

Arthropod pattern theory and Cambrian trilobites

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Abstract

An analysis of duplome (= segment) distribution within the cephalon, thorax, and pygidium of Cambrian trilobites was undertaken to determine if the Arthropod Pattern Theory (APT) proposed by Schram & Emerson (1991) applies to Cambrian trilobites. The boundary of the cephalon/thorax occurs within the predicted duplome node 1 (duplomeres 4 or 6). The boundary between the thorax and pygidium generally occurs within node 2 (duplomeres 11–13) and node 3 (duplomeres 18–20) for corynexochids and ptychopariids, respectively. This boundary occurs within field 4 (duplomeres 21–n) for olenellids and redlichiids. The termination of the body generally occurs within node 3 for corynexochids and within field 4 for olenellids, redlichiids, and ptychopariids. In addition, the location of macropleural spines, which may indicate the location of the gonopores or anus, generally falls at the predicted duplomeres. The boundary between the prothorax and opisthothorax of olenellids occurs within or near node 3. These results indicate that the number and distribution of duplomeres within Cambrian trilobites were somewhat constrained by some genetic patterning program. However, the common distribution of boundaries outside of the predicted locations and the possible shifting of nodes suggest that other factors were also controlling the number of duplomeres within the body parts. This variation supports the idea that Cambrian arthropods, unlike modern arthropods, had a simpler genetic program, which easily allowed for changes in the *Bauplan*.

Résumé

Une analyse a été entreprise de la distribution des duplomères (= segments) dans le céphalon, le thorax, et le pygidium des Trilobites du Cambrien, afin de vérifier si l'Arthropod Pattern Theory (APT) proposée par Schram & Emerson (1991) s'applique à ces fossiles. La limite céphalon/thorax se trouve, comme pronostiqué, au niveau du node duplomère 1 (duplomère

4 ou 6). La limite thorax/pygidium se trouve généralement au niveau du node 2 (duplomères 11–13) et du node 3 (duplomères 18–20) pour les Corynexochides et respectivement pour les Ptychopariides. Cette limite se trouve dans le champ 4 (duplomères 21–n) dans le cas des Olenellides et des Redlichiides. L'extrémité du corps se trouve généralement au niveau du node 3 chez les Corynexochides, et au niveau du champ 4 chez les Olenellides, les Redlichiides et les Ptychopariides. D'autre part, les épines macropleurales, qui pourraient indiquer l'emplacement des gonopores ou de l'anus, sont généralement situées au niveau des duplomères pronostiqués. La limite prothorax/opisthothorax des Olenellides est située dans le node 3 ou près de celui-ci. Ces résultats indiquent que nombre et distribution des duplomères des Trilobites du Cambrien ont été en quelque sorte sous la contrainte d'un certain programme de patterning génétique. Cependant, l'emplacement fréquent des limites ailleurs que dans les endroits pronostiqués, ainsi que le déplacement possible des nodes suggèrent que d'autres facteurs ont été aussi impliqués dans le nombre des duplomères des diverses parties du corps. Cette variabilité rend plausible l'idée que les Arthropodes du Cambrien, à la différence de ceux récents, avaient un programme génétique plus simple, ce qui facilitait l'apparition de modifications dans le *Bauplan*.

Introduction

Interpreting morphological characters to decipher phylogenies of organisms is always a challenge. This is especially true when organisms are extinct, where there are no soft-body or biochemical remains to supplement the limited amount of information provided by skeletal remains. Thus, when generalizations on *Bauplane* can be made for a specific group, guidelines can be generated to help interpret the morphological patterns observed and to construct phylogenies. Such a generalization has

recently been proposed by Emerson & Schram (1990) and Schram & Emerson (1991). They suggested that the location of tagmata transitions, gonopores, the anus, and body terminations occurs at specific regions within the *Bauplan* of arthropods. This Arthropod Pattern Theory (APT) was based on both fossil and modern taxa, comparative anatomy of exterior and interior morphology, ontogeny, and developmental genetics, although this theory has not been statistically tested. APT implies that there are only a limited number of arrangements of segments and other morphological features available to arthropods. This could increase the potential of convergence among distantly related groups because the number of segments within the body and body parts or the location of the gonopores or anus are limited. Conversely, closely related taxa also would be expected to have similar distributions of segments in the body.

Schram & Emerson (1991) have also proposed that most biramous arthropods are composed of duplomeres, each containing two primary segments. Both of these segments are typically fused together and in some taxa the individual segments can only be recognized by the internal organization of soft parts. Schram & Emerson recognized two types of sequences of duplomeres, nodes and fields (Fig. 1). They observed that morphological changes generally occurred at three nodes within the *Bauplan*: node 1 = duplomeres 5 and 6; node 2 = duplomeres 11–13; and node 3 = duplomeres 18–20. The fields are duplomeres that are relatively stable because they do not generally show morphological change (field 1 = 1–4, field 2 = 7–10, field 3 = 14–17, field 4 = 21–n). In some notable exceptions, duplomeres 9 and 16 within fields 2 and 3, respectively, can possess gonopores or anus; and several taxa have an anus and terminate in field 4.

The isopod *Ligia* provides an example of morphological changes and other features occurring with the nodes (from Schram & Emerson, 1991). *Ligia* has its head, thorax, and abdomen terminate at the ends of nodes 1, 2 and 3, respectively. In addition, the female gonopore of *Ligia* occurs in the first duplomere of node 2, the male gonopore is in the last duplomere of node 2 and the anus is located in the last duplomere in node 3.

APT implications to trilobite *Baupläne*

As a prediction of APT, changes in arthropod *Baupläne* should occur in quantum jumps, from node to node. This prediction appears to hold true for those extinct and extant taxa discussed by Schram & Emerson (1991) with only a few exceptions. Trilobites would be a good test of APT in that, unlike most modern arthropod groups, they vary widely in their number of segments (= duplomeres). If APT is universal for all arthropods, then changes in the number of segments within trilobites would be in jumps, from one node to the next. In addition, the locations of tagmata transitions (cephalon/thorax and thorax/pygidial boundaries) should occur within the nodes.

Other morphological features that may display APT distributions may be the location of macropleural spines and the boundary between the prothorax and opisththorax in some Olenellida. According to Harrington et al. (1959, p. O73), macropleural spines may indicate the location of the gonopores. If they do, then they would be expected to occur either within a node or at duplomeres 9 or 16.

Schram & Emerson's preliminary study suggested that trilobites display a pattern where tagmata boundaries occur at nodes. They studied the trilobites *Triarthrus*, *Naraoia*, *Olenoides*, and *Agnostus* and in each case the cephalon/thorax transition occurred in node 1. In *Olenoides* and *Triarthrus*, the thorax/pygidium transition occurred in nodes 2 and 3, respectively. If these patterns hold true in other trilobites, then the number of thoracic and pygidial segments, as well as the location of macropleural spines, could be important in determining the evolutionary relationship among taxa. If the pattern does not hold true, then APT is not completely applicable to trilobites, which could potentially make them different from most other arthropods.

Methods

This test of APT is limited to Cambrian trilobites because of the difficulty in deciphering their supergeneric classification

