first appear. "M" is the macropleural segment. Major developmental events and stages are shown to the left, morphological terms for these stages are given to the right. Fused trunk segments are shown in darker grey, freely articulating trunk thoracic segments are shown in lighter grey.

habit yielded sequential instars that can be arranged into ontogenetic series, now known for many species (Chatterton and Speyer, 1997). The earliest instars of trilobites consisted of a single fused shield, the protaspis, although these are not known for all trilobite clades. Trilobites that displayed the morphology of a protaspis are said to have belonged to the protaspid developmental stage (Fig. 5). The protaspis was composed of a cephalic region made up of serially repeated segments most clearly expressed in the axis. Although the morphology of the cephalic region changed markedly during ontogeny, the number of segments defined in the cephalic exoskeleton apparently remained constant throughout all stages, as far as preservation permits determination of segment counts. In cases in which furrows are clearly defined, there appear to have been at least 4 segments, including the occipital segment (*e.g., Neocobboldia chinlinica* [Zhang, 1989]). The most common condition is that of 5 axial cephalic segments examples of which include the protolenid *Inchangia inchangensis* (Zhang and Pratt, 1999), the phacopids *Flexiclaymene senaria*, *Cybeloides prima*, and *Calyptaulax annulata*, the lichid *Hemiarges* aff.

H. turneri (Chatterton and Speyer, 1997), and early meraspis of the olenelloid *Nephrolenellus geniculatus* (Webster *et al.*, 2001).

The stability of cephalic segmentation contrasts with that seen in the trunk region (Fig. 5). The onset of the protaspid developmental stage apparently represented the ontogenetic advent of preservable exoskeletal calcification but, with respect to overall size of the smallest calcified individual or the development of somatic features, calcification was not congruent in all taxa (Speyer and Chatterton, 1990). The relationships between the number and size of individual segments and the overall size of the animal have yet to be explored in detail, but it is clear that the segment expression of the earliest protaspids of many taxa was restricted to the cephalic region, with the protopygidium—the terminal region composed of fused trunk segments at the posterior of the A/P axis—terminal, tiny, and dorsally undifferentiated (Fig. 5). Whether all cephalic segments were first expressed simultaneously or sequentially is currently unknown, expression apparently having occurred prior to preservable calcification. Subsequent molts witnessed both an increase in the size of previously formed cephalic segments, accompanied by significant modification of cephalic structure, and the anamorphic appearance of new trunk segments within the protopygidium, each of which shared a similar overall morphology. Hence the protaspid phase was characterized by two morphological trends. Firstly, while cephalic segments were stable in number, the appearance of the cephalon changed markedly during growth. Secondly, the protopygidium was characterized by the appearance of additional segments that increased their relative proportions relatively rapidly through growth, but which resembled one another closely in overall form.

The transition to the next major phase, the meraspid developmental stage, was defined by the appearance of an articulation between the cephalon and the trunk region, yielding a hinge-like body structure (Fig. 5). The advent of this phase was not developmentally homologous among all taxa with respect to numbers of segments in the trunk region. For example, many species transitioned into the meraspid phase with 3 or 4 trunk segments, but the cheirurid *Ceraurinella typa* apparently did not transition into the meraspid phase until it had 14 trunk segments (Whittington and Evitt, 1953). The caudal region was composed of fused segments and in the meraspid phase is known as the transitory pygidium. Newly expressed trunk segments are known to have first appeared towards the rear of this structure. This view was based on the site of first appearance of distinctive macropleural segments during ontogeny, and the subsequent appearance of additional segments behind them (Stubblefield, 1926) (Fig. 5). The thorax was first differentiated when segments were released, in a ratchet-like manner, from the anterior of the transitory pygidium.

The dynamics of segment accretion in the trunk region remain incompletely described, but were apparently quite complex in detail. The complement of segments that comprised the transitory pygidium continually changed as new segments appeared near the posterior, transitioned through, and subsequently budded-off from the anterior of the transitory pygidium. The balance of segment appearance and release rates varied during ontogeny among taxa, and some showed an early growth phase of incremental accretion of segments in the transitory pygidium, known as the accumulation phase (Kopaska-Merkel, 1987). This was followed by a phase in which the segment number declined, called the shedding phase, as segments were released from the anterior of the transitory pygidium into the thorax at a rate faster than their appearance near the posterior of the transitory pygidium. The balance of the accumulation and shedding phases varied among taxa, even those with the same total numbers of trunk segments (McNamara *et al.*, 2003). Much work remains to be done in documenting the details of trunk segment appearance and allocation, its relationship to overall body size with respect to the sizes of individual segments (Minelli *et al.*, 2003), and to the evolution of caudalization.

The transfer of segments from the transitory pygidium to the thorax continued throughout meraspid ontogeny, and the final phase of trilobite ontogeny, the holaspid phase, is generally defined to have begun at the point at which a stable number of thoracic segments was reached (Raw, 1925). An alternative definition for holaspis, being the stage after the full complement of trunk segments was expressed (Stubblefield, 1926), has not been generally applied because of the operational utility of Raw's (1925) definition and the fact that completion of the thorax and full expression of trunk segments were commonly coincident. The advent of holaspid phase is widely taken to mark the onset of adulthood, and is used in that sense in this paper although there is no morphological evidence of trilobite reproductive tissue or mode to support such a claim. A recent claim that the proetide *Aulacopleura konincki* retained the capacity to express new segments throughout life (Hughes and Chapman, 1995), including in a phase comparable to holaspis of other trilobites, is currently being re-evaluated. It appears likely that the holaspid phase of the great majority of, and perhaps all, trilobites was epimorphic in that the number of trunk segments remained constant despite continued growth and molting (Minelli *et al.*, 2003).

Trilobite ontogenetic sequences can be reconstructed most reliably in those cases in which morphological changes between molt instars were modest and incremental. Such gradual change apparently typified the majority of trilobite clades, and although there are some early growth stages that cannot be confidently linked to any adult form (Chatterton and Speyer, 1997), such cases are relatively rare. The transition between ''non-adult like'' protaspids, diagnostic of the Order Asaphida and inferred to live pelagically, and the ''adult like'' meraspids of the same species, presumed to be benthic, has been interpreted as an ex-
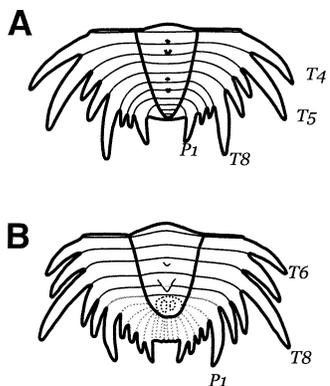
FIG. 6.   Two transitory pygidia of *Dentaloscutellum hudsoni* showing the trunk region divided into two morphological batches of segments prior to onset of holaspis. A. Degree 3 meraspid with the anteriormost seven segments destined to become part of the adult thorax, of which three prominent spines are labeled. P1 is destined to become the anterior segment of the adult pygidium. B. Degree 5 meraspid, with many segments destined to become the adult pygidium defined by a distinct morphology (smaller size, furrows less firmly incised) and a distinctly different rate of appearance: the rate at which these pygidial furrows became defined near the posterior of the pygidium greatly exceeded the rate of release of segments at the anterior. Modified from Chatterton (1971).

ample of metamorphosis, although this transition is not the radical reorganization of body patterning to which the term metamorphosis is commonly applied among extant arthropods (see Williamson, 1982).

