

TAGMATA AND SEGMENT SPECIFICATION IN TRILOBITES

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ABSTRACT. As in some Recent arthropods, the link between segmentation as expressed in the dorsal exoskeleton of trilobites and that of ventral appendages is not always exact, suggesting that specification at a cellular level and the morphological appearance of segments may have been significantly dissociated during trilobite ontogeny. It is possible that the cellular primordia of all segments to be expressed later morphologically were specified during a short sequence of events early in ontogeny. Such a mechanism is invoked in the multiplicative model of segmentation suggested for centipedes, and could apply to all arthropods, trilobites included. This model contrasts with the additive model for trilobite postcephalic segmentation, which suggests that segments were both specified in and budded from a posterior generative zone in a gradual manner that extended late into ontogeny. Discriminating between these ideas in trilobites will require careful exploration of the dynamic relationship between the size of individual segments and the size of the entire organism. The trilobite postcephalic region also shows a dynamic exchange of segments between the transitory pygidium and the thorax. This contrasts with how tagmata are defined among living arthropods, and thus the adult pygidium of trilobites is a kind of 'frozen' postcephalic growth zone, following the cessation of the appearance of new segments in the dorsal exoskeleton. As such, we suggest that the trilobite exoskeletal bodyplan should be regarded as consisting of only two tagmata, the cephalic and postcephalic tagma.

KEY WORDS: trilobite, segmentation, tagmosis, body plan, developmental evolution.

TRILOBITES offer an unique opportunity for understanding the nature and evolutionary potential of two fundamental units of the arthropodan body plan: segments and body regions (tagmata). The group displays marked diversity in terms of total segment number, intraspecific variability in the number of segments, and allocation of segments to the thorax and to the adult pygidium respectively. This contrasts with the prevailing stability in segment number and precise allocation of segments to each body region exhibited by most other arthropods. In addition, their geological range places trilobites in a temporal framework that offers a glimpse into the early stages of arthropodan evolution, and for documenting the long-term evolution of segmentation in one well-represented arthropod clade. Lastly, some well-preserved ontogenetic series provide detailed developmental information which is seldom available for fossil arthropods.

Recent progress in arthropod developmental biology (including molecular developmental genetics in a few model species) adds to the traditional database of comparative morphology and developmental biology of Recent taxa. New insights from the evolutionary developmental biology of extant arthropods invite comparisons which may benefit both trilobite palaeontology and arthropod zoology.

In this paper we reconsider aspects of the postcephalic region of trilobites in the light of some current understanding of segment production and patterning in Recent arthropods. In addition to arguing that the postcephalic region of most trilobites should be considered as a single body region, our primary aim is to draw attention to the need for and promise of further research on trilobite segmentation patterns in the light of increasing knowledge of arthropod developmental genetics. We also highlight some of the diversity of segmentation patterns among trilobites and the difficulties that may hinder a straightforward interpretation of trilobite segmentation patterns.

SEGMENTS

Number of postcephalic segments in adults. Among adult trilobites, the total number of postcephalic segments ranges from five (based on ventral appendages in *Agnostus pisiformis*) to more than 45 (based on

dorsally expressed segments in olenellids). At the upper end, these numbers exceed those found in most Recent arthropods. Numbers larger than *c.* 15 postcephalic segments are found only in centipedes (Chilopoda), millipedes (Diplopoda) and a few putatively basal Crustacea.

Counting segments in trilobites, however, is commonly not straightforward. Firstly, while counts of postcephalic segments in trilobites are usually based on exoskeletal patterns, we generally do not know whether exoskeletal segments matched the number of pairs of postcephalic appendages. In some cases, as in *Olenoides serratus* (Walcott 1921; Raymond 1920; Whittington 1975, 1980), the two counts apparently correspond; in others, such as *Triarthrus eatoni* (Cisne 1981; Whittington and Almond 1987) and *Agnostus pisiformis* (Müller and Walossek 1987), they do not. Secondly, some species exhibit individual variation in the number of postcephalic segments expressed in the dorsal exoskeleton (Hughes *et al.* 1999). Thirdly, the last pygidial segments are often small and indistinctly developed. Fourthly, there are commonly discrepancies between the numbers of segments expressed in the axial and pleural regions of the pygidium (see Adrain and Edgecombe 1997, for numerous examples).

As for the number of segments in the adult thorax, most species are invariable, but many examples of intraspecific variability are also known. Hughes *et al.* (1999) list 20 species (mainly Cambrian) with intraspecific variation in the number of adult thoracic segments. Polymorphs in these species may differ by one segment in some cases to as many as eight in others (M. Webster, pers. comm. 2001), but work is now needed to assess the controls and prevalence of such polymorphism within variable species. Intraspecific variation for the number of pygidial segments is more common. This is partly because new segments in the dorsal exoskeleton first appeared near the posterior of the pygidium and are often indistinct. Another reason may be the tendency within derived clades for the number of segments in the pygidium to increase at the expense of the number of thoracic segments (Stubblefield 1959; Fortey and Owens 1997). The degree of variation in segment numbers is related to the number of segments within a given region (Hughes *et al.* 1999). Accordingly, for any given total number of postcephalic segments, the chance of finding variation in the number of pygidial segments increases as the ratio of segments in the thorax to the pygidium declines. If the trilobite postcephalic region is one body region, as we argue below, analyses of the combined numbers of thoracic and pygidial segments will be vital for assessing evolutionary trends in trilobite segmentation. Developmental mechanisms notwithstanding, adaptations such as those related to the mechanics of encapsulated enrollment (Hughes *et al.* 1999) may explain the apparent tendency toward increased constancy of postcephalic numbers among derived clades (McNamara 1983; Hughes and Chapman 1995; Hughes *et al.* 1999).