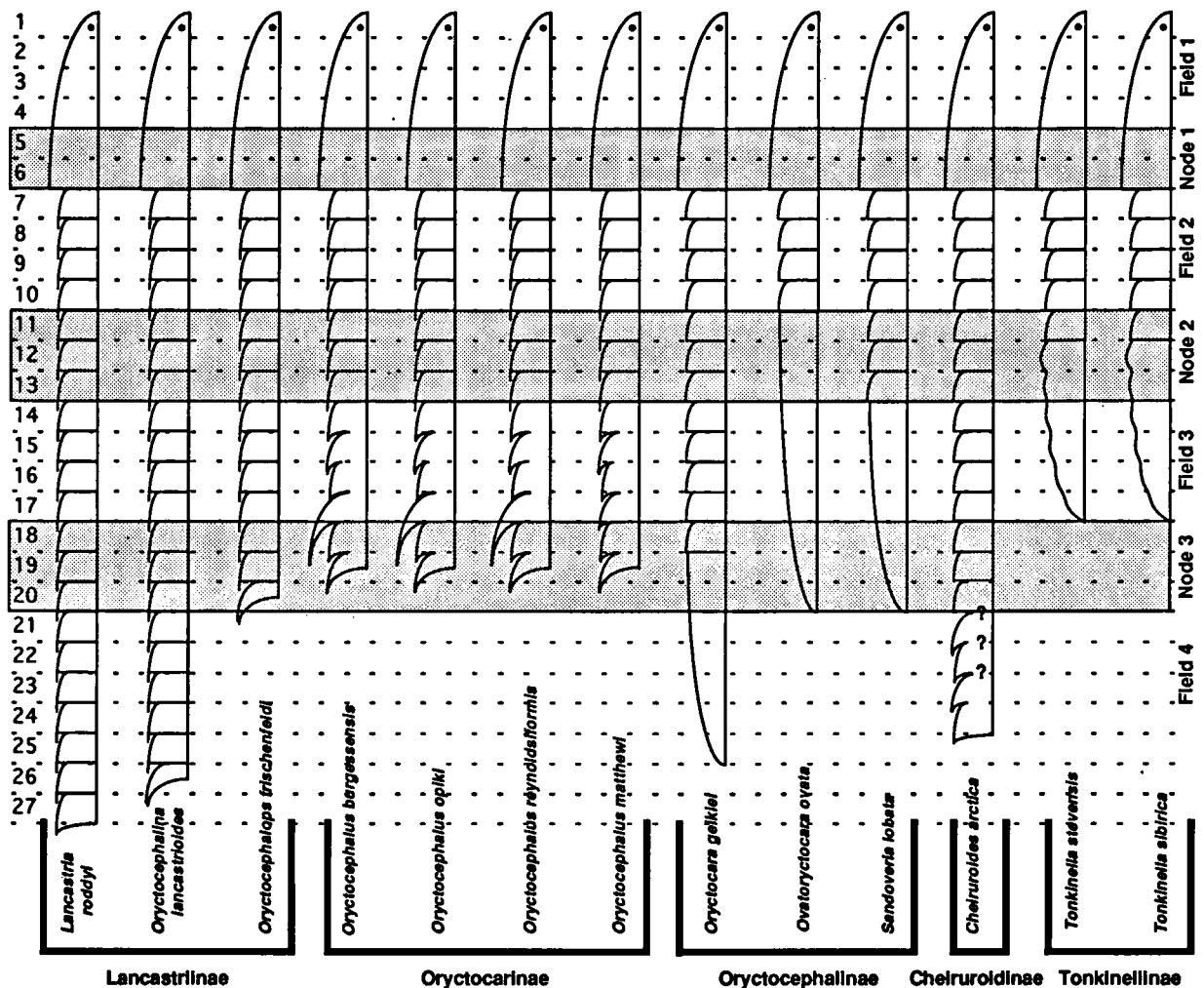


Fig. 1. Distribution of duplomeres (= segments) of representatives of Oryctocephalidae (Corynexochida) relative to the fields and nodes predicted from APT.

(Palmer & Halley, 1979) and their apparent plasticity in morphology (McNamara, 1986, 1988; Hughes, 1991). This contrasts to later trilobite groups, where phylogenies are somewhat better understood and some groups are fixed in their number of thoracic segments (Harrington et al., 1959; McNamara, 1986). The analysis here consisted of establishing the node/field location of: (1) the boundary between the cephalon and thorax; (2) the boundary between the thorax and pygidium; (3) the termination of the trilobite (i.e., total number of segments); (4) the location of the macropleural spine if present; and (5) the boundary between the prothorax and opisthothorax if present.

Information for the analysis is derived from both published and unpublished sources (see Appendix). The data consist of the duplomere location of boundaries or features determined from descriptions, photographs, and/or drawings of complete trilo-

bite specimens. A total of 348 trilobite specimens representing 291 species from Olenellida, Redlichiida, Corynexochida, and Ptychopariida were studied (Appendix). Only a single specimen was recorded per species unless holaspids of a species were reported as varying in the number of either thoracic or pygidial segments. Agnostids and eodiscoids were not included in this analysis due to the uncertainty in the number of duplomeres in the cephalon and/or pygidium.

In this paper, a one-to-one correlation of sclerites (dorsal exoskeleton segment) to somites (soft-body segments) is assumed. Bergström (1973) and Müller & Walossek (1987) discussed the appropriateness of this correlation. However, there are known deviations where the number of appendages do not correlate to the number of *apparent* sclerites. In a recent review of trilobite limbs, Whittington (1992) notes some of these deviations. Trilo-

bite cephalons contain only four appendages (antenna and three walking legs), which suggests four segments. This differs from the common six-part division of the glabella (frontal lobe, four pairs of glabellar lobes, and occipital ring, see below), which suggest six segments instead of four. Each thoracic segment typically possesses only one pair of walking legs, but the soft-shelled trilobite *Tegopelte gigas* Simonetta & Delle Cave, 1978, has three pairs of limbs per thoracic segment. The number of appendages in the pygidia of *Olenoides*, *Phacops*, and *Agnostus* matches the number of segments visible in the pygidial axis, but in the Upper Ordovician *Triarthrus eatoni* (Hall, 1847), the pygidium contains 12 pairs of limbs with only five apparent pygidial segments on the dorsal surface. The Ordovician *Cryptolithus* also contains 12 pairs of limbs with a fewer number of pygidial segments apparent on the dorsal surface. From this discussion, it is apparent that a strict adherence to the one-to-one correlation of sclerites to somites will result in some errors, especially in the number of somites in the pygidium; but, with the limited number of trilobites with known appendages (*Olenoides serratus* (Rominger, 1887); *Kootenia dawsoni* (Walcott, 1889); *Triarthrus eatoni*; *Ceraurus pleurexanthemus* Green, 1832; *Phacops* sp.; *Rhenops* sp.; *Cryptolithus tessellatus* (Green, 1832); *Agnostus pisiformis* (Linnaeus, 1758); *Tegopelte gigas*; and *Naraoia compacta* Walcott, 1912), a more accurate assessment is not possible.

Schram & Emerson (1991) suggested that the segments within trilobites were duplomeres (instead of diplosegments or monosegments) based on the trilobite biramous limbs. Further support for each trilobite segment being at least a diplosegment, if not a duplomere, is provided by the bipartite division of thoracic pleurae (anterior and posterior pleural bands), axial rings (ring and articulating half ring), and pygidial pleurae (anterior and posterior pleural bands). Hessler (1962) suggested that some of these features represent a secondary segmentation, however, an alternative interpretation is that these features represent an expression of the duplomere construction of trilobite somites. In addition, Öpik (1961) illustrated anterior and posterior pairs of "diverticulata" caeca for each thoracic and/or pygidial segment in Redlichiida (*Redlichia* and *Centropheura*) and Ptychopariida (*Papyriaspis*), which also supports a duplomere construction of these segments.

Counting the number of duplomeres (= segments) within the thorax is usually straight forward, each duplomere is well defined. Counting of the number of duplomeres in the cephalon and pygidium from photographs is more difficult. Individual lateral glabellar furrows are commonly effaced or very shallow. This is especially true for the most anterior pair of lateral glabellar furrows, thus the counting of individual lobes in the cephalon can be unreliable. However, the presence of six duplomeres in the cephalon is justifiable, as discussed below. As a result, the initial duplomere in the thorax is deemed number seven (7). The number of duplomeres in a pygidium is also difficult to determine because of the effacement of axial ring furrows. This can occasionally be circumvented by using internal molds of the pygidium, which will commonly display better defined furrows.

Results

An initial study on the number of duplomeres within taxa was undertaken using the corynexochid family Oryctocephalidae. The results of this study were promising for the APT so that a larger study involving other taxonomic groups was undertaken. The results of both analyses are presented because they are not entirely consistent with each other.

Cephalon/thorax boundary

In an initial study of the corynexochid family Oryctocephalidae, all taxa appear to have their cephalon/thorax boundary located at the end of node 1 (duplomere 6, Fig. 1). As mentioned above, the establishment of the number of cephalic duplomeres is sometimes difficult to determine due to the effacement of the lateral glabellar furrows. In most species of Oryctocephalidae, five glabellar lobes and the occipital ring are visible. Very shallow and very short lateral glabellar furrows typically separate the frontal lobe of the glabella from the adjacent lateral glabellar lobes.

In some other groups of trilobites, the number of cephalon duplomeres is more difficult to establish. However, in groups where the lateral glabellar furrows are well defined, there are some taxa that contain six cephalic duplomeres. For example, Palmer & Halley (1979, pls. 1, 8–11, 13–16) alone illustrated several specimens from a variety of taxa that contain six glabellar lobes (including the frontal and occipital ring): (1) in Olenellida the genus *Bristolia* (pl. 1, fig. 6); (2) in Corynexochida the genera *Albertelloides* (pl. 10, figs. 16, 17), *Glossopleura* (pl. 16, fig. 8), *Paralbertella* (pl. 9, fig. 19), *Poliella* (pl. 11, figs. 2, 3), *Ptarmiganoides* (pl. 11, figs. 12, 18), and *Zacanthoides* (pl. 11, fig. 19); and (3) in Ptychopariida the genera *Alokistocarella*? (pl. 15, fig. 21), *Kochiellina* (pl. 8, fig. 3), *Mexicella* (pl. 13, fig. 16), and *Nyella* (pl. 14, figs. 3, 6, 7, 11, 12). In most instances, the anteriormost lateral glabellar furrow is very shallow and located at the junction between the axial furrow and the eye ridge. In taxa with only five cephalic lobes visible, a furrow projecting from this junction is not

visible. If the junction of the eye ridges and axial furrows is homologous in taxa with six and five visible lobes, then this homology indicates that the frontal lobe in taxa with only five lobes is composed of two duplomeres.