A critical question from the point of view of the controls of segment specification is when during ontogeny did a trunk segment acquire its ultimate identity as an adult segment? This question can be answered in those cases in which the segments of the adult thorax and pygidium differed markedly in morphology. The meraspid transitory pygidia of the scutelluids *Dentaloscutellum hudsoni* and *Scutellum calvum* clearly show that, from their first appearance in ontogeny, segments that would later comprise the adult pygidium were distinctly different from those that would be released into the thorax (Chatterton, 1971) (Fig. 6). Hence identity as a thoracic or pygidial segment was specified prior to the onset of the holaspid phase. It is unclear whether this was the case among all trilobites—especially those in which adult thoracic and pygidial segments resembled one another closely and which show intraspecific variation in holaspid segment numbers. The occurrence of incompletely released segments at the anterior of the pygidium in some individuals belonging to these forms is of interest in this regard (Hughes and Chapman, 1995).

Limited evidence is available to assess whether the form of individual limbs was modified during ontogeny, but given the general homonomy of the adult biramous appendages any such changes were probably minor. This inference is supported by ontogenetic stability of limb form seen among meraspid molts of *Agnostus pisiformis* (Müller and Walossek, 1987).

TRILOBITE SEGMENT SPECIFICATION AT THE CELLULAR LEVEL

The sequential appearance of additional segments near the rear of the pygidium has been termed "teloblastic" by some authors (*e.g.*, Hessler, 1962; Hu, 1971; Størmer, 1942), implying a direct linkage between cell division in a sub-terminal generative zone (Patel, 1994) and the appearance of new segments. For such a pattern to be universally applicable to trilobites, we may expect different aspects of the expression of segmentation to be correlated and tightly controlled. Although this is generally true in trilobites there were mismatches between dorsal and ventral aspects of segmentation, as discussed above. Hence the appearance of segments or appendages during the ontogeny of trilobites cannot be assumed to directly mirror their cellular specification. Indeed, it has been argued, based on patterns seen in some Recent multisegmented arthropods, that the cellular primordial of all segments later to be expressed morphologically in trilobites may all have been specified early in ontogeny (Minelli, 2001; Minelli *et al.*, 2003). That said, the general congruence among trilobites in the numbers of dorsal segments and ventral appendages suggest that both patterns may share common aspects of specification, and the likelihood remains that the cellular primordia of segments later to become expressed in the exoskeleton or as appendages were specified sequentially.

TRILOBITE TAGMATA

Tagmosis refers to the partition of the serially homologous arthropod body plan into discrete regions, but not all specialists agree on the boundaries between tagmata, even within extant groups (Minelli *et al.*, 2003). With regard to trilobites, each of the adult cephalon, thorax, and pygidium have been considered as a distinct tagma (Burmeister, 1846), although the dynamic interchange of segments between fused and articulating portions of the pre-adult trunk has caused some to question whether the adult pygidium was really a distinct tagma or simply a "frozen growth zone" within a serially homonomous trunk (Minelli *et al.*, 2003). If the morphological expression of segments corresponded even approximately to their sequential cellular specification, the segments that comprised the adult pygidium could simply be interpreted as the complement that happened to comprise that structure at the point adulthood was reached. According to this view segments that may have had the potential to become functional thoracic segments were captured or "frozen" as part of the adult pygidium by whatever control mitigated onset of epimorphosis (here we do not use "growth zone" to imply a region of undetermined cells, as is common among developmental biologists, but rather simply as a morphological category). As mentioned above, this does not appear to have been the case, at least in scutelluids, in which the adult thoracic identity was expressed even while the segments were part of the pre-adult transitory pygidi-

um. Whether fate as a thoracic or pygidial segment was preallocated among all trilobites is a fascinating question, requiring detailed analysis of growth modes in species, such as *Aulacopleura konincki*, that showed intraspecific variation in the numbers of thoracic segments. The evolution of modularization of the trilobite trunk lies at the heart of this question, because if some trilobites did not have tightly controlled pre-specification of segment fate this suggests that a fundamental aspect of body plan specification may have been modified during the evolution of the group.

Ventral appendages suggest a different pattern of tagmosis, especially if tagmata are defined as zones of functional specialization, as is commonly the case when considering arthropod appendages (*e.g.,* Flessa *et al.,* 1975). According to this view, the only tagmatic distinction within the cephala of most trilobites is that between the uniramous antennae and the subsequent biramous appendage pairs. The terminal uniramous cerci of *Olenoides serratus* would constitute another functional appendage tagma. The situation among the best-preserved trilobite appendages, those of *Agnostus pisiformis*, is controversial (see above).

During trilobite ontogeny additional dorsal segments were first expressed near the posterior of the pygidium, but the exact position of appearance is hard to determine. It has generally been assumed that the appearance of new segments corresponded to their sequential cellular specification in a "teloblastic" growth zone authors (Størmer, 1942; Hessler, 1962; Hu, 1971). By analogy with modern arthropods this zone was inferred to lie at the anterior of a terminal ventral body segment—the telosoma (Lauterbach, 1980)—and the antenniform cerci of *Olenoides serratus* might be interpreted as belonging to that segment (H. B. Whittington, personal communication, 2002). The tiny, segment-poor pygidia seen in some basal redlichid trilobites include this terminal segment and the one just expressed at its leading margin.

In summary, the major A/P body divisions that seem of fundamental morphological, ontogenetic, and inferred functional significance to all trilobites are the antennae/biramous appendage transition within the cephalon, the cephalic/trunk transition, and the possible presence of a terminal trunk segment. Superimposed upon this pattern are the profound modifications of adjacent dorsal segments within the cephalon, the subdivision of the trunk into allocated batches of segments seen in some trilobites (although these distinctions are never as profound as those among cephalic segments), and the unusually proportioned "macropleural" trunk segments of some trilobites.

It should be noted that many trilobites show other variations, such as axial nodes or spines (Fig. 6), among trunk segments that might be used to advocate division of the trunk into additional sub-regions. For example, Sundberg (2000) divided the adult thorax into anterior and posterior regions based on posterior axial nodes seen in three species. The difficulty with such interpretations is that the distributions of such features are highly variable (or, more commonly, absent) among trilobites, weakening any case that they are integral features of trilobite tagmosis. Moreover, features of segmentation such as these were commonly modified during ontogeny. For example, the segments of the transitory pygidium of *Dentaloscutellum hudsoni* apparently showed periodic variation in the length of the pleural spines (Fig. 6) in addition to various axial nodes, but by the time these segments were part of the adult thorax such differences had disappeared (*c.f.,* Fig. 3B). Likewise, Sundberg (2000) also recognized the occipital segment and anteriormost pygidial segment to represent tagmatic distinctions within trilobites. The occipital segment of many trilobites is, in some ways, of intermediate morphology between the cephalon and the thorax (perhaps necessary for functional reasons), but the anterior pygidial segment is most similar either to other pygidial segments in those "two batch" taxa with markedly modified segments in the adult pygidium, or to all trunk segments in those forms with an uniform trunk segment morphotype. It is unique when it happens to be macropleural, but there is no reason to think that macropleural segments were preferentially situated at this position.