Among Recent arthropods, as in derived trilobites, the number of trunk segments is generally constant, not just at the specific level, but also within larger clades, such as Eumalacostraca or several insect orders. Intraspecific variability, coupled with generally high to very high total number of segments, is known only in a few clades, that is, in well-defined subgroups of the above-mentioned clades of multisegmented arthropods (geophilomorph centipedes, juloid millipedes, notostracans; conditions in remipedes are uncertain: F. Schram, pers. comm. 2001; J. Yager, pers. comm. 2001). Variation in segment numbers occurs within each sex; in geophilomorphs, females generally have more segments than the conspecific males. It is perhaps noteworthy that, as Hughes *et al.* (1999) claimed for trilobites and Fusco and Minelli (2000) for centipedes, high and variable numbers of segments is not necessarily a plesiomorphic condition for arthropodan clades (see below, discussion of Williston's law).

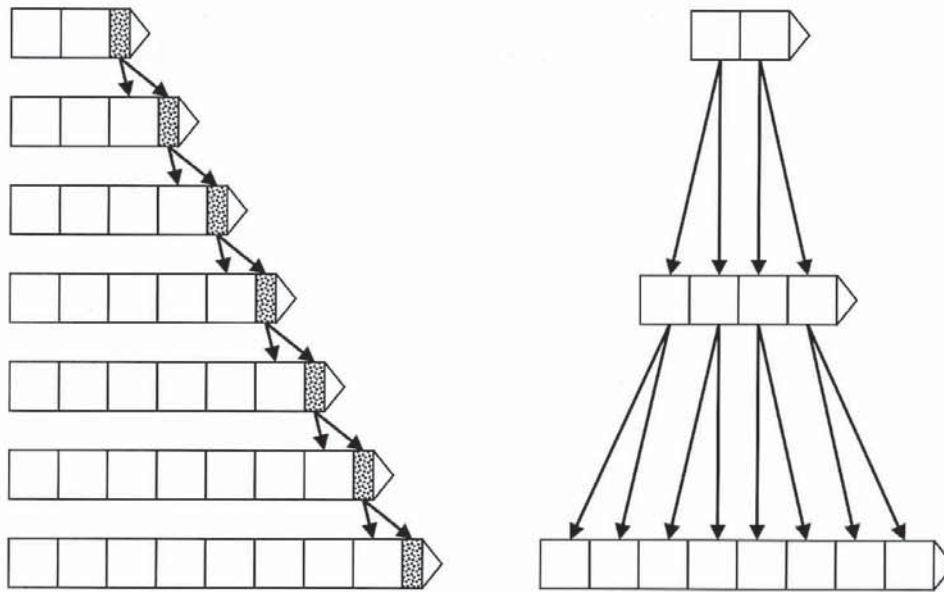
The common mismatch between the number of exoskeletal segments expressed in the axial and pleural regions of the pygidium has led to the suggestion of secondary segmentation in the pleural region (Størmer 1942; Hessler 1962). According to this model, the boundaries between somatic segments in the pleural regions of trilobites coincide with the pleural furrows, as opposed to the interpleural furrows (i.e. those structures along which the thoracic segments articulate). Trilobite soft tissues apparently attached to apodemes within the axial region, a portion of the exoskeleton that was not proposed to show evidence of secondary segmentation. This fact makes it difficult to assess the spatial relationships between somatic and exoskeletal boundaries within the pleural region, and the idea of secondary segmentation has not received widespread acceptance (e.g. Bergström 1973a). Nevertheless, the presence of two furrows within the pleural region for every one in the axial region emphasises that there can be conflicting interpretations of segmentation patterns even within the dorsal exoskeleton.

Dorsoventral mismatch (number of segments). But . . . what is a segment? Recent progress in developmental biology has clearly shown that segments as *developmental* units are not the same thing as the (admittedly, often quite idealized) units of the traditional comparative anatomy of arthropods. Following Lawrence (1992, p. 91), we can define segments, as morphogenetic units, as precisely defined sets of cells serially repeated along the main body axis. Such are the parasegments defined by the expression of pair-rule genes in *Drosophila*. That is, a segment is not necessarily, or only, the conventional structural unit of arthropod comparative anatomy. Moreover, we must be prepared to acknowledge the existence, within one and the same animal, of different degrees of segmentation, e.g. on the dorsal and ventral aspect, both as mismatch between tergites and sternites (Scutigerozoa, Pauropoda, Symphyla) or as mismatch between exoskeletal segments and appendages (Diplopoda, Notostraca) (Minelli and Fusco 1995).