As a result, trilobites in this study are believed to have six duplomeres in the cephalon, whether or not they are expressed in the glabella. Bergström (1973) came to the same conclusion that the cephalon consisted of six “segments”, based on the study of olenellids and appendages of other trilobites. However, as noted above, all trilobites species that have known ventral appendages have only four pairs of appendages in the cephalon (Whittington, 1992) with the possible exception of *Rhenops* sp., which may have five pairs of appendages (Bergström & Brassel, 1984). In Crustacea, the number of segments and appendages within the head do not always display a one to one match (Schram, written communication 1993). Thus, the number of limbs in trilobites may not be a reliable indication of cephalic segments. At this time, it cannot be established if the dorsal shield illustrates more duplomeres than actually present or if trilobites underwent a reduction of limbs in the head region. As a result, this analysis will treat the cephalon as containing six duplomeres, but will later explore the shift in the distribution of body segments if the cephalon contains only four duplomeres.

Thorax/pygidium boundary

The analysis of the position of the thorax/pygidium boundary is based on the assumption that the cephalon contains six duplomeres. This assumption is based on several taxa from different trilobite groups containing six cephalic duplomeres and the likelihood of the frontal lobe of other taxa containing two duplomeres (see above).

In the Oryctocephalidae, the position of the thorax/pygidial boundary varies among the different subfamilies and to some extent within the subfamilies (Fig. 1). Lancastriinae have a thorax/pygidium boundary in node 3 or field 4. Oryctocariinae show the thorax/pygidium boundary consistently at the end of node 2. Oryctocephalinae show the thorax/pygidium boundary in either nodes 2 or

3. Cheiruroidinae show the boundary at the end of node 3 and Tonkinellinae show the boundary within node 2.

If APT is correct, then the boundary between the thorax and pygidium should fall at the end of duplomeres 10, 11, 12 or 13 (node 2) or 17, 18, 19, or 20 (node 3). In the analysis of 80 corynexochids, the distribution of the number of duplomeres is not limited to the predicted node regions, but rather clustered in and around node 2 and field 3 (Fig. 2). In fact, the data resemble normally distributed data, although a goodness of fit *G*-test illustrates that they are not ($G = 54.6 > \chi^2_{0.001 [17]} = 40.8$, $p < 0.001$). Corynexochids have a mean boundary location at 14.2 duplomeres (i.e., having 8.2 thoracic segments, $s = 2.6$) with a peak at duplomere 13. The mean falls in or near node 2, as does the peak at duplomere 13, however, only 52% of the corynexochids fall within the nodes. If we assume an expected normal distribution around the mean of 14.2 ± 2.6 , then we see that node 2 contains 75% more specimens than expected, whereas node 3 contains 50% less than expected, although this last value is not significant (Table I). This illustrates a tendency for the thorax/pygidial boundary to occur within node 2. It should be noted that duplomeres 13, 14, and 15 contain 75% of the specimens.

An analysis of 197 ptychopariids shows little correspondence between the thorax/pygidium boundary and the location of the nodes (Fig. 2). These data also resemble normally distributed data, although they too are in fact not ($G = 44.8 > \chi^2_{0.025 [27]} = 43.194$, $p < 0.025$). Ptychopariids have a mean boundary location of 19.7 duplomeres (i.e., having 13.7 thoracic segments, $s = 4.1$) with two peaks: one at duplomere 15 and the other at duplomere 19. The mean falls within node 3 as does the peak at duplomere 19, however, the peak at duplomere 15 falls within field 3. Only 53% of the ptychopariids fall within the nodes. If we again assume a normal distribution around the mean of 19.7 ± 4.1 , then we see that node 2 contains 30% less specimens than expected (not significant, Table I), whereas node 3 contains 45% more than expected. This illustrates a small tendency for the thorax/pygidial boundary to occur within node 3.

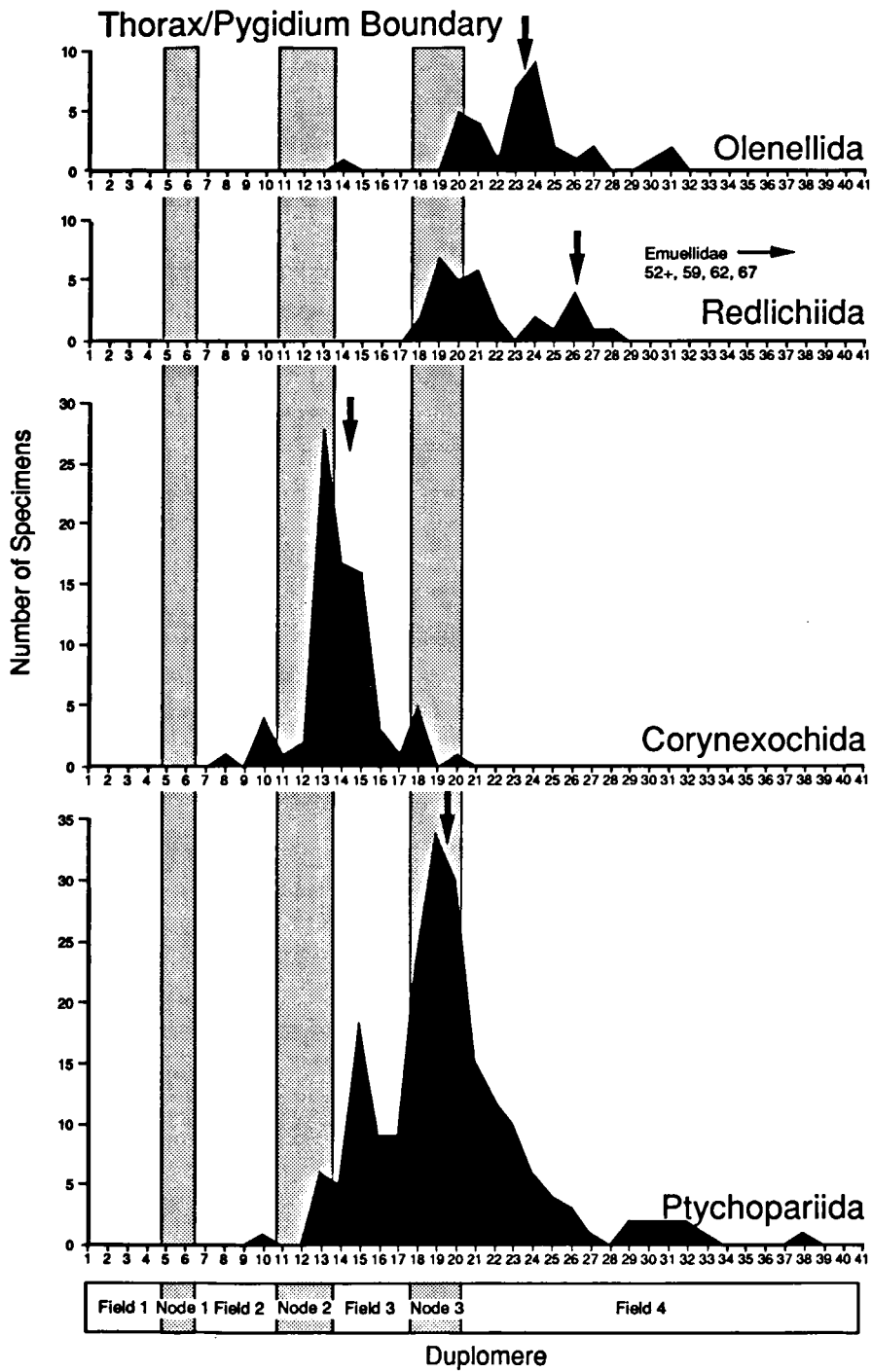


Fig. 2. Distribution of the thorax/pygidium boundary denoted by the number of the last diplomere in the thorax of olenellids, redlichiids, corynexochids, and ptychopariids. Six duplomeres are assumed in the cephalon. Arrows indicate mean values.