INFERRED DEVELOPMENTAL CONTROLS OF TRILOBITE TAGMOSIS

This discussion of trilobite tagmosis highlights some key features of trilobite body structure and its development. Many of these features have counterparts among extant arthropods and this fact invites a consideration of trilobite body regionalization from the perspective of current knowledge of arthropod development. The discovery of conserved aspects of the development of the A/P axis throughout the Metazoa pointed to the deep homology of Hox-gene controls, and unique aspects of Hox gene identity and number characterize individual clades. For example, the *Ultrabithorax* gene is apparently synapomorphic of the ecdysozoan clade, and the basal arthropod condition was a complement of ten Hox genes (see Akam *et al.,* 1994; Warren *et al.,* 1994; Averof, 1997; Grenier *et al.,* 1997; Carroll *et al.,* 2001; Hughes and Kaufman, 2002*a, b*). It has been clear for some time that trilobites, being arthropods, not only possessed the Hox genes characteristic of the triploblasts as a whole, but were likely to have possessed the particularities of Hox genes share among extant euarthropods (Hughes and Chapman, 1995). More recently, an explicit attempt was made to relate the morphology of adult trilobites to zones of Hox gene expression (Sundberg, 2000). This paper offers an evaluation of the Sundberg model by considering correlations known to exist between regions of Hox gene expression and morphological features among extant arthropods and their relatives, and considers some broader aspects of the evolution of trilobite tagmosis.

Attempts to directly relate developmental controls witnessed among modern organisms to fossils are sub-

ject to myriad difficulties (Minelli *et al.*, 2003). For example, much of our knowledge of arthropod developmental genetics comes from studies of a select group of model organisms, of which the holometabolous fly *Drosophila melanogaster* is a prominent example. Developmental regulation in this fly is peculiarly modified in association with its syncytial organization in the earliest embryonic stage and with larval metamorphosis, and this has resulted in cooption of certain Hox genes into unique roles related to these unusual developmental patterns (Akam *et al.*, 1994; Telford and Thomas, 1998*b*; Telford, 2000; Hughes and Kaufman, 2002*a*, *b*). However, until comparative analysis of the development of other arthropods permitted identification of this derived modification, it appeared that the Hox gene array seen in *Drosophila* might be the basal arthropod condition. Accordingly, Sundberg (2000) assumed that the eight Hox genes present in *Drosophila* represented the ground state of arthropods as a whole, rather than the ten Hox genes that are considered pan-arthropodal today (Akam, 2000; Hughes and Kaufman, 2002*a*, *b*). This issue is important because Sundberg (2000) then equated the inferred expression domains of these eight genes to an equivalent number of regionalized zones within the trilobite body. This implies that an unique Hox gene or combination of Hox genes (Fig. 7A) specified each region. An alternative approach, presented herein, seeks to identify aspects of tagmosis that can be considered general among trilobites and other arthropods, and then use these to consider possible ties to developmental controls, while acknowledging that connections between Hox gene expression domains and arthropod tagmosis are not always direct.

Given our incomplete knowledge of the developmental genetics of extant arthropods any attempt to infer aspects of trilobite genetics is bound to encounter pitfalls, but this does not invalidate attempts to view the trilobite body plan in the broader context of the evolution of arthropod tagmosis. Indeed, information from fossil arthropods could be critical for evaluating the evolutionary history of arthropod body patterning (see Akam *et al.*, 1994, p. 212; Budd, 1996, 1998, 2002). Furthermore, recent advances in knowledge of the distribution of Hox genes within the Ecdysozoa allows firmer constraints to be placed on the likely complement present within extinct members of the clade (Averof, 1997; de Rosa *et al.*, 1999; Grenier *et al.*, 1997), and how they may have been deployed.

Given that trilobites probably had 10 Hox genes what, if anything can we say about how might these have been used? This can be considered in the context of patterns of trilobite tagmosis, moving posteriorly along the A/P axis.

Uniramous/biramous appendages

The transition between the uniramous antennae and first biramous appendage pair seen in trilobites is mirrored in wide range of arthropods. Among these, the antennae form in the absence of a Hox gene expression
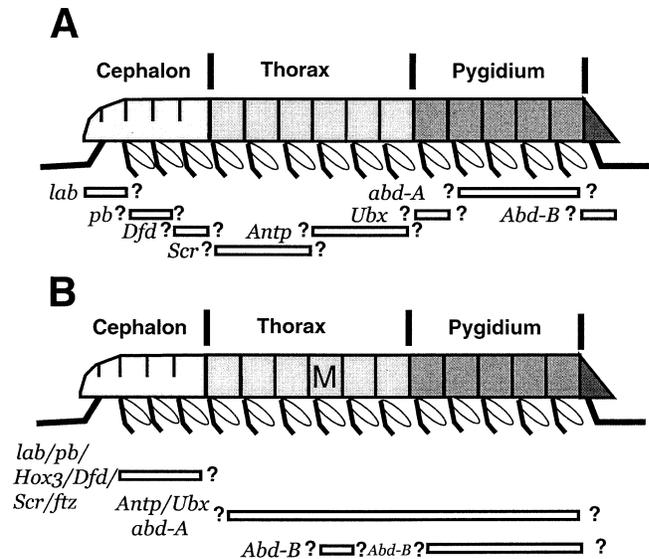

FIG. 7. Alternative inferred Hox gene expression domains in trilobites mapped with respect to major body plan divisions in the dorsal exoskeleton and ventral limbs. This idealized form is shown as having posterior cerci, as in *Olenoides serratus*, but is based on the exoskeletal segmentation pattern of adult *Shumardia (Conophrys) salopiensis*. A. Hox gene expression in relation to trilobite body plan discussed in this paper, based on the views of Sundberg (2000). Note that the expression domains of individual Hox genes may extend beyond the zones specified, but that the model assumes that particular Hox genes have a critical role in specifying each particular body region. B. One alternative model based on generalized correlations between Hox gene expression and tagmosis patterns seen among extant arthropods. The major features are the absence of Hox domains in regions where uniramous antennae and cerci are specified, concentration of anterior Hox gene expression domains within the cephalon, broad overlap among domains with uncertain boundaries, and a possible tie of *Abdominal-B* expression to the macropleural segment. Numerous alternative schemes could be posited (see text).

domain (Akam, 2000), and uniramous antennae is the state to which appendages default when Hox genes are deleted (Beeman *et al.*, 1993). If trilobite and mandibulate first antennae are homologous and a similar control applied in trilobites, trilobite antennae could be interpreted as a region in which Hox genes were not expressed (Fig. 7B). It is possible that the terminal trunk antenniform cerci of *Olenoides serratus* also represent a region in which Hox genes did not play a role in specifying appendage morphology. Among modern arthropods some cercal segments do express Hox genes (Peterson *et al.*, 1999) but in the case of *Olenoides serratus* the cerci, apart from bearing small spines, appear to be identical in form and size to the anteriormost antennae. If correct, this view could support interpretation of the terminal trunk region as a distinct tagma. Fossilized basal arthropods such as *Kerygmachela* (Budd, 1999*b*) also show cerci, and it is possible that these structures and antennae represent the first jointed arthropod appendages (Akam, 2000), although recent evidence suggests that a leg-like structure, as opposed to antennae, may be the ground state of ventral appendages (Casares and Mann, 2001). Pos-

terior cerci do not appear to be ubiquitous among basal arachnates (Edgecombe and Ramsköld, 1999), and so the prominent cerci in *Olenoides serratus* apparently represent a derived condition in this case. The suggestion that antennae could mark the absence of Hox gene influence on appendage form in trilobites contrasts with the view of Sundberg (2000) who saw the anterior lobe of the glabella and the frontal area of trilobites to correspond to a Hox expression domain. Assuming colinearity (see below), Sundberg's model suggests this is the anteriormost gene of the *Drosophila* Hox cluster, *labial*.