We can hardly hope to identify 'developmental segments' in fossil animals such as trilobites. Nevertheless, the occurrence in these arthropods of different degrees of segmentation is suggested by two kinds of evidence. First, in the pygidium, irrespective of whether we count axial rings or pleural ribs, there can be a mismatch between the number of dorsal units and the number of pairs of ventral appendages, as is shown in *Triarthrus eatoni* (Whittington and Almond 1987). A corresponding arrangement of appendages and tergites is known from the extinct euthycarcinoids. Second, there is marked variation among trilobite clades in the extent to which the morphology and degree of expression of pygidial segments differs from that of thoracic segments (see Hughes *et al.* 1999, fig. 1). In many trilobites, such as *Aulacopleura konincki*, individual pygidial segments are barely distinguishable from individual thoracic segments. In others, such as *Planiscutellum planum*, pygidial segments are strikingly different from thoracic segments. Whether this difference was also expressed in the structure of ventral appendages, as Bergström (1973b, p. 44) suggested in *Iliaenus crassicauda*, is largely unknown because forms in which softparts have been described generally show similar morphologies in thoracic and pygidial segments. Nevertheless, this seems unlikely to be a universal rule for two reasons. Firstly, thoracic and pygidial appendages of *Agnostus pisiformis* appear similar (Müller and Walossek 1987) despite exoskeletal differences. Even in *Rhenops*, in which a marked difference between thoracic and pygidial limbs has been claimed (Bergström and Brassel 1987, p. 70), these differences relate more to relative size than to differentiation of limb structure. Secondly, trilobites show little anterior-posterior differentiation among biramous appendages even across the cephalic/postcephalic boundary, a division apparently more fundamental in trilobite ontogeny than the thorax/pygidium divide. The cephalic region shows no ontogenetic variation in its dorsal segmentation during protaspid development and onwards, in striking contrast to the postcephalic region.

Although dissecting the relationships between these different meanings of segmentation is difficult in trilobites, the issues discussed above provide a basis for questioning some implicit assumptions about trilobite growth. We explore these in the next section.

Segmental markers and segmental specification. Stubblefield's (1926) paper on the development of *Shumardia (Conophrys) salopiensis* demonstrated progressive terminal appearance of postcephalic segments by charting the position of new segments with respect to the macropleural segment during ontogeny. This elegant work identified the site of appearance of new postcephalic segments to be at the posterior of the pygidial axis, but has since been interpreted to imply that the morphological appearance was correlated with initial cellular differentiation of new segments from a terminal, possibly teloblastic, generative disc (Størmer 1942, p. 118; Hessler 1962; Hu 1971, p. 64). However, Stubblefield's observations do not rule out the possibility that the appearance of segments as expressed in the trilobite exoskeleton may have been ontogenetically dissociated from an earlier determination of segments at the cellular and molecular level, as found in Recent arthropods (e.g. Nüsslein-Volhard and Wieschaus 1980; Patel *et al.* 1989). Accordingly, we now explore the implications of the idea that segments were produced in trilobites according to a *multiplicative* (rather than additive) process of segmentation. Such a mechanism was first suggested by Maynard Smith (1960) to explain the high level of developmental control in segmentation exhibited by arthropods with a very high number of segments, as some centipedes. This model suggests that the main body axis becomes subdivided in a small number of primary developmental units very early in development (Text-fig. 1). These units later undergo a further



TEXT-FIG 1. Schematic representation of additive (left) versus multiplicative (right) mode of segmentation. Squares are segmental units, the grey belt (in the left scheme) represents a generative zone, and the terminal triangle is a posterior non-segmental unit (telson).

subdivision into secondary units which provide the definitive segmental architecture of the animal. The number of adult trunk segments would be therefore precociously determined, even when their full morphological expression appears progressively during post-embryonic development. This progression is not necessarily antero-posterior. Exceptions occur, for instance, in some stomatopod crustaceans: in the pseudozoea I larval stage of *Squilla* the appendages of the most caudal body region (the pleon) are already differentiated, whereas those of the preceding tagma (the pereion) are not (Minelli and Fusco 1995). Building on Maynard Smith's model, Minelli and Bortoletto (1988) and Minelli (2000, 2001) developed a more elaborate model in which all arthropods have the same number of primary units (eosegments) which undergo a further subdivision into secondary units (merosegments) following a stereotyped pattern. It must be stressed that this model clearly distinguishes between an early determination and a later full expression of segments. Determination is assumed to be completed long before the full deployment of the segments is brought about by the activity of a generally posterior (preanal) zone, during later embryonic development (in the generality of arthropods) and also during a more or less extended part of the post-embryonic development (in the anamorphic arthropods, such as trilobites and many myriapod groups; see below).

A multiplicative model of segment production is supported by three lines of evidence. First, the occurrence of dorso-ventral mismatch in segmentation. Second, the conservation of overall body shape irrespective of the number of body segments. Third, the position of segmental markers.