Table I. Goodness of fit *G*-test for the number of samples (taxa) with tagmata boundaries within the predicted APT nodes. The first set of nodes assumes the cephalon contains 6 duplomeres and the second set (†) assumes 4 duplomeres. No. of observed = the number of samples that have a tagmata boundary within the predicted nodes; No. of expected = the number of samples that would occur in the predicted node if we assume a normal distribution with the parameters listed behind tagmata boundary; % Change = the difference between the observed and expected counts divided by the expected count; + = percentage increase above the predicted counts; – = percentage decrease below the predicted counts; numbers in the χ^2 column are *p* values.

Taxa/Tagmata boundary	Node	No. of observed	No. of expected	% Change	<i>G</i>	$\chi^2_{0.001[1]} = 10.828$
Corynexochida						
Thorax/pygidium ($\bar{x} = 14.2$, $s = 2.6$, $n = 80$)						
	Node 2	35	20	+ 75%	32.869	< 0.001
	Node 2†	63	38	+ 66%	43.320	< 0.001
	Node 3	7	14	– 50%	– 1.420	> 0.1
	Node 3†	1	1	0%	– 0.152	> 0.5
Total segment ($\bar{x} = 19.6$, $s = 2.4$, $n = 80$)						
	Node 2	1	0	+ 100%	1.603	> 0.1
	Node 2†	4	3	+ 33%	3.448	> 0.05
	Node 3	57	39	+ 46%	24.744	< 0.001
	Node 3†	54	46	+ 17%	18.204	< 0.001
Ptychopariida						
Thorax/pygidium ($\bar{x} = 19.7$, $s = 4.1$, $n = 197$)						
	Node 2	7	10	– 30%	2.353	> 0.1
	Node 2†	29	22	+ 32%	14.339	< 0.001
	Node 3	97	67	+ 45%	40.510	< 0.001
	Node 3†	91	72	+ 26%	28.333	< 0.001
Total segment ($\bar{x} = 24.0$, $s = 3.5$, $n = 192$)						
	Node 2	0	0	–	–	–
	Node 2†	0	0	–	–	–
	Node 3	17	23	– 26%	– 0.969	> 0.1
	Node 3†	57	47	+ 21%	16.936	< 0.001

The analyses of 35 olenellids and 36 redlichiids also show little correspondence between the thorax/pygidium boundary and the location of the nodes (Fig. 2). Olenellids have a mean of boundary location at 23.4 duplomeres (17.4 thoracic segments, $s = 3.3$), which falls within field 4. Redlichiids have a mean of boundary location at 26.1 duplomeres (20.1 thoracic segments, $s = 12.7$), which also falls within field 4. The majority of olenellids (one exception) and all redlichiids have their thorax/pygidium boundary occurring within node 3 or field 4.

Total number of duplomeres

In the Oryctocephalidae, the termination of the exoskeleton also varies among and within the dif-

ferent subfamilies (Fig. 1). Most taxa terminate at node 3, either at the beginning, within, or at the end of the node. Some taxa in Cheiruroidinae, Lancastriinae, and Oryctocephalinae terminate in field 4.

The analysis of 80 corynexochids shows a relatively strong correlation to the termination of the pygidium in node 3, which contains 70% of the sample (Fig. 3). Corynexochids have a mean termination at 19.6 duplomeres ($s = 2.4$) with a single peak at duplomere 19, which falls in node 3. If we assume a normal distribution, then we see that node 3 contains 46% more specimens than expected (Table I). This illustrates a tendency for the termination of the body to occur within node 3.

The analysis of 192 ptychopariids shows little correspondence of body termination to occur in node 3 (Fig. 3). Ptychopariid terminations general-

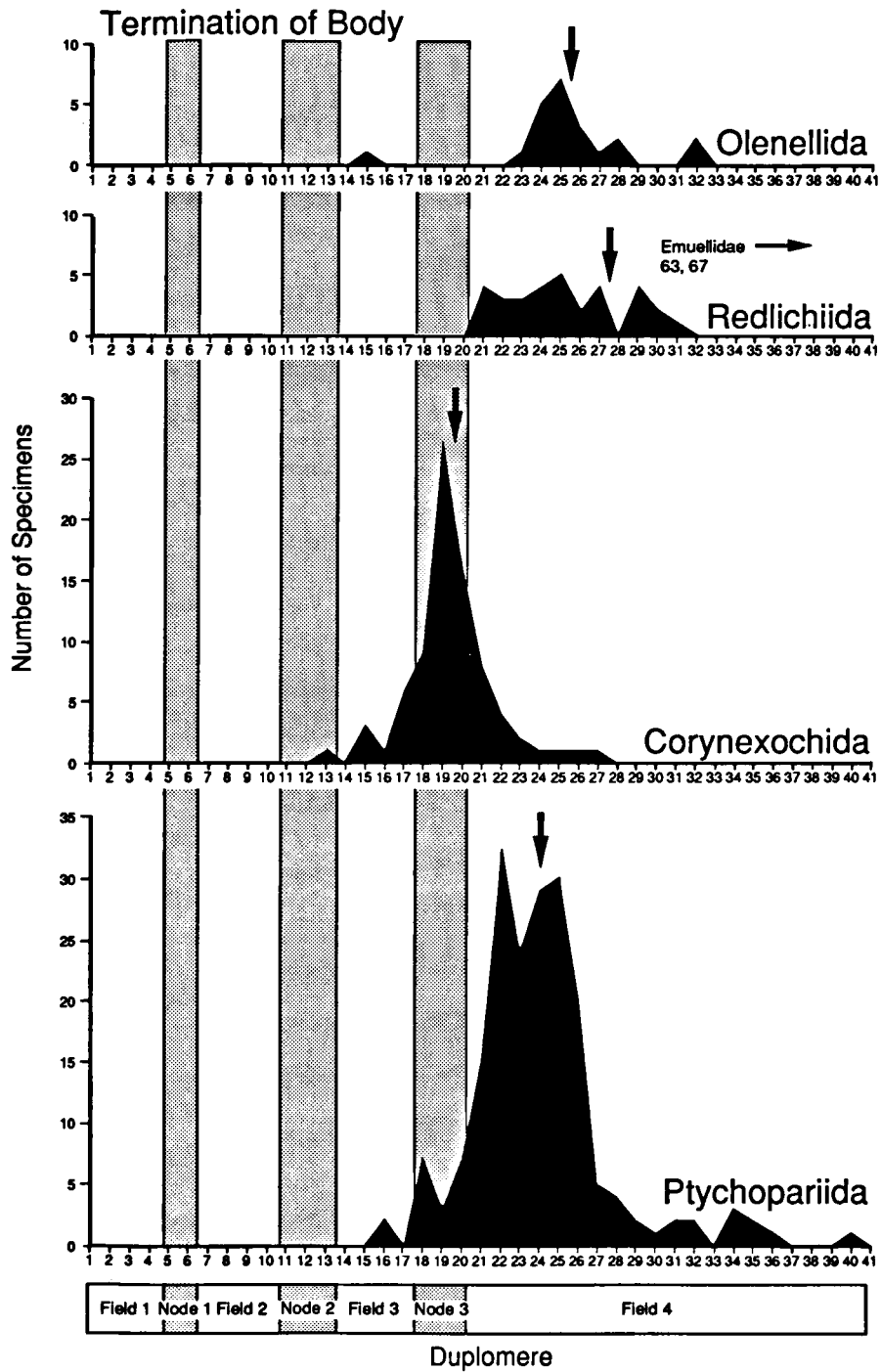


Fig. 3. Distribution of the total number of duplomeres in the olenellids, redlichiids, corynexochids, and ptychopariids. Six duplomeres are assumed in the cephalon. Arrows indicate mean values.

Table II. Macropleural spine duplomere location.