Cephalon

The cephalic/trunk divide marks a sharp morphological discontinuity in the dorsal exoskeleton of trilobites and, apparently, also in the pattern of ontogenetic appearance of segments. This discontinuity is also generally consistent with regard to the number of cephalic appendages. However, it does not correlate with a marked change in appendage morphology (except, perhaps, in *Agnostus pisiformis*). Assessing the homologies of particular segments among arthropods remains difficult, even with the aid of molecular markers because, inevitably, an initial criterion for alignment has to be adopted (*e.g.,* Damen *et al.*, 1998; Budd, 2002). In trilobites this is particularly difficult, due to the generally homonomous nature of the biramous limbs, and disagreements about the number of preantennal segments. Different criteria for homology suggest alternative patterns, discussed below.

The number of cephalic limbs might be used as a basis for estimating homologies of trilobites with extant arthropods, and thus to infer likely Hox gene expression patterns. In the trilobite head there appears to have been at least three and no more than four biramous appendages. This would equate the cephalic/trunk boundary, at least approximately, to the head/thorax boundary of insects and crustaceans. The homology with chelicerates based on segment counts is less clear because of the absence of antennae in this clade (Damen *et al.*, 1998), but the posterior boundary of the trilobite cephalon would likely lie within the chelicerate prosoma, perhaps near the third leg. However, the pattern of segmentation expressed in the trilobite dorsal exoskeleton might suggest the presence of two or more appendage-less segments anterior to the antennae and so homologies based strictly on appendage number and order of segments should be treated with caution (see also Sundberg, 1995).

An alternative criterion for assessing segment homologies relates to the profound morphological and, apparently, ontogenetic distinction between the cephalic and trunk segments of trilobites. The division between early and broadly synchronous specification of head segments, and the sequential appearance of trunk segments, is a common developmental feature among arthropods (*e.g.,* Anderson, 1982; Freeman, 1991; Sekiguchi *et al.*, 1988; Davis *et al.*, 2001, fig. 5). There is some evidence that such a division also

reflected the initial controls of early embryonic patterning both in arthropods with the sequential appearance of trunk segments (including the "short germ band" insects (Tautz *et al.*, 1994) and even also in long germ band forms such as *Drosophila* that specify all segments simultaneously in the syncytium (Cohen and Jürgens, 1991). Damen and others (1998, p. 10669) have used these patterns to correlate the prosoma/opisthosoma division in spiders with the region anterior of parasegment 4 in *Drosophila*, which equates to the first thoracic segment in this fly. Although different segment homologies might be postulated, these studies all support the notion that the cephalic/trunk boundary region generally equates to a fundamental boundary between tagma among euarthropods.

How, then, might trilobites have deployed their Hox genes? The conserved colinearity of Hox gene expression domains is of relevance here (see Carroll *et al.*, 2001). One of the most remarkable facts about Hox genes is that the order of the *Drosophila* Hox genes as arranged on chromosomes, and the sequence of Hox gene domains along the A/P axis of the fly, are coincident. The same A/P sequence of Hox gene domains appears to be widely conserved among triploblasts. Hence it is highly likely that the deployment of trilobite Hox genes followed the same general A/P order as is seen among other arthropods. With regard to trilobites, the lack of differentiation among trilobite biramous appendages might indicate that all belong to a single homeotic domain—a suggestion that has been mooted, at least for the trunk segments of trilobites (Budd, 1999*a*, p. 330). This is because the morphological consequences of Hox gene expression are most evident in the distinctions among appendages of extant arthropods (Abzhanov and Kaufman, 2000). The noticeable, though relatively slight, differences among cephalic appendages in *Agnostus pisiformis* may be of relevance in this regard. Crustaceans, insects, myriapods, and chelicerates all express *labial, proboscipedia, Deformed*, and *Sex combs reduced* and their homologs exclusively within the head region or near the head/trunk boundary (Carroll *et al.*, 2001; Hughes and Kaufman, 2002*a, b*) and *Hox3* and *fushi tarazu* are also expressed in the heads of myriapods and chelicerates (Hughes and Kaufman, 2002*a, b*). Hence it is possible that all these genes had expression domains within the trilobite cephalon (Fig. 7B).

Sundberg (2000) interpreted the cephalon to be composed of three domains of Hox gene expression, presumably *labial, proboscipedia*, and *Deformed* (Fig. 7A). The expression domains of these genes probably did lie within the cephalon, but the possibility that other Hox genes were also expressed in that region remains open. There is no reason to suppose that the occipital ring was specifically related to the expression zone of the third of the *Drosophila* Hox cluster—*Deformed*, as a strict interpretation of Sundberg's (2000) scheme would imply.

One general relationship between arthropod limbs and Hox genes appears to be that patterns of Hox gene

expression are more sharply localized in forms with high degrees of limb tagmosis (Abzhanov and Kaufman, 1999a, b, 2000; Hughes and Kaufman, 2002a, b). Hence the expression domains of individual Hox genes in the anterior region of crustaceans shows a higher degree of localization than that seen in the chelicerates (Damen *et al.*, 1998; Telford and Thomas, 1998a), which are characterized by less marked cephalic limb tagmosis (Wills *et al.*, 1997). Given the relatively low degree of cephalic biramous limb differentiation seen in trilobites (even when accepting *Agnostus pisiformis* as a member of the clade), and the phylogenetic placement of trilobites within the arachnates, it may be that the overlap of trilobite cephalic Hox gene expression domains were more similar to those of the chelicerates (Damen *et al.*, 1998; Telford and Thomas, 1998a) than to those of the more highly modularized crustaceans and insects (Fig. 7B). The functions of these genes, in the absence of marked limb regionalization (except, perhaps, in *Agnostus pisiformis*), may have related to the profound morphological differences among the dorsal segments of the cephalon, and/or to cell specialization in the mesoderm or nervous system. In this regard it is notable that the majority of the vital organs of trilobites including digestive, sensory, and possibly reproductive organs (Fortey and Hughes, 1998; Whittington, 1992), were concentrated within the cephalon. This was a necessary condition, as most vital functions must have been operative shortly after hatching, which may have coincided with the onset of calcification.

Given recent advances in developmental genetics, and the wealth of ontogenetic series now available for trilobites, a fresh review of trilobite cephalic segmentation patterns is warranted for it is possible that features may exist that will anchor putative serial homologies more securely.