It is quite difficult indeed to account for the widespread occurrence of dorso-ventral mismatch in segmentation mentioned above in terms of additive production of new segments during embryonic and postembryonic development. The growth zone would be required to produce dorsal and ventral elements at different and often variable rates, at the same time accounting for an error-free and species-specific dorso-ventral pairing. By contrast, the multiplicative model would simply require that dorsal vs. ventral features imply more or less advanced degrees of secondary segmentation.

A second argument that might support a multiplicative process of segmentation applies specifically in trilobites. Hughes and Chapman (1995) suggested that in the adults of *Aulacopleura konincki* the length of individual segments could be modified to give the thorax a fixed share of the whole postcephalic region. Adult specimens with 18–22 trunk segments shared almost identical sagittal proportions (Hughes and Chapman 2001); the same behaviour was observed in conspecific geophilomorph centipedes belonging to different cohorts (Berto *et al.* 1997). Although in *A. konincki* there may be functional reasons for this pattern, related to enrollment mechanics, no obvious adaptive explanation can be offered for the centipedes. In both cases, this pattern could be interpreted in terms of a fixed growth potential (e.g. a

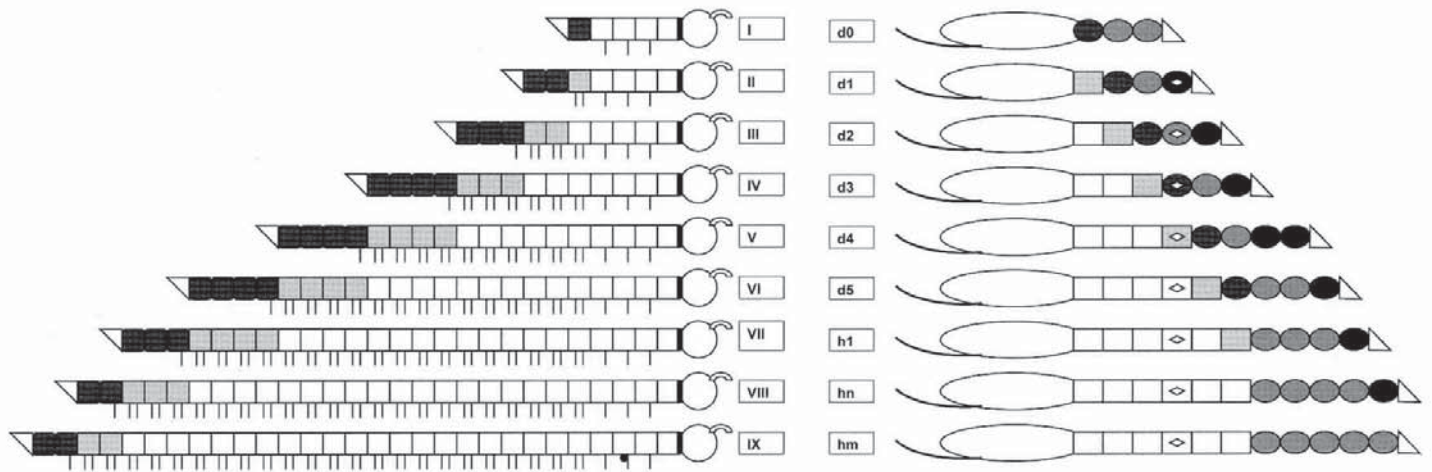
fixed number of cells, in an early developmental stage) allocated to a given eosegment, thus constraining its future growth, irrespective of the number of merosegments into which it will eventually split. It will be interesting to check whether the relative sizes of segments behave in the same way in basal trilobites that did not enroll but vary in adult segment numbers.

The third argument, that the location of some morphological markers correlates with the relative rather than the absolute segmental position, was first observed in a Recent geophilomorph centipede (Minelli 1992). This observation supports a mode of segmentation obtained through a multiplicative process, as it seems that morphological features invariably occur at the same relative position along the trunk irrespective of the total number of segments. Many trilobites possess macropleurae (here we use this term in a general sense to imply any postcephalic segment that has a morphology markedly distinct from those adjacent to it), features which could be used as a marker of segmental position when comparing individuals in species with variable number of segments. Unfortunately, there are no published records of any species with both macropleurae and intraspecific variability in the number of thoracic segments. Nevertheless, hints on trilobite segmentation arise at another level of comparison, when confronting the segmental arrangement of the major arthropodan clades. In some Recent arthropods, one or more trunk segments are marked by the presence of unique features which interrupt the otherwise uniform sequence of segments within a tagma, that is, without constituting a boundary between two distinct tagmata (Minelli, 2001). In other words, the segments immediately following the unique segmental marker are identical to those immediately preceding it. The most widespread among these segmental markers is the (female) gonopore, which occurs, for instance, on the sixth pereonite of malacostracan crustaceans, on the fourth trunk segment of symphylans, and on the second opisthosomal segment of arachnids. In those arthropods in which the gonopore is secondarily displaced to a more cephalic (millipedes) or more caudal position (insects, centipedes), features other than the gonopore may remain to mark the segmental position originally occupied by the latter. The most conspicuous of these features are the male gonopods (legs modified as claspers) present in the majority of millipedes. Minelli (2001) sees a good correspondence between some segmental positions in arthropods with different total number of segments, building on the alignment of specific segmental markers, that apparently mark a fixed position in the context of a first layer of body segmentation (eosegments).