Species	Thoracic	Pygidial
REDLICHIIIDA		
<i>Balcoracania bailyi</i> Pocock, 1970	15	
<i>Balcoracania flindersi</i> Pocock, 1970	15	
<i>Bathynotellus yermolaevi</i> Lermontova, 1940	17	
<i>Bathynotus holopyga</i> (Hall, 1859)	17	
<i>Despujolsia rochi</i> Neltner & Poctey, 1949	17	
<i>Emuella dalgarnoi</i> Pocock, 1970	15	
<i>Emuella polymea</i> Pocock, 1970	15	
<i>Resserops resserianus</i> Richter & Richter, 1940	15	
<i>Richterops falloti</i> Hupé, 1953	17	
OLENELLIDA		
<i>Biceratops nevadensis</i> Pack & Gayle, 1971	9	
<i>Fallotaspis</i> sp.	9	
<i>Fallotaspis typica</i> Hupé, 1953	9	
<i>Olenelloides armatus</i> Peach, 1894	9	
<i>Olenellus bonnensis</i> Resser & Howell, 1938	9	
<i>Olenellus clarki</i> (Resser, 1928)	9	
<i>Olenellus fremonti</i> Walcott, 1910	9	
<i>Olenellus georgiensis</i> Resser & Howell, 1938	9	
<i>Olenellus getzi</i> Dunbar, 1925	9	
<i>Olenellus lapworthi</i> Peach & Horne, 1892	9	
<i>Olenellus reticulatus</i> Peach, 1894	9	
<i>Olenellus roddyi</i> Resser & Howell, 1938	9	
<i>Olenellus similaris</i> Resser & Howell, 1938	9	
<i>Olenellus thompsoni</i> (Hall, 1859)	9	
<i>Olenellus transitans</i> (Walcott, 1910)	9	
<i>Olenellus vermontanus</i> (Hall, 1859)	9	
<i>Olenellus yorkensis</i> Resser & Howell, 1938	9	
CORYNEXOCHIDA		
<i>Albertella bosworthi</i> Walcott, 1908	10, 13	14
<i>Albertella nitida</i> Resser, 1936	9, 13	14
<i>Anoria tontoensis</i> (Walcott, 1916)	11	
<i>Bathyriscus adaeus</i> Walcott, 1916		17
<i>Oryctocephalus burgessensis</i> Resser, 1938		17
<i>Oryctocephalus reynoldsi</i> Reed, 1899		17
PTYCHOPARIIDA		
<i>Damesella paronai</i> (Airaghi, 1902)		19
<i>Drepanura premesnili</i> Bergeron, 1899		20
<i>Irvingella nuneatonensis</i> (Sharman, 1886)	8	
<i>Levisella brevifrons</i> Rasetti, 1944	11	
<i>Loganellus macropleurus</i> Rasetti, 1944	11	
<i>Proceratopyge rectispinus</i> (Troedsson, 1937)		16

ly occur in field 4 (90%), which is not incompatible with APT. Ptychopariids have a mean termination at 24.0 duplomeres ($s = 3.5$) with two peaks at 22

and 25 duplomeres. Only 9% of the specimens fall within node 3, 26% less than expected from a normal distribution (not significant, Table I).

The terminations of nearly all olenellids and redlichiiids studied fall or would fall (if the pygidium was preserved) in field 4. *Olenellus armatus* Peach, 1894, provides the only exception with eight thoracic segments and probably one pygidial segment. Olenellids have a mean termination location at 25.4 duplomeres ($s = 3.3$, $n = 22$), with a peak at 25 duplomeres. Redlichiiids have a mean termination location at 27.6 duplomeres ($s = 12.3$, $n = 36$), with no prominent peak.

Macropleural spines

The total number of taxa possessing macropleural spines is limited ($n = 38$). However, some distinctive patterns are present (Table II). In the olenellids ($n = 17$), when macropleural spines occur, they occur in thoracic segments at duplomere 9. In the redlichiiids ($n = 9$), macropleural spines occurred in thoracic segments at duplomere 15 ($n = 5$) or 17 ($n = 4$). Corynexochids show three groups of duplomeres where macropleural spines are located. Data for this group consist of only six species, however, two species of *Albertella* possess three pairs of macropleural spines, thus $n = 10$. The highest "concentration" of macropleural spines is at duplomere 17, which is in the pygidium. However, this "concentration" consists of only 3 species. Ptychopariids ($n = 6$) also show three groups of duplomeres with macropleural spines, four fall within nodes and one each at duplomeres 8 and 16. However, the species count is too low for any further meaningful discussion about these distributions.

Prothorax/opisthothorax boundary

The boundary between the prothorax and opisthothorax is marked by an "abrupt" reduction in the size of pleurae in some genera of Olenellida. The boundary between the prothorax and opisthothorax occurs at the end of duplomeres 19 (*Ellip-tocephala*), 20 (*Bristolia*, *Callavia*, and *Olenellus*),

and 23 (*Fallotaspis* and *Nevadia*). Duplomeres 19 and 20 fall within node 3, whereas duplomere 23 falls within field 4.

The Emuellidae are multisegmented Redlichiida, which can contain 46+ to 61 thoracic segments (*Emuella* and *Balcoracania*; Pocock, 1970). Pocock made a distinction between the pleurae that are anterior of the macropleural spine (duplomere 21, field 4) to those posterior of the spine based on their size, thus they could be interpreted as prothoracic and opisthothoracic segments. However, the pleurae posterior of the macropleural spine are roughly the same shape as the pleurae anterior of the spine. Excluding the macropleural spine, the pleurae gradually decrease in size from the first thoracic segment to the last. Thus, the posterior segments of the Emuellidae probably do not represent an opisthothorax.

Evaluation of the arthropod pattern theory and Cambrian trilobites

The morphology of Cambrian trilobites appears to be constrained at least to a limited degree by some genetic patterning program. Olenellida, Redlichiida, Corynexochida, and Ptychopariida all appear to have six duplomeres within the cephalon. This pattern agrees with the APT, for this places the boundary between the cephalon and thorax at the end of node 1. However, the locations for the thorax/pygidium boundaries, locations of gonopores and anus, and body terminations differ from the predicted locations.

Corynexochids may be the group of trilobites most constrained by duplomere patterns as predicted by APT. Beside the location of cephalon/thorax boundary being in node 1, a high proportion of taxa have their thorax/pygidium boundaries in node 2 and their body terminations in node 3. The applicability of APT to corynexochids is best observed in the Oryctocephalidae, with all taxa investigated conforming to the predicted APT distributions. The investigation of a larger data set, however, illustrates that the corynexochids were not entirely constrained in the location of thorax/pygidium boundary or the body termination. This

would also suggest that some taxonomic groups within the corynexochids are more constrained than others.

Harrington et al. (1959) suggested that macropleural spines mark the location of reproductive organs. Although, Whittington (1992) proposed that macropleural spines may have served as a stabilizer or aided in digging. If the idea of Harrington et al. and APT are true, then macropleural spines should occur within nodes or at duplomeres 9 or 16. These positions in other arthropods are the common location of gonopores and/or the anus (Schram & Emerson, 1991). This pattern was not observed in the corynexochids, but instead, when present, the macropleural spines occurred on the pygidium at duplomere 17. This location is one more segment than predicted by APT, but, Schram & Emerson (1991) place the anus of the corynexochid *Olenoides* at duplomere 17. Perhaps the macropleural spine at this location reflects the position of the anus. However, the anus of the Devonian trilobites *Phacops* and *Asteropyge* (= *Rhenops* sp.) is located at the posterior end of the pygidium (Bergström, 1973), as it is in *Olenoides* (Whittington, 1992), which has a total of 18 duplomeres. No macropleural spines are located at the end of the pygidium in corynexochids, thus it is unclear what the macropleural spine indicates in corynexochids.

Ptychopariids appear to be less constrained in their location of the thorax/pygidium boundary and body termination. The thorax/pygidial boundary ranges over several duplomeres, but there is a peak location at duplomere 19 within node 3. However, ptychopariids have a secondary peak at duplomere 15 in field 3. This location is one duplomere less than would be predicted from other arthropods (Schram & Emerson, 1991). Nearly all ptychopariids have body termination in field 4. The common termination in field 4 is compatible with APT, correlating with several groups discussed by Schram & Emerson (1991) that terminate in field 4. The data on macropleural spines are meager, but the five of the six species used contain macropleural spines within nodes 2 or 3 or at duplomere 16 in field 3. These results suggest that a sequence pattern program is functioning within the ptychopariids,

but unlike that predicted by APT, morphology is not strictly limited in the number of duplomeres.

The olenellids and redlichiids generally show their thorax/pygidium boundary and body termination in field 4, which is compatible with APT. The boundary between the prothorax and opisthothorax in olenellids falls in either node 3 or field 4, which is also compatible with APT. The location of macropleural spines cluster at duplomere 9 in the olenellids and duplomeres 15 and 17 in the redlichiids. The macropleural spines in the olenellids at duplomere 9 in field 2 are in agreement with Harrington et al.'s (1959) interpretation of macropleural spines representing the location of the gonopores. The situation of macropleural spines in redlichiids at duplomere 15 is one off from the predicted duplomere 16 in field 3 and may also indicate the location of the gonopores. As in the corynexochids, the macropleural spines at duplomere 17 may also represent the location of the gonopores and/or anus.