Trunk

Possible linkages between Hox gene expression domains and the trilobite body plan become more difficult to evaluate toward the posterior, because the zones of expression of Hox genes generally expressed in the arthropod trunk (*Antennapedia, Ultrabithorax, abdominal-A,* and *Abdominal-B*) are apparently more variable than those of the cephalic Hox genes. This is perhaps related to the homonomous nature of the trunk region of many arthropods.

This difficulty is compounded by uncertainty about the homology of the thorax of adult trilobites. It is not clear what portion, if any, of the trilobite trunk was homologous with the thorax, as it is understood in crustaceans or in insects, (Minelli *et al.*, 2003), or to the opisthosoma of chelicerates. Nor is it clear in what, if any, sense the trilobite pygidium equated to the crustacean abdomen (contra Cisne *et al.*, 1980). Sundberg's (2000) scheme broadly equated the trilobite thorax with that of insects and crustaceans, for he divided the trilobite thorax into an anterior batch of segments that on the basis of his inferred Hox domain/body re-

gion correlation would be the *Sex combs reduced* expression domain, and a posterior batch of segments that would be the *Antennapedia* expression domain. This cannot easily be refuted on the grounds of homologies between Hox expression and individual trilobite segments because the termination of Hox gene expression domains may occur amid batches of homonomous segments (an example is the posterior of *Antennapedia* expression in centipedes [Hughes and Kaufman, 2002a]). Nevertheless, the division of the adult trilobite thorax into two discrete portions based on morphology, the basis for Sundberg's (2000) inference, is untenable as a general aspect of the trilobite body plan and this division cannot be considered of general significance to trilobite tagmosis. Furthermore, the fundamental similarity of all trilobite pre-terminal trunk segments, both in exoskeletal and limb structure, makes it difficult to see the trunk region as comprised of distinct, highly regionalized domains of Hox gene expression, such as envisioned by Sundberg (2000) (see also Budd, 1999a).

On the basis of the plausible head/trunk homology with other arthropods, the anterior boundary of the expression of the anterior trunk Hox genes, such as *Antennapedia* may have been situated near the trilobite cephalic/trunk boundary rather than toward the posterior thorax, but it is difficult to constrain where its domain of expression might have ended, and where the anterior of the *Ultrabithorax* and *abdominal-A* expression domains began (Fig. 7B). The anterior of *Ultrabithorax* expression occurs within the thorax of insects and crustaceans and at the anterior of the trunk of a centipede, and the evolution of the position of *Ultrabithorax* and *abdominal-A* expression can be related to major morphological modifications of limb structures among crustaceans (Averof and Patel, 1997). Such evidence as is available from chelicerates suggests that the anterior boundary of *Ultrabithorax* expression is consistently expressed within the second opisthosomal segment, even in basal crown group members such as limulids (Popodic and Nagy, 2001). However, the segmental homologies of the opisthosoma and the adult trilobite pygidium remain unclear. A firmer basis for speculating on the Hox controls of the trilobite cephalic/trunk boundary awaits further characterization of the Hox gene expression domains among arthropods and onychophorans, and further resolution of phylogenetic relationships among basal crown group arachnates and myriapods.

Sundberg's (2000) model was based on the body plan of an adult trilobite, but has implications for Hox gene expression domains earlier in ontogeny. A segment near the posterior of the adult thorax would have passed through the meraspid transitory pygidium during anamorphic ontogeny. The three morphological zones of the adult pygidium inferred, according to Sundberg's model (2000), to be the *Abdominal-B, abdominal-A* and *Ultrabithorax* Hox gene expression domains (Fig. 7A), can also be distinguished within the transitory pygidium. This is because they are defined

by relative position rather than by unique morphological aspects of individual segments. Hence grounds exist for questioning whether these morphological divisions actually represent tagmatic divisions. If they do, and each of these zones was specified by a Hox gene expression domain, then one of two explanations is possible. If each topological position was tied to a specific Hox gene, then individual segments initially expressed posterior Hox genes, and then, during ontogeny, switched to express anterior Hox genes as they moved forward relative to the terminal zone. Although the boundaries of Hox gene expression zones may shift during ontogeny (*e.g.,* Castelli-Gair, 1998; Abzhanov and Kaufman, 1999*b*; Hughes and Kaufman, 2002*a, b*), given the broadly homonomous structure of trilobite trunk segments it seems unlikely that an individual segment would pass through as many as five discrete Hox gene expression domains during ontogeny on its way to the anterior of the adult thorax. Alternatively it is possible that morphologically defined regions considered in the Sundberg model to relate explicitly to zones of gene expression in adulthood bore no relation to Hox gene expression in pre-adult ontogeny, but such an explanation would undermine the basis for equating morphology with gene expression domains in adulthood.

Can we place any constraints on the likely Hox gene expression domains in the trunk region? Firstly, the homonomous nature of trunk segments may suggest overlapping zones of Hox gene expression domains. Secondly, there is a persistent tendency for Hox genes to influence batches of segments, as opposed to individual segments (Akam, 2000) (for a possible exception, see below). Thus the division of the trunk into regions of distinct segment identity in such trilobites as scutelluids (Fig. 3B) may be congruent with expression of a Hox gene related control (Fig. 8). The fact that some trilobites varied in the numbers of thoracic segments in adulthood, implying relatively flexible control of trunk segment fate, while in others fate was more tightly determined, could suggest that aspects of Hox gene expression and their downstream effects were modified during the evolution of the group. The distinct adult thorax and pygidia evident in some trilobites probably do deserve recognition as separate tagmata, but this may not be the case among all trilobites (Minelli *et al.*, 2003).

The condition, such as seen in *Aulacopleura konincki* (Fig. 3A), in which all trunk segments appeared as a single morphological batch, occurred widely across the Trilobita, and was apparently the basal condition for the clade as a whole (Fig. 8A). Trilobite evolution repeatedly witnessed departures from this condition, and this apparently occurred according to either of two modes. In the first mode, exemplified by some Early Cambrian olenelloid (Fig. 2) and emuellid trilobites, the thoracic region of adults was divided into two batches of similar segments (the prothorax and the opisthothorax), and the adult thoracic/pygidial divide, situated very close to the posterior of the animal, ap-
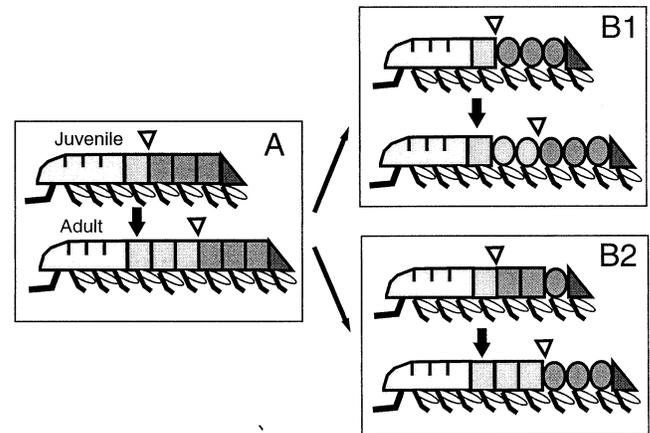