At present, we do not have any evidence of the position possibly occupied by the gonopore in trilobites but macropleural segments could potentially form an unique marker equivalent to those of the other arthropods, irrespective of whether they were associated with the trilobite gonopore, or not. Correlations between the segmental position of the macropleurae and the total number of postcephalic segments, however, are not as good as the correlations between the segmental position of the 'mid-body anomaly' and the total number of body segments in some Recent arthropods. Trilobite macropleurae occur on a wide range of postcephalic segments (see Bergström 1973a), and in some cases more than one segment within an individual may be macropleural (e.g. *Akoldinioidia shanjiangensis*, Peng *et al.* 2003).

One other issue has direct relevance to the multiplicative model, and this concerns the variability of segmentation dynamics among different trilobite clades. The meraspid phase of some trilobites, such as *Aulacopleura konincki* (Hughes and Chapman 1995), shows a constant balance between the release of exoskeletal segments into the thorax and the appearance of new segments in the transitory pygidium (in this case apparently a one-to-one balance). Other trilobite taxa show more variable patterns (see Chatterton and Speyer 1997). A simple departure from the one-to-one balance is provided by *Shumardia* (*Conophyrus*) *salopiensis*, in which the early transitory pygidium had a stable balance between the release of one segment from the anterior of the transitory pygidium and the appearance of one new segment in the terminal portion (Text-fig. 2). This proceeded until the transition into meraspid degree 4, but at this point only, two new segments were expressed in the dorsal exoskeleton, apparently within one moult, while only one was released into the thorax (see Fortey and Owens 1997, fig. 13). Following that transition, the trilobite reverted to the usual one-to-one balance for meraspid degree 5, but then continued to add at least one more segment to the pygidium following completion of the adult thorax (Stubblefield 1926; Fortey and Owens 1991) (Text-fig. 2).

More extreme variations in the growth dynamics of the transitory pygidium apparently characterize



TEXT-FIG. 2. Schematic representation of anamorphic development in a millipede (left) and a trilobite (right). Rounded blocks are not completely developed segmental units in the millipede and pygidial segments in the trilobite. Dark grey rounded blocks are segmental units that will form a fully developed segmental unit in the following stage in the millipede, or pygidial segments that will be released into the thorax in the following meraspid degree in the trilobite. Black rounded blocks are newly-formed pygidial segments. Squared blocks are fully developed segmental units (trunk segments in the millipedes, thoracic segments in the trilobite). Light grey squared blocks are the last fully developed segmental units added at that stage. The terminal triangle is the telson or its equivalent. In the millipede, the dark circle marks the appearance of female genitalia. In the trilobite, a diamond marks the macropleural segment, d0–d5 are meraspid degrees, h1 is the first holoaspis and hn and hm are two later holoaspis stages. The millipede ontogeny illustrated is based on the development of *Nanogona polydesmoides* and follows Geoffroy (1984). The trilobite ontogeny illustrated is based on the development of *Shumardia (Conophrys) salopiensis* and follows Stubblefield (1926) and Fortey and Owens (1991).

certain cheiruriniids and scutelloids. *Ceraurinaella typa* evidently possessed the entire complement of postcephalic segments at meraspid degree 0 (Whittington and Evitt 1953, pp. 68–71, pl. 12, figs 1–2), and passed through the meraspid period by progressively releasing segments from the anterior of its unusually segment-rich transitory pygidium. Latest stage protaspids of some *Meridioscutellum* possessed all of the ten segments that would ultimately comprise the mature thorax (Feist 1970). These examples indicate that trilobites could express all exoskeletal segments within early growth phases. Unfortunately the protaspid ontogeny of *C. typa* is unknown, although late-stage protaspids of *Ceraurinaella zhoui* (Edgecombe *et al.* 1999, figs 5.8–5.10) appear similar to those of other trilobites in that they show few postcephalic segments. It would now be interesting to track the development of the sizes of individual segments through meraspid ontogeny to trace whether the unusual pattern in *C. typa* and *Meridioscutellum* is related to the early appearance of segments each of an anomalously small size, or whether the pattern is related to an extraordinarily extended protaspid and meraspid degree 0 ontogeny. The expression of the complete postcephalic segmentation early in ontogeny could be construed as evidence for the multiplicative model, but only if the sizes of individual segments were smaller than meraspids with more conventional development.

Another interesting example is that reported, but not documented in detail, in *Hintzeia* from the Broken Skull Formation of the District of MacKenzie, Canada (Kopaska-Merkel 1987), in which variations in the number of segments added per instar correlated with variations in the growth rates of existing exoskeletal segments. These examples suggest that a more detailed review of the dynamics of segment accretion and size would be of value in assessing whether there are underlying patterns controlling this relationship.