Four duplomere cephalon

If we assume the cephalon contains four duplomeres, as indicated by the number of appendages in the head region, then the location of boundaries and other morphological features will shift to a lower duplomere (this would be equivalent to shifting the distributions shown in Figs. 2 and 3 to the left by two duplomeres). In general, the use of a four duplomeres cephalon provides for better alignment of trilobite species to the predicted APT patterns. However, given the spread of data points, this shifting of duplomere counts still fails to fit all of the data into the predicted nodes.

If the cephalon contains only four duplomeres, then the boundary between the cephalon and thorax occurs at the *beginning* of node 1, which still agrees with APT.

In the corynexochid family Oryctocephalidae, the presence of only four duplomeres in the cephalon would align some of the thorax/pygidium boundary and body termination to the fields away from the nodes. For example, in Tonkinellinae, the thorax/pygidium boundary would fall within field

2 and the body termination would fall within field 3. In contrast, the boundaries of Oryctocarinae would still be located within nodes or at node boundaries. Thus, the Oryctocephalidae would yield fewer examples that would agree with the APT predictions.

In the broader study of corynexochids and ptychopariids, the assumption of a four duplomere cephalon typically provides more examples of trilobites that align with the nodes (Table I). The occurrence of corynexochids increased in the nodes from 51% to 79% for the thorax/pygidium boundary and no overall change in the 72% for the body termination. The occurrence of ptychopariids increased in the nodes from 53% to 61% for the thorax/pygidium boundary and from 9 to 30% for the body termination. The largest changes were the thorax/pygidium boundary of corynexochids in node 2, which changed from 35 to 63 specimens, and the body termination in ptychopariids in node 3, which changed from 17 to 57 specimens. However, in some individual examples the changes are trivial, e.g. an increase from one corynexochid to four in node 2 for the body termination.

The shift of boundaries in olenellids and redlichiids provides only a few significant changes. A few redlichiids would have their thorax/pygidium boundary within field 3 or at the boundary between field 3 and node 3. Perhaps the most significant change is the location of the macropleural spine in the olenellids and redlichiids. Where these spines originally occurred at the predicted duplomere 9 in olenellids, they would now occur at duplomere 7 in field 2, which does not agree with the APT predictions. In redlichiids, the shift would place the spine at duplomere 13, which is at the end of node 2, and duplomere 15, which is one less than the predicted node 16 in field 3.

Implications

The results of this analysis indicate that Cambrian trilobites are relatively limited in the number of duplomeres that they can possess in the cephalon, thorax, pygidium, and the body as a whole. The corynexochids appear to be the most constrained,

with tagmata boundaries commonly occurring at nodes 2 and 3. This may imply that corynexochids possessed a genetic program that constrained the number of duplomeres and that they could not vary in the number of segments to any major degree. This accords with the general nature of corynexochids being geographically widespread, stratigraphically long ranging, and morphologically conservative.

Whereas there are examples of the limitation on the placement of the macropleural spines and the end of the thorax and pygidium in Cambrian trilobites, these limitations are not strict. For example, the ptychopariids illustrate a trend of the thorax/pygidium boundary occurring in node 3, but there are several examples of the boundary occurring in field 3. Even within the relatively constrained corynexochids, there are several taxa that have their morphologic boundaries falling outside the nodes. This variation suggests that there are other processes controlling the placement of tagmata boundaries, gonopores, and the anus in Cambrian trilobites that are not influencing the same morphological features in modern arthropods.

The duplome location of nodes and fields may have differed in Cambrian trilobites compared to later taxa. In the corynexochids, 75% of the taxa studied had the thorax/pygidium boundary at the end of duplomeres 13, 14, and 15. Perhaps in corynexochids the location of node 2, which is normally duplomeres 10–13, had shifted to the posterior to occur at duplomeres 13–15. Ptychopariids have a peak of the thorax/pygidium boundary at duplome 15, which may represent an anterior shift from the predicted occurrence at duplome 16. There is also a concentration of macropleural spines of corynexochids and redlichiids at duplome 17 instead of the predicted duplome 16. This may again represent a shift in location.

An alternative explanation for the apparent shift in some of the nodes discussed above may be that the cephalon contains only four duplomeres. If this is true, then the peak values at duplomeres 13, 14, and 15 in the corynexochids would change to encompass node 2 and, thus, no shift is needed for this example. However, universal application of only four duplomeres in the cephalon does not

solve all of the “offset” peaks from the expected nodes (e.g., duplome 17 then becomes duplome 15, which is one *less* than the expected location) and the shifting of nodes may have still occurred.

The trend of tagmata boundaries to concentrate in or near nodes suggests that genetic patterning programs that controlled the discrete placement of morphologic boundaries existed in Cambrian trilobites. However, variation of the boundary placements away from the nodes and the potential shifting of nodes within the duplome sequence suggest that the genetic program could be easily changed. This variation is similar to other Cambrian arthropods (Briggs, 1990), but contrasts to the limited range of variation proposed for most modern groups of arthropods (Schram & Emerson, 1991). If modern arthropods are genetically constrained in the distribution of morphological features as predicted by APT, then this contrast between Cambrian and modern arthropods supports the hypothesis that Cambrian organisms contained relatively simple genetic codes that could easily accommodate changes to produce new *Baupläne* (Vermeij, 1974; McNamara, 1983, 1986, 1988; Runnegar & Bentley, 1983; Erwin & Valentine, 1984; Jacobs, 1987, 1990).

Conclusions

The Arthropod Pattern Theory proposed by Schram & Emerson (1991) appears to hold true to a certain degree for Cambrian trilobites. The boundary between the cephalon and thorax occurs at the end of node 1 (duplome 6) in olenellids, redlichiids, corynexochids, and ptychopariids. The boundary between the thorax and pygidium is in field 4 (post duplome 20) for most olenellids and redlichiids, in and around node 2 for corynexochids, and in and around node 3 for ptychopariids. The termination of the body occurs in field 4 for most olenellids, redlichiids, and ptychopariids, but they cluster in and around node 3 for corynexochids. The occurrence of macropleural spines in olenellids, redlichiids, and corynexochids cluster at either duplomeres 9 or 17, which closely match the predictions from APT. The boundaries between

the prothorax and opisthothorax of some olenellids cluster around node 3.

The existence of many trilobite taxa matching the predicted pattern of tagmata boundary location suggests that a genetic control that fixes their location had developed in Cambrian trilobites. However, the spread of the boundary location away from expected nodes suggests that Cambrian trilobites were not strictly constrained by this genetic control and that other factors influenced the number of duplomeres within the different body parts. This flexibility in boundary locations supports the idea that Cambrian trilobites possessed relatively simple genetic control that allowed changes in the *Bauplan* that is not exhibited by modern arthropods.

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Appendix. Listing of trilobite taxa, number of thoracic and pygidial segments, age and reference.