FIG. 8. Two patterns of modularization of the trunk segments of trilobites. The contrast in shading and open arrows within the trunk region represent the boundary between freely articulating thoracic segments and the fused segments of the caudal plate (transitory pygidium or pygidium). Each box shows a degree 1 meraspid as the upper figure, with four trunk segments plus the terminal piece (triangular). The lower figure represents an holaspid with three thoracic segments and three pygidial segments plus the terminal piece. In A, the most common and apparently basal condition of the clade (Fig. 3A), all trunk segments shared a similar morphology, represented by rectangular cells. In B1 and B2 two trunk segment morphotypes are expressed during ontogeny, the second of which represented by oval cells. In B1 the position of the transition between morphotypes did not coincide with the boundary between freely articulating and fused trunk segments in adulthood (Fig. 2). This condition characterized some olenelloid and emuellid trilobites, known from Lower Cambrian rocks. The upper figure in box B1 is hypothetical as articulated meraspids are poorly known in these taxa. In B2 the transition between segment morphotypes corresponds with the boundary between freely articulating and fused trunk segments in adulthood (Fig. 3B). This condition characterized certain derived trilobite clades, common in Ordovician and later rocks. The modularization the trunk into two batches of segments apparently occurred repeatedly and independently during trilobite evolution and may suggest the iterative modification of the boundary between the domain of expression of Hox genes, or several such domains. The numbers of trunk segments in the adults of these stylized examples have been reduced for clarity.

parently did not coincide with a marked shift in segment morphology (Fig. 8B1) (see Whittington *et al.*, 1997, p. 410). The second mode occurred in scutelluid and in some lichid trilobites, in which adult trunk also displayed two distinct batches of segment morphotypes, the boundary of which was consistently correlated with the boundary between the thorax and the adult pygidium (Fig. 8B2). This distinction is consistent with the observation that later, derived clades were more caudalized, such that their adult pygidia contained many more segments. It could be that the boundary of the pro- and opisthothorax of olenelloids is homologous with the thoracic/pygidial divide of these more caudalized trilobites, at least in respect to the controls of body patterning. These early clades were not the primitive sister taxa of the derived lichids or scutelluids, nor were lichids and scutelluids close relatives. Hence it appears that trilobite evolution witnessed repeated experimentation in the developmental controls of trunk segment regionalization, with the

transition from the ''one batch'' condition (Fig. 8A) to the ''two batch'' condition (Fig. 8B1/2) occurring repeatedly and independently several times during the history of the group. As such trilobites may offer an opportunity for exploring the evolution of a major aspect of body plan organization in the aftermath of the Cambrian radiation (Hughes, 2003).

Evolutionary transitions among tagmatic boundaries across modern arthropods apparently relate to shifting zones of Hox gene expression (*e.g.,* Averof and Patel, 1997) and perhaps also to the regulation of Hox expression during ontogeny (Abzhanov and Kaufman, 1999*b*). It is possible that similar mechanisms pertained in trilobites with regard to the evolution of increased regionalization across the thoracic/pygidial boundary, although the particular Hox genes involved cannot be identified with confidence. Whether the thoracic/pygidial boundary constitutes a fundamental divide in Hox gene expression domains in all trilobites (as claimed by McNamara *et al.* [2003]) is questionable because the morphology of segments either side of this boundary was similar in most trilobites. This point is reiterated by the dynamic nature of the trunk region during pre-adult ontogeny (Minelli *et al.*, 2003), and the truly transitory compliment of segments within the caudal plate during meraspis. With regard to the form of trunk segments it appears that in at least some two batch taxa the regional fate of segments in adulthood was evident early in larval ontogeny, long prior to attainment of the epimorphic articulation state. In these cases the form of the segments that were eventually to become the adult pygidium was clearly independent of their state as fused or articulating segments. What controlled onset of the epimorphic articulation state among trilobites is unknown. Possibilities include either a specific predetermined fate for each individual segment (presumably mitigated by a different control from that which specified segment morphology), or a ''regional'' control that constrained the topographic position of the boundary with respect to overall body proportions as the individual reached the meraspid/holaspid transition. In such a situation cells in segments within the thoracic/pygidial transition zone would have remained receptive to new regulatory cues. Morphological transitions such as these may have been effected by ontogenetic changes in the expression of transcription factors, such as a Hox gene or genes of which *Abdominal-B* is a candidate based on its expression among extant arthropods. Documenting the co-evolution of different aspects of segmentation may be instructive in understanding the evolution of the two batch morphotype (Hughes, 2003).

Regardless of the specific of the controls of the thoracic/pygidial boundary, they were at least partially independent of the controls determining modularization into the ''two batch'' trunk condition. Similarly the transition into two batches of exoskeletal trunk segments is not obviously mimicked by a sharp transition in trunk appendage morphology, at least in *Agnostus pisiformis* (it should be reiterated that scutelluid and lichid trunk appendages are unknown, and any within the opisthothorax of olenelloids and emuellids were surely much smaller than those of the prothorax). The evolution of modularity within the trilobite trunk may have been a step-wise process in derived clades such as scutelluids and lichids, building firstly upon the functional distinction between fused and articulating exoskeletal segments, but perhaps not necessarily accompanied by a sharp transition in ventral appendage form. In this respect the transition may have been akin to the correlated progression model advocated for basal arthropod evolution (Budd, 1996), in which fundamental transitions in body plan evolution are thought to have been achieved through a graded series of functional intermediates, rather than from sudden macroevolutionary changes affecting multiple characters synchronously.

Macropleural segments

Among modern arthropods expression of the *Abdominal-B* Hox gene appears to be correlated with the position of the genital opening (Averof and Akam, 1995; Damen and Tautz, 1999; Akam, 2000; Minelli, 2001). The reproductive tissues of trilobites are entirely unknown, but it has been speculated that the position of macropleural segments marks the position of the genital opening (Harrington, 1959, p. O73; Sundberg, 1995). This argument was based on the fact that the genital opening of modern arthropods is commonly coincident with unusually modified segments or segment pairs. While there is no direct evidence by which to assess this in trilobites, it seems improbable that the genital opening was terminal in the trunk region in all species. This is because in *Triarthrus eatoni* the posterior most appendage pairs were tiny and, apparently, all of similar form. It seems unlikely that so critical a structure as the genital opening would have been placed in a region of tiny subterminal appendages. Furthermore, indirect evidence based on phylogenetic relationships may suggest that the majority of trilobite tissues involved in producing and storing gametes were situated cephalically (Fortey and Hughes, 1998), far from the terminal trunk region. Thus it remains plausible that trilobite macropleural segments did coincide with the genital opening. If *Abdominal-B* is indeed consistently expressed in this zone in extant arthropods (Averof and Akam, 1995; Damen and Tautz, 1999), this may also have been the condition in trilobites (Fig. 7B). Functional reasons for why the genital opening should be situated at the macropleural segment remain obscure, and the common absence of macropleural segments must be acknowledged. It should be noted that the relative positions of macropleural segments within the trunk varied among trilobites, with some near the anterior of the thorax, some near the posterior, and some within the pygidium.

Terminal or Sub-terminal Cerci?

The single most striking variation in trilobite tagmosis is the presence of cerci in *Olenoides serratus*.