TAGMATA

Caution is in order when comparing body regions of different arthropod clades, and definitions of arthropod tagmosis vary within the group. Some have used tagmosis to refer to specializations of entire

sets of limbs on an arthropod body (Flessa *et al.* 1975, p. 72). Others view tagmosis as a property of the dorsal exoskeleton, and this has been the general practice of those working on trilobites. These conflicting definitions partly reflect the different types of segmentation that can be recognised in arthropod bodies (see above). To be sure, it is nearly impossible to avoid some degree of subjectivity in defining an arthropod's tagmosis; nevertheless, in accordance with neontological usage we advocate defining a tagma as a discrete morphological entity which is distinct, in the dorsal exoskeleton at least, from its first appearance in ontogeny, that is, its boundaries with adjacent regions are never crossed by newly recruited or released segments.

Trunk regions of different clades that seem to be equivalent in morphological terms (e.g. a leg-bearing thorax followed by a leg-less abdomen) do not necessarily correspond in terms of *Hox* gene expression (Averof and Akam 1993, 1995). Therefore, we cannot take for granted that what is called thorax in trilobites corresponds, in any definite sense, to the tagma also called thorax in other arthropod clades (see also Hughes 2003 for additional comments on trilobite tagmosis). We suggest that a comparison to millipedes and centipedes may help in obtaining a clearer view of trilobite tagmosis.

Post-embryonic developmental schedules and post-cephalic body regions in myriapods vs. trilobites. Recent millipedes (Diplopoda) offer a good model for interpreting the post-embryonic development of trilobites and the apparently unique way they allocate segments to the two postcephalic body regions, the thorax and the pygidium. Both groups are clearly anamorphic, i.e. they progressively add new exoskeletal segments, during a sequence of moults, to the small number of fully deployed segments present in the first larval stage. The same is true of two of the five orders of Recent centipedes (Chilopoda), i.e. the Scutigermorpha and the Lithobiomorpha and, to a lesser extent, of a third order, the Craterostigmomorpha. Among millipedes, three different kinds of anamorphosis can be distinguished (Enghoff *et al.* 1993): (1) *euanamorphosis*, in which the posterior addition of new segments continues until the last moult the animal undergoes, without any clear evidence of a fixed terminal number to be eventually reached; (2) *teloanamorphosis*, in which the millipede does not moult any more after it has reached a final, tightly determined number of segments which is usually the same for all species in a family or order; (3) *hemianamorphosis*, when the final and fixed number of segments is reached after a few moults, but growth continues through further moults without further increase in the number of body segments. Hemianamorphic is also the development of the centipede orders mentioned above. Most trilobites probably grew by hemianamorphosis, with the meraspid/holaspid boundary coinciding with, or close to the transition phase between accretion and constancy, but euanamorphosis cannot be ruled out in the case of taxa with very high and intraspecifically variable number of segments [for example in the olenellid *Olenellus* (*Olenellus*?) *fowleri*].

The dissociation between determination and full expression of segments implied by the multiplicative model referred to above seems, in fact, to apply in myriapods (Minelli and Bortoletto 1988; Minelli *et al.* 2000). It is true that no gene expression pattern of the pair-rule kind has been found in the first few studies on the developmental genetics of these arthropods (Hughes and Kaufman 2002a, b; Kettle *et al.* 2003), but many features of the post-embryonic development of representatives of this group seem to support a very early determination of the full complement of body segments or, at least, of the full set of the primary segmental units envisaged in the multiplicative model. For instance, different centipedes such as *Lithobius* and *Scutigera* obtain an identical adult segment complement, although proceeding from moult to moult through completely different schedules of post-embryonic addition of complete segments; the same is true for millipede genera such as *Glomeris* and *Trachysphaera* where, again, the same adult condition is the target of different post-embryonic schedules of (full) segment accretion. Suggestive of a very early determination of the segments is also the seemingly counterintuitive condition of the centipedes, where the more basal clades (Scutigermorpha, Lithobiomorpha, Craterostigmomorpha), all with a fixed number of 15 leg-bearing segments in the adult, contrast with the more derived clades (Scolopendromorpha and Geophilomorpha) where a higher or much higher segment number (up to 191 leg-bearing segments in the latter group) is not accompanied by a temporally more extended phase of segment accretion but, on the contrary, by a transition from hemianamorphosis to epimorphosis (all segments been fully formed at hatching). Thus, differences between epimorphosis and anamorphosis (in its diverse modes) are possibly

nothing else than heterochronic variations on a common theme, affecting the activity of cell proliferation in the posterior part of the body but without affecting an already established pattern of segmentation.