Taxa	Thorax	Pygidium	Age	Reference
REDLICHIIIDA				
<i>Acadoparadoxides sacheri</i> (Barrande, 1852)	20	3?	Middle Cambrian	Horný & Bastl, 1970
<i>Balcoracania bailyi</i> Pocock, 1970	53	4?	Lower Cambrian	Pocock, 1970
<i>Balcoracania flindersi</i> Pocock, 1970	61	?	Lower Cambrian	Pocock, 1970
<i>Bathynotellus yermolaevi</i> Lermontova, 1940	13	5?	Middle Cambrian	Harrington et al., 1959
<i>Bathynotus holopyga</i> (Hall, 1859)	13	3	Lower Cambrian	Harrington et al., 1959
<i>Bergerroniellus asiaticus</i> Lermontova, 1940	15	1	Lower Cambrian	Harrington et al., 1959
<i>Despujolsia rochi</i> Neltner & Poctey, 1949	14	4?	Lower Cambrian	Harrington et al., 1959
<i>Dolerolenus zoppii</i> (Meneghini, 1882)	15	2	Middle Cambrian	Harrington et al., 1959
<i>Eccaparadoxides brachyrachis</i> Linnarsson, 1883	18	2	Middle Cambrian	Courtesole, 1973
<i>Eccaparadoxides pusillus</i> (Barrande, 1846)	16	3?	Middle Cambrian	Horný & Bastl, 1970
<i>Eccaparadoxides rouvillei</i> Miquel, 1905	20	3	Middle Cambrian	Courtesole, 1973
<i>Edelsteinaspis ornata</i> Lermontova, 1940	15	6	Middle Cambrian	Suvorova, 1964
<i>Ellipsocephalus hoffi</i> (Schlotheim, 1823)	12	3	Middle Cambrian	Whittington, 1992
<i>Ellipsocephalus gripi</i> (Kautsky, 1945)	14	1	Lower Cambrian	Harrington et al., 1959
<i>Emuella dalgarnoi</i> Pocock, 1970	56	5?	Lower Cambrian	Pocock, 1970
<i>Emuella polymeia</i> Pocock, 1970	46+	?	Lower Cambrian	Pocock, 1970
<i>Galahetes fulcrosus</i> Öpik, 1975	13	6	Middle Cambrian	McNamara, 1981
<i>Gigantopygus bondoni</i> Hupé, 1953	15	3	Lower Cambrian	Harrington et al., 1959
<i>Hicksina elvensis</i> (Vogdes, 1925)	19	2	Lower Cambrian	Harrington et al., 1959
<i>Hindermeyeria insecta</i> (Richter & Richter, 1940)	14	1	Lower Cambrian	Harrington et al., 1959
<i>Lermontovia dzevanowskii</i> Suvorova, 1956	23	1	Lower Cambrian	Harrington et al., 1959
<i>Longianda termieri</i> Hupé, 1953	15	4	Lower Cambrian	Harrington et al., 1959
<i>Paradoxides carens</i> (Barrande, 1852)	18	3?	Middle Cambrian	Horný & Bastl, 1970
<i>Paradoxides davidis</i> Salter, 1863	20	3	Middle Cambrian	Whittington, 1992
<i>Paradoxides gracilis</i> (Boeck, 1838)	20	3	Middle Cambrian	Whittington, 1992
<i>Paradoxides hicksii</i> Salter, 1866	22	2	Middle Cambrian	Morris & Fortey, 1985
<i>Paradoxides paradoxissimus</i> (Wahlenberg, 1821)	21	4	Middle Cambrian	Harrington et al., 1959
<i>Redlichia chinensis</i> Walcott, 1905	16	2	Lower Cambrian	Harrington et al., 1959
<i>Redlichia mansayi</i> Resser & Endo, 1937	15	1?	Middle Cambrian	Whittington, 1992
<i>Resserops resserianus</i> Richter & Richter, 1940	12	7	Lower Cambrian	Harrington et al., 1959
<i>Richterops falloti</i> Hupé, 1953	14	7	Lower Cambrian	Harrington et al., 1959
<i>Xystridua saintsmithi</i> (Chapman, 1929)	13	4	Middle Cambrian	Harrington et al., 1959
<i>Xystridura altera</i> Öpik, 1975	13	7	Middle Cambrian	McNamara, 1981
<i>Xystridura carteri</i> Öpik, 1975	13	4	Middle Cambrian	McNamara, 1981
<i>Xystridura templetonensis</i> (Chapman, 1929)	13	6?	Middle Cambrian	McNamara, 1981
<i>Yunnanocephalus yunnanensis</i> (Mansuy, 1912)	14	1	Lower Cambrian	Harrington et al., 1959
OLENELLIDA				
<i>Biceratops nevadensis</i> Pack & Gayle, 1971	18	1?	Lower Cambrian	Whittington, 1992
<i>Bondonella typica</i> Hupé, 1953	17	2	Lower Cambrian	Harrington et al., 1959
<i>Callavia broeggera</i> (Walcott, 1890)	18	1	Lower Cambrian	Harrington et al., 1959

Appendix. Continued.

Taxa	Thorax	Pygidium	Age	Reference
<i>Daguinaspis ambroggii</i> Hupé & Abadie, 1950	17	1	Lower Cambrian	Harrington et al., 1959
<i>Ellipsocephala asaphoides</i> Emmons, 1844	18	1	Lower Cambrian	Harrington et al., 1959
<i>Fallotaspis</i> sp.	15		Lower Cambrian	Nelson, 1977
<i>Fallotaspis typica</i> Hupé, 1953	21	1	Lower Cambrian	Harrington et al., 1959
<i>Holmia kjerulfi</i> (Linnarsson, 1871)	16	2	Lower Cambrian	Whittington, 1992
<i>Holmia lapponica</i> Ahlberg & Bergström, 1982	15	2	Lower Cambrian	Ahlberg & Bergström, 1982
<i>Holmia rowei</i> Resser & Howell, 1938	17	1	Lower Cambrian	Resser & Howell, 1938
<i>Holmiella</i> sp.	18		Lower Cambrian	Nelson, 1977
<i>Judomia rossea</i> Jell & Repina, 1992	17	1	Lower Cambrian	Jell & Repina, 1992
<i>Kjerulfia lata</i> Kiar, 1917	18	1	Lower Cambrian	Harrington et al., 1959
<i>Neltneria jaqueti</i> (Nelter & Poctey, 1950)	17	3?	Lower Cambrian	Harrington et al., 1959
<i>Neopholenellus multinodus</i> (Palmer, 1979)	17		Lower Cambrian	Palmer & Halley, 1979
<i>Nevadella</i> sp.	24		Lower Cambrian	Nelson, 1977
<i>Nevadia</i> sp.	15		Lower Cambrian	Nelson, 1977
<i>Nevadia weeksi</i> Walcott, 1910	21	1	Lower Cambrian	Whittington, 1992
<i>Olenelloides armatus</i> Peach, 1894	8	1?	Lower Cambrian	Harrington et al., 1959
<i>Olenellus bonnensis</i> Resser & Howell, 1938	18	?	Lower Cambrian	Resser & Howell, 1938
<i>Olenellus clarki</i> (Resser, 1928)	14		Lower Cambrian	Nelson, 1977
<i>Olenellus fremonti</i> Walcott, 1910	14		Lower Cambrian	Nelson, 1977
<i>Olenellus geogensis</i> Resser & Howell, 1938	25	1	Lower Cambrian	Resser & Howell, 1938
<i>Olenellus getzi</i> Dunbar, 1925	18	1	Lower Cambrian	Resser & Howell, 1938
<i>Olenellus lapworthi</i> Peach & Horne, 1982	14	?	Lower Cambrian	Cowie & McNamara, 1978
<i>Olenellus reticulatus</i> Peach, 1894	14	?	Lower Cambrian	Cowie & McNamara, 1978
<i>Olenellus roddyi</i> Resser & Howell, 1938	19	1?	Lower Cambrian	Resser & Howell, 1938
<i>Olenellus similaris</i> Resser & Howell, 1938	18		Lower Cambrian	Resser & Howell, 1938
<i>Olenellus</i> sp.	14		Lower Cambrian	Nelson, 1977
<i>Olenellus thompsoni</i> (Hall, 1859)	19	1	Lower Cambrian	Resser & Howell, 1938
<i>Olenellus thompsoni</i> (Hall, 1859)	18	1	Lower Cambrian	Whittington, 1992
<i>Olenellus transitans</i> (Walcott, 1910)	15 +		Lower Cambrian	Resser & Howell, 1938
<i>Olenellus vermontanus</i> (Hall, 1859)	25	1	Lower Cambrian	Resser & Howell, 1938
<i>Olenellus yorkensis</i> Resser & Howell, 1938	20	1	Lower Cambrian	Resser & Howell, 1938
<i>Wanneria walcottanus</i> (Wanner, 1910)	17	1	Lower Cambrian	Harrington et al., 1959
CORYNEXOCHIDA				
<i>Abakania usitata</i> Repina, 1973	7	2	Lower Cambrian	Poletaeva, 1973
<i>Albertella bosworthi</i> Walcott, 1908	7	6	Middle Cambrian	Rasetti, 1951
<i>Albertella helena</i> Walcott, 1908	7	5	Middle Cambrian	Schwimmer, 1973
<i>Albertella microps</i> Rasetti, 1951	7	4	Middle Cambrian	Rasetti, 1951
<i>Albertella nitida</i> Resser, 1936	7	5	Middle Cambrian	Rasetti, 1951
<i>Anoria baton</i> (Walcott, 1916)	7	6	Middle Cambrian	Schwimmer, 1973
<i>Anoria baton</i> (Walcott, 1916)	8	6	Middle Cambrian	Schwimmer, 1973
<i>Athabaskia bithus</i> (Walcott, 1916)	8	6	Middle Cambrian	Campbell, 1974
<i>Athabaskia howelli</i> (Walcott, 1886)	8	4	Middle Cambrian	Palmer, 1954
<i>Athabaskia wasatchensis</i> (Resser, 1939)	8	5	Middle Cambrian	Campbell, 1974
<i>Bathyriscus adaeus</i> Walcott, 1916	8	7	Middle Cambrian	Rasetti, 1951
<i>Bathyriscus brighamensis</i> Resser, 1939	9	5	Middle Cambrian	Campbell, 1974
<i>Bathyriscus brighamensis</i> Resser, 1939	9	6	Middle Cambrian	Campbell, 1974
<i>Bathyriscus fimbriatus</i> Robison, 1964	8	7	Middle Cambrian	Robison, 1971
<i>Bathyriscus fimbriatus</i> Robison, 1964	8	8	Middle Cambrian	Robison, 1971
<i>Bathyriscus haydeni</i> (Meek, 1873)	9	6	Middle Cambrian	Schwimmer, 1973
<i>Bathyriscus rotundatus</i> (Rominger, 1887)	9	6	Middle Cambrian	Rasetti, 1951
<i>Bathyriscus rotundatus</i> (Rominger, 1887)	9	5	Middle Cambrian	Rasetti, 1951

Appendix. Continued.