Their absence appears to be firmly established in taxa such as *Triarthrus eatoni* and *Phacops* (*Chotecops*) *ferdinandi*. In both these taxa the terminal appendage pairs were apparently biramous, although the tiny size of the posteriormost appendages inhibits clear determination. Whatever their construction they could not have been functionally analogous to the extended cerci in *O. serratus*. The absence of the well-developed cerci can be viewed in various ways. The terminal tagma may simply been of small relative size in most trilobites, and only seen in *O. serratus* because the terminal tagma was large in that species. This is here called the "terminal cerci" model.

An alternative way in which to view the cerci is that they represent the terminal appendage pair of the trunk region, and that they lay to the anterior of the zone within new segments were expressed morphologically. This is the "sub-terminal cerci" model. If this is correct, *O. serratus* could be viewed has having expressed a complete complement of trunk segments, ensuring that each of the segments obtained complete development in both form and size by later in the holaspid developmental phase. This view receives some support from Whittington's (1975) opinion that all appendage pairs were fully developed in adults of this species. On the other hand, it is seemingly in conflict with apparent insertion of additional biramous appendages anterior to the cerci during holaspid growth (Whittington, 1975), and the mismatch between dorsal and ventral segment numbers in the pygidium.

If the "sub-terminal cerci" model is correct, this pattern might indicate two different growth strategies in trilobites. In *O. serratus*-type development the trunk region deployed its full complement of segments. This could have been coincident with the precise allocation of segments to the thorax or adult pygidium (as in those derived trilobites with two batches of trunk segments), because regulation of the precise size and shape of all segments may have been necessary in such forms to effect encapsulated enrollment. (This argument would not apply to the multisegmented olenelloids and emuellids, which could not encapsulate.) In *T. eatoni*-type development the full potential of segment generation was never achieved and the adult pygidium merely represented a "frozen growth zone" (Minelli *et al.*, 2003). In this type of growth the onset of holaspis would presumably have been partially independent of the numbers of trunk segments differentiated per se, and may be more characteristic of those trilobites, such as *T. eatoni*, in which thoracic and pygidial segments apparently belonged to a single batch and in which there was intracollectional variation in segment numbers among adults (Cisne, 1973; Hughes *et al.*, 1999).

The expression of cerci in the absence of Hox gene control, as considered above, favors the "terminal cerci" model because it suggests that the cerci do equate to a different tagma (an opinion maintained by Prof. Whittington, personal communication, 2002), but these ideas may be tested more definitively by further anal-

ysis. Examination of the extensive new collections of *Olenoides serratus* from the Burgess Shale may reveal whether cerci appeared in ontogeny prior to specification of the most posterior pair of biramous appendages. Similarly, detailed examination of when, in ontogeny, the final number of segments is determined in those trilobites showing intraspecific variation in thoracic segment number will be critical in determining if individual trunk segments in "one batch" forms have a particular developmental fate. An opportunity exists to examine this in detail in the Silurian proetide *Aulacopleura konincki*.

TRUNK SEGMENT NUMBERS

Trilobites modified their total numbers of trunk segments profoundly during evolution and this capacity was apparently exploited most fully early in the evolutionary history of the clade (Minelli *et al.*, 2003). In fact, derived clades were characterized by higher and more stable total numbers of trunk segments (Raymond, 1920; Stubblefield, 1959; Hughes *et al.*, 1999). There has been continuous argument about whether the basal arthropodal condition was one of many or few segments (*e.g.,* Raw, 1953; Akam, 2000; Minelli *et al.*, 2003). Trilobite evolutionary history draws attention to the capacity of an early clade of euarthropods to vary profoundly in trunk segment numbers, rather than be defined by large or small numbers per se (Akam, 2000). Selection pressure for encapsulated enrollment in order to foil predators (McNamara, 1988; Hughes *et al.*, 1999) remains a candidate explanation for why later trilobites showed reduced intraspecific variability in the numbers of trunk segments. This is because most of the early forms with very large numbers of trunk segments could only partially enroll, and could not have encapsulated (Bergström, 1973*a*). They may thus have tolerated greater flexibility in trunk segment specification. The relationship between this trend, the increased caudalization (*i.e.,* proportion of the trunk segments allocated to the adult pygidium) long observed in trilobites (Raymond, 1920; Stubblefield, 1959; Fortey and Owens, 1997), and the evolution of developmental controls remains to be explored. Increased caudalization may been another way of foiling predators by limiting the numbers of articulations between segments to a smaller proportion of the entire trunk, and thus reducing the number of surfaces along which rupture could easily occur.

TRILOBITES AS BASAL EUARTHROPODS?

Although the Trilobita had distinctive synapomorphies and apparently nested within a clade of euarthropods (Edgecombe and Ramsköld, 1999; Budd, 2002) the question of their overall proximity to a basal euarthropod condition remains unanswered. The suggestion that trilobites were among the most morphologically derived euarthropods (Wills *et al.*, 1997) is likely an artifact of the operationally expedient but biologically tenuous assignment of *a priori* equal weighting to all characters (Budd, 2000). This is be-

cause features of basic body plan design of trilobites—such as the patterns of exoskeletal and limb tagmosis discussed herein—are less modularized than those witnessed among many modern arthropods. Nevertheless, uncertainties in the resolution of higher taxonomic relationships among euarthropods, and in particular the position of the Myriapoda, place limits on which major features of the trilobite body plan may be judged representative of a basal euarthropod condition. Features of the Trilobita that may bear on current thinking on this matter include the following: 1) a fundamental body division into a stable and differentiated cephalon and a dynamic trunk region composed of broadly homonomous segments, 2) preoral antennae followed by homonomous leg appendages, of which there were apparently three postoral pairs within the cephalon, 3) morphological expression of segments in the trunk region proceeding in an anamorphic (step-like) manner late into ontogeny, 4) dynamic release of segments from the terminal caudal region to the anterior portion of the trunk. Many of these features were likely shared with other basal arachnates and with myriapods (Minelli *et al.*, 2003).

Perhaps the most striking difference between the Hox gene expression patterns of chelicerates and those arthropods with specialized gnathal cephalic appendages is that of the broadly overlapping Hox domains in chelicerates. Myriapod Hox gene expression domains were apparently intermediate between the chelicerate and crustacean/insect condition (Hughes and Kaufman, 2002*a*). Based on current phylogenetic understanding it is possible that the intermediate state seen in myriapods is the basal condition for euarthropods. However, cephalic appendages of extant myriapod are clearly dedicated to particular roles in feeding. Perhaps a more likely scenario is that the chelicerate condition of overlapping Hox domains is indeed basal, and the myriapod condition is derived, regardless of the relationship of myriapods with the crustacean/insect lineage (Fig. 1).

Sloppy Hox Deployment as Condition of Basal Trilobites?

McNamara (1997, p. 54) argued that the patterns of expression among Hox genes in trilobite evolutionary history were "pretty wayward early on, becoming more settled as the group evolved." This view supposed that number of trunk segments, which was most variable among early trilobites, was under Hox gene control. Among modern arthropods the role of Hox genes is understood most clearly with regard to regional differentiation rather than opposed numbers of segments per se, which commonly relate to other genetic controls, upstream of Hox expression (Carroll *et al.*, 2001). Based on the associations inferred herein there is no clear evidence to suggest that Hox gene expression was more variable among early, as opposed to later, trilobites. While the trend toward more stable numbers of thoracic segments among derived trilobite clades is firmly established, what is meant be "hard-

ening" of trilobite genetic regulation (McNamara, 1983) in this context remains uncertain. Such evidence as currently exists indicates that at least some derived trilobites retained the ability to respond flexibly in the generation of trunk segments (Hughes *et al.*, 1999).