In so far as the comparison between trilobites and Recent myriapods can be stretched, the latter offer a process comparable to that operating in the trilobite transitory pygidium (Text-fig 2). In the larva I of the centipede *Lithobius forficatus* (Andersson 1976), for instance, there are seven trunk segments each with a pair of fully developed legs, followed by an eighth segment with half-developed limbs and a terminal, incompletely segmented region with two pairs of limb buds in the growth zone. In the larva II, the eighth pair of legs is fully developed, whereas the other two are still in a bud stage; but these are fully developed in the larva III (which has, therefore, ten pairs of legs), whereas two additional pairs of legs appear as leg buds on the two next differentiating segments. Three more moults will respectively add two, one and two (or two, zero, three) pairs of legs, until the final number of 15 pairs is eventually reached. In millipedes, no external leg bud is visible in the terminal region of the larval body, but it is clear that, following each moult, the most anterior of the apodous rings forming the posterior part of the larval body are promoted to the state of complete, leg-bearing segments, whereas new apodous rings appear behind them. The apodous rings of the larval millipedes and the posterior part of the trunk of the hemianamorphic centipedes (with its incompletely developed appendages) is thus broadly comparable to the trilobite transitory pygidium. Interestingly, in many Lithobiomorpha the posterior corners of some tergal plates (in fixed segmental positions, typically those of leg-bearing segments (7), 9, 11, and 13) are prolonged into more or less distinct projections, analogous to trilobite macropleurae in that they can be used as positional reference points. Indeed, the lithobiomorph segments with posteriorly prolonged tergites are 'released' from the posterior growth zone during post-embryonic development in a way strictly paralleling Stubblefield's (1926) observations on the progression of the macropleural segment of *Shumardia* out of the transitory pygidium. At least in *Triarthrus eatoni*, dorsal exoskeletal segments appear to correlate with fully-formed ventral appendages, rather than legs or half developed legs as in myriapods, although these appendages could be of sub-adult proportions.

In most myriapods, the growth zone comparable to the trilobite transitory pygidium is more or less completely 'exploited' during post-embryonic development; that is, there is no terminal set of segments retaining and consolidating the larval condition, as in the mature pygidium of trilobites. There are, however, millipede clades in which a couple of apodous rings are retained in the adult. In centipedes, the last leg-bearing segment is followed by a genital region (probably consisting of two segments) which mostly bears just one pair of small genital appendages. In myriapod morphology, however, there has never been the temptation to recognise these few final segments as a separate tagma: these are simply regarded as the terminal segments of the trunk. Things are quite different, therefore, from the situation in other arthropods, in which two distinct postcephalic tagmata (say, thorax and abdomen, or pereion and pleon) are clearly distinguishable. In our opinion, then, the distinction between thorax and adult pygidium, although useful in strictly descriptive terms, does not correspond to consolidated tagmata. We prefer to regard the pygidium instead as a kind of 'frozen' growth zone.

Williston's law and the evolution of arthropod segmentation. In organisms with a variable and often high number of repetitive parts, such as vertebrate ribs and vertebrae, annelid and arthropod segments, or petals and stamens in flowers, it is often taken for granted that evolution generally proceeds according to the so-called Williston's law (Saunders and Ho 1984): that is, that more primitive forms have a high number of uniform parts (e.g. ribs, vertebrae, segments) whereas in more advanced forms there is a reduction in the number and an increase in the degree of specialisation of those parts. Thus, Lauterbach's (1980) suggested groundplan of the Arachnata exhibits a huge number of essentially uniform segments, smoothly declining in size in antero-posterior progression. Correspondingly, geophilomorph centipedes and juloid millipedes, with their often huge number of segments, are commonly held as morphologically close to a putative worm-like arthropod ancestor, but this view has been repeatedly negated by modern phylogenetic analyses of these groups, molecular and morphological alike (Dohle 1985; Enghoff 1990; Giribet *et al.* 1999; 2001), associated with studies on morphological complexity (Fusco and Minelli 2000). Hence the status of Williston's law requires consideration in other multisegmented groups.

Trilobites have traditionally been considered to be basal within the Arthropoda based on their early stratigraphic occurrence and their lack of appendage specialisation: with the exception of the antennae and antenniform cerci, all trilobite appendages were apparently homonomous. Opinion has differed as to whether primitive trilobites possessed few (e.g. Matthew 1889; Beecher 1897) or large numbers of (e.g. Raw 1925, 1953) segments. Recent phylogenetic analyses favour the latter (e.g. Fortey and Whittington 1989; Edgecombe and Ramsköld 1999) and some analyses suggest that trilobites were derived from within the arachnomorphs, implying that their largely homonomous condition was derived (Briggs and Fortey 1989; Wills *et al.* 1994). Hence, although early trilobites were probably multi-segmented, it is not clear that their homonomous limb structure represents the basal arachnomorph condition, although there is evidence that the majority of Cambrian arthropods had a reduced degree of limb differentiation compared to modern forms (Cisne 1974; Wills *et al.* 1997; Budd 2000).

That early workers debated whether the basal members of the Trilobita had few or many postcephalic segments attests to the fact that both segment-rich (e.g. redlichiids and olenellids) and segment-poor (e.g. eodiscids) forms occur in Lower Cambrian rocks. Indeed, the range of variation in numbers of postcephalic segments among Early Cambrian trilobites may equal that known at any time in their subsequent history. Such a pattern is consistent with a multiplicative process of segment specification at a cellular level, in that different degrees of subdivision of a small number of primary developmental units could result in a high variance in the total numbers of segments. On the other hand, in the alternative model of sequential segment specification, profound ontogenetic displacement of the controls of the termination of segment accretion would be required. Again, ontogenetic relationships between the sizes of individual segments and overall body size in trilobites may provide some insights as to which of these alternatives is the more likely.