Taxa	Thorax	Pygidium	Age	Reference
<i>Bathyriscus wasatchensis</i> (Resser, 1939)	9	4	Middle Cambrian	Campbell, 1974
<i>Bathyriscus wasatchensis</i> (Resser, 1939)	9	5	Middle Cambrian	Campbell, 1974
<i>Bonnaspis stephenensis</i> (Walcott, 1889)	7	4	Middle Cambrian	Rasetti, 1951
<i>Bonnia globosa</i> Tomashpolskaja, 1964	8	4	Middle Cambrian	Suvorova, 1964
<i>Bonnia</i> sp.	6	6	Lower Cambrian	Nelson, 1977
<i>Borovikovia plana</i> Romanenko, 1969	6	8	Upper Cambrian	Romanenko, 1969
<i>Cheiruroides arctica</i> Tchernysheva, 1962	14?	4?	Lower Cambrian	Tchernysheva, 1962
<i>Erbiopsis coangustus</i> Romanenko, 1969	12	10	Lower Cambrian	Romanenko, 1969
<i>Glossopleura boccar</i> (Walcott, 1916)	7	6	Middle Cambrian	Schwimmer, 1973
<i>Glossopleura gigantea</i> Resser, 1939	8	8	Middle Cambrian	Campbell, 1974
<i>Glossopleura gigantea?</i> Resser, 1939	7	9	Middle Cambrian	Campbell, 1974
<i>Glossopleura producta</i> (Hall & Whitfield, 1877)	7	7	Middle Cambrian	Palmer, 1954
<i>Glossopleura producta</i> (Hall & Whitfield, 1877)	7	6	Middle Cambrian	Palmer, 1954
<i>Glossopleura templensis</i> Rasetti, 1951	7	5	Middle Cambrian	Rasetti, 1951
<i>Hemirhodon amplipyge</i> Robison, 1964	7	6	Middle Cambrian	Robison, 1964
<i>Hemirhodon amplipyge</i> Robison, 1964	7	5	Middle Cambrian	Robison, 1964
<i>Klotziella ornata</i> (Walcott, 1908)	8	5	Middle Cambrian	Rasetti, 1951
<i>Kootenia burgessensis</i> Resser, 1942	7	5	Middle Cambrian	Rasetti, 1951
<i>Kootenia dawsoni</i> (Walcott, 1889)	7	6	Middle Cambrian	Rasetti, 1951
<i>Kootenia germana</i> (Resser, 1939)	7	4	Middle Cambrian	Palmer & Halley, 1979
<i>Kootenia jakutensis</i> Lermontova, 1940	8	7	Middle Cambrian	Suvorova, 1964
<i>Kootenia spencei</i> Resser, 1939	7	6	Middle Cambrian	Campbell, 1974
<i>Lancastria roddyi</i> (Walcott, 1912)	20	1	Lower Cambrian	Harrington et al., 1959
<i>Milaspis citata</i> Romanenko, 1969	12	3	Lower Cambrian	Romanenko, 1969
<i>Milaspis jaroshewitchi</i> Suvorova, 1964	10	3	Middle Cambrian	Suvorova, 1964
<i>Ogygopsis typicalis</i> (Resser, 1939)	8	9	Middle Cambrian	Palmer & Halley, 1979
<i>Olenoides nevadensis</i> (Meek, 1870)	7	5	Middle Cambrian	Robison, 1971
<i>Olenoides serratus</i> (Rominger, 1887)	8	5	Middle Cambrian	Rasetti, 1951
<i>Olenoides</i> sp.	7	4	Middle Cambrian	White, 1973
<i>Oryctocara geikei</i> Walcott, 1908	12	7	Middle Cambrian	Campbell, 1974
<i>Oryctocephalina lancastrioides</i> Shergold, 1969	19	1	Middle Cambrian	Shergold, 1969
<i>Oryctocephalops frischenfeldi granulatus</i> Solov'yev, 1988	12	2	Middle Cambrian	Solov'yev, 1988
<i>Oryctocephalops frischenfeldi</i> Lermontova, 1940	12	2	Lower Cambrian	Suvorova, 1964
<i>Oryctocephalus burgessensis</i> Resser, 1938	7	6	Middle Cambrian	Rasetti, 1951
<i>Oryctocephalus matthewi</i> Rasetti, 1951	7	6	Middle Cambrian	Rasetti, 1951
<i>Oryctocephalus öpiki</i> Shergold, 1969	7	6	Middle Cambrian	Shergold, 1969
<i>Oryctocephalus reynoldsi</i> Reed, 1899	8	5	Middle Cambrian	Whittington, 1992
<i>Oryctocephalus reynoldsi</i> Reed, 1899	7	6	Middle Cambrian	Rasetti, 1951
<i>Oryctocephalus reynoldsiiformis</i> Lermontova, 1940	7	6	Middle Cambrian	Tchernysheva, 1962
<i>Oryctocephalus walcotti</i> Resser, 1938	7	6	Middle Cambrian	Campbell, 1974
<i>Ovatoryctocara ovata</i> Tchernysheva, 1960	4	10	Lower Cambrian	Kriskov et al., 1960
<i>Parkaspis decamera</i> Rasetti, 1951	10	4	Middle Cambrian	Rasetti, 1951
<i>Parkaspis endecamera</i> Rasetti, 1951	11	4	Middle Cambrian	Rasetti, 1951
<i>Poliella denticulata</i> Rasetti, 1951	10	4	Middle Cambrian	Rasetti, 1951
<i>Poliella prima</i> (Walcott, 1908)	8	3	Middle Cambrian	Rasetti, 1951
<i>Polyleuraspis insignis</i> Rasetti, 1951	7	10	Middle Cambrian	Rasetti, 1951
<i>Sandoveria lobata</i> Shergold, 1969	7	7	Middle Cambrian	Shergold, 1969
<i>Stephenaspis bispinosa</i> Rasetti, 1951	9	4	Middle Cambrian	Rasetti, 1951
<i>Thorococare minuta</i> (Resser, 1939)	2	5	Middle Cambrian	Campbell, 1974
<i>Tonkinella sibirica</i> Tchernysheva, 1962	4	5	Middle Cambrian	Tchernysheva, 1962
<i>Tonkinella stephensis</i> Kobayashi, 1935	4	6	Middle Cambrian	Rasetti, 1951
<i>Tonkinella stephensis</i> Kobayashi, 1935	4	5	Middle Cambrian	Rasetti, 1951

Appendix. Continued.

Taxa	Thorax	Pygidium	Age	Reference
<i>Vanuxemella nortia</i> Walcott, 1916	5	6	Middle Cambrian	Rasetti, 1951
<i>Wenkchemnia spinicollis</i> Rasetti, 1951	9	5	Middle Cambrian	Rasetti, 1951
<i>Wenkchemnia walcotti</i> Rasetti, 1951	9	4	Middle Cambrian	Rasetti, 1951
<i>Zacanthoides cnopus</i> Walcott, 1917	9	5	Middle Cambrian	Schwimmer, 1973
<i>Zacanthoides cnopus</i> Walcott, 1917	9	4	Middle Cambrian	Schwimmer, 1973
<i>Zacanthoides divegens</i> Rasetti, 1951	9	4	Middle Cambrian	Rasetti, 1951
<i>Zacanthoides idahoensis</i> Walcott, 1908	8	6	Middle Cambrian	Campbell, 1974
<i>Zacanthoides planifrons</i> Rasetti, 1951	9	4	Middle Cambrian	Rasetti, 1951
<i>Zacanthoides romingeri</i> Resser, 1942	9	4	Middle Cambrian	Rasetti, 1951
<i>Zacanthoides typicalis</i> (Walcott, 1886)	9	4	Middle Cambrian	Palmer, 1954
PTYCHOPARIIDA				
<i>Agraulos ceticephalus</i> (Barrande, 1846)	16	2	Middle Cambrian	Horný & Bastl, 1970
<i>Agraulos longicephalus</i> (Hicks, 1872)	16	3	Middle Cambrian	Courtessole, 1973
<i>Alokistocare idahoensis</i> Walcott, 1939	24	2	Middle Cambrian	Campbell, 1