Homeosis in Trilobites

There have been several recent suggestions that morphological characteristics seen in particular segments in ancestral species occurred within other segments in descendents (Sundberg, 2000; McMenamin, 2001; McMenamin and McMenamin, 2001). Such arguments are strongest when unique features localized to a particular segment or segments appeared in a different position in descendents with relative to a stable total number of segments. McMemanin and McMenamin (2001, p. 108) argued that third thoracic segment that was macropleural in the certain early Cambrian olenellid trilobites was "trying to transform itself" into the rearmost segment of the cephalon. This argument was based on supposed homologies unique to these two segments. A difficulty is that these putative homologies were either characters general to all segments with clearly defined pleurae (*e.g.,* the posterior border), or they were analogous characters (such as the genal angles of both the posterior cephalic and macropleural segments) that were required functionally to permit flexure along the posterior margins of the segments.

Even when the case for a pattern of homeosis is more firmly established, such as in the glabellar pits of oryctocephalid trilobites studied by Sundberg (2000), the underlying mechanism responsible for the pattern is not easily accessible. The kinds of morphological changes that are related to ectopic expressions of Hox genes in modern arthropods are unknown among trilobite appendages (Minelli *et al.*, 2003). Nevertheless McMemanin and McMenamin (2001, p. 108) named a specific but hypothetical allele of *Antennapedia, Antp^{Tgl}*, that they considered responsible for a variety of morphological changes in the olenellid thorax and cephalon. While attempts to identify integrated patterns of morphological change within trilobite ontogeny and phylogeny offer a promising approach for better understanding of trilobite developmental evolution, such approaches require a firm empirical basis. That presented by McMenamin and McMenamin (2001) in their discussion of the role of *Antp^{Tgl}* in the development of cephalic morphology is inconsistent with current knowledge of olenellid ontogeny (Webster, 2003). Furthermore, as *Antennapedia* expression is largely confined to the trunk and posterior cephalic body regions among extant arthropods (Hughes and Kaufman, 2002*b*) the suggestion that it played an important role in patterning of the anterior trilobite cephalon is surprising.

Trilobite Modularity

Trilobites showed relatively little differentiation among appendages and low values of appendage tag-

mosis compared to some other arthropods (Cisne, 1974; Wills *et al.*, 1997; Budd, 2000). (I accept that the notable variation in structure among cephalic biramous limbs of *Agnostus pisiformis*, but consider that these differences do not equate in magnitude to those seen among several Orsten crustaceanomorphs.) It is often thought that the homonomous state was primitive for the Arthropoda (Cisne, 1974; Averof, 1997; Akam, 2000). Trilobites were, nevertheless, notably diverse in both overall form and numbers of trunk segments. The variety of ecological roles exploited by trilobites was also diverse (Fortey, 1985; Fortey and Owens, 1999), although probably less so than among modern aquatic arthropods. A relatively low degree of tagmosis is characteristic of the marine arachnates when compared to that of insects or crustaceans (Wills *et al.*, 1997). As marine arachnates are better known from fossils than from extant forms, whereas the reverse is true for crustaceans, it seems that early arthropods, in general, had lower degrees of tagmosis than modern arthropods (Wills *et al.*, 1997, p. 58; Budd, 2000, fig. 18.2). Nevertheless, relatively enhanced tagmosis appears to have been a consistent characteristic of the crustaceans, because even the least differentiated Cambrian crustacean, *Odaraia*, showed notably higher tagmosis values than that of many arachnates. Hence, there are some grounds for thinking that arachnates may, as a group, have had a lower propensity to differentiate appendage morphologies than that of crustaceans, and that they diversified while retaining an essentially homonomous body plan (Akam *et al.*, 1994).

An interesting question that can best be addressed using fossil arthropods is whether enhanced tagmosis is a general feature of all derived arthropod clades, or is specific to the crustacean/insect lineage. The broadly overlapping domains of Hox genes among modern chelicerates may reflect the fact that arachnates in general show limited modularity compared to some other euarthropods. This interpretation may be supported if ontogenetic transitions that characterize arachnates are modest in comparison to other arthropods. Trilobites are known for their "track-like" ontogenetic series with progressive and subdued morphological change between instars compared to the profound transitions witnessed among insects and some derived crustaceans (Hughes and Chapman, 1995). Trilobite "metamorphosis" (Speyer and Chatterton, 1989; Chatterton and Speyer, 1997) did not equate to the truly radical reorganization of the entire body plans, with adults derived from a small population of specialized cells set aside from those of the larval body, characteristic of holometabolous insects. Nor is there evidence of radical modification of limb structure between instars, as is seen in crustaceans, that can be mitigated by changes in Hox gene expression (Abzhanov and Kaufman, 1999b), or their products (Akam, 2000).

The question of why trilobites (and other arachnates), while sharing the same developmental toolkit of Hox genes that were employed successfully by crustaceans and insects to effect high degrees of modular-

ity, failed to do likewise, remains unanswered. The answer likely lies not in the Hox genes themselves, but in how they were regulated. A striking aspect of trilobite body patterning is the contrast between the observed variability in numbers or trunk segments in the clade and the constancy of their form. This may have been related to the extension of segment appearance late into ontogeny, akin to that seen in "short germ band" mandibulates but in trilobites occupying a substantial portion of post-embryonic life. Such post-embryonic changes took place in free-living individuals in which the form of each molt instar was directly subject to selection. This may have constrained the extent of morphological transitions adaptively possible between anamorphic instars, among which segments were still differentiating. Thus retention of terminal addition late into trilobite ontogeny may have facilitated variation in numbers of homonomous segments, but limited the degree of heteronomy possible in their form.

If the ability to effect complex tagmosis evolved uniquely near the base of the crustacean/insect lineage, the low degree of modularization in trilobites and other marine arachnates could be seen simply as a plesiomorphic arthropod feature. If Paleozoic arachnates and crustaceans competed for many of the same resources this could have been a factor in the long-term demise of the marine arachnates. In 1981 David Raup posed the question of whether trilobites went extinct due to "bad genes or bad luck" and supported the former explanation (Raup, 1981). Today it's tempting to quizzically rephrase the answer as "Good genes, bad deployment" for although trilobites likely had the genes other arthropods used to modularize, they may have failed to exploit them in a comparable manner. In this regard, perhaps the modularization of the trilobite pygidium seen repeatedly among trilobites is relevant in the context of Budd's (1999a) concept of "homeotic takeover" in which selection for regional limb specialization ultimately drives the localization of Hox gene expression patterns. One modification in trilobites might be that the selection was primarily for exoskeletal morphology rather than limb structure. But when we can identify those factors that hindered trilobites from modularizing in the manner of other successful arthropods we may approach one half of the ultimate question of trilobite evolutionary history: Where did they come from and why did they go (Hughes, 1993)?

Hughes for teasing me out of my trilobite exoskeleton for a dip into comparative development.

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