Hox genes and tagmosis. There are phylogenetic reasons to believe that segment patterning in trilobites was regulated by *Hox* genes as it is in Recent arthropods (Hughes and Chapman 1995, 2001; Hughes *et al.* 1999; Sundberg 2000; Hughes 2003, in press). Nevertheless, we cannot subscribe to Sundberg's (2000) analysis, in which the trilobite body was divided into eight regions that were inferred to correspond to the expression of as many *Hox* genes (this number of *Hox* genes being considered by Sundberg 2000 to be plesiomorphic in the onychophoran-arthropod clade).

Only a tiny minority of trilobites allow recognition of Sundberg's (2000) eight 'regions'. Moreover, there is no evidence that the putative distinction of these regions in dorsal segmentation correspond to any differentiation in the associated ventral appendages (see above). Finally, three of the eight morphological regions that Sundberg (2000) recognised in the holaspis of some species are ontogenetically dynamic during the meraspid of the same taxa. This is because any segment destined to become an anterior thoracic segment in the holaspid phase was firstly a segment of the pygidial axis and then the pygidial articulating ring during the meraspid phase. Thus, a postcephalic segment formed early in ontogeny would apparently shift through at least three of Sundberg's (2000) supposedly distinct morphological regions during its growth. If these regions do not represent distinctive morphological entities in themselves, then the grounds for their inferred relationship to particular developmental genes becomes tenuous indeed. Moreover, more recent studies (Hughes and Kaufman 2002c) suggest that ten *Hox* genes, rather than eight, is the plesiomorphic condition in arthropods.

A more convincing case for the operation of homeotic mutations affecting particular *Hox* genes in trilobites would be cases in which trilobites showed two pairs of antennae rather than one, or with their antennae displaced to a 'wrong' segment, but nothing like that is yet known. Therefore, we currently have little factual basis for advancing suggestions as to the body patterning specified by *Hox* genes in trilobites. The ubiquitous homonomous condition of the biramous appendages known in trilobites may further frustrate efforts in this regard. Moreover, it is important to stress that the correspondence between pattern of expression of the *Hox* genes and specification of segmental (or regional) identity is not a simple one and much depends on the evolutionarily varying patterns of control by upstream genes, and in the downstream targets of *Hox* proteins (Carroll *et al.* 2001). It is, therefore, dangerous to try to infer from the tagmosis a causal relationship between variation in *Hox* gene expression pattern and morphological variation (Rogers *et al.* 1997; Gellon and McGinnis 1998; Akam 1998; Hughes and Kaufman 2000).

SUMMARY

In this paper we have reviewed trilobite segmentation and tagmosis with reference to mechanisms and models of segment specification and patterning in Recent arthropods. As in some other arthropods, myriapods in particular, the link between segmentation as expressed in the dorsal exoskeleton of trilobites and that of ventral appendages is not always exact. We draw attention to the fact that the first expression of postcephalic segments in the dorsal exoskeleton need not, and in some cases cannot, coincide with their first specification as developmentally defined segmental units. This fact allows us to posit that segment specification at a cellular level and the morphological appearance of segments may have been significantly dissociated during trilobite ontogeny. This raises the possibility that the cellular primordia of all segments later to be expressed morphologically, in either dorsal exoskeleton or ventral appendages, were specified at the same time. Such a mechanism is invoked in the multiplicative model of segmentation suggested for centipedes (Minelli *et al.* 2000). Direct testing of this idea is impossible in trilobites, but a prediction of this model is that in forms with intraspecific variation in the numbers of postcephalic segments the mean size of individual segments in proportion to body length in segment-rich morphs should be smaller than that of segment-poor forms. Indeed, the dynamics of the relationship of overall body size to individual segment size throughout ontogeny provides the most promising source of data for testing and discriminating between the multiplicative and additive models.

The trilobite postcephalic region shows a dynamic exchange between segments from the transitory pygidium and the thorax. This contrasts with how tagmata are defined among nearly all living arthropods, in which each tagma is a discrete morphological entity from its first appearance in ontogeny and does not recruit new segments from adjacent regions. The only exception is represented by copepods, where the postcephalic trunk is divided into an anterior prosome and a posterior urosome and the earliest segments budded off from the telson during the copepodid phase pass from the larval urosome to the adult prosome (Huys and Boxshall 1991). We argue that the adult pygidium with stable numbers of segments merely represents a 'frozen' postcephalic growth zone, following the cessation of the appearance of new segments in the dorsal exoskeleton. As such, we suggest that the trilobite exoskeletal bodyplan should be regarded as consisting of two distinct regions: the cephalic and postcephalic regions. What we know of ventral appendages suggests that even this distinction does not correlate well with ventral appendage morphology because all known biramous appendages in trilobites, whether cephalic or postcephalic, appear to be homonomous.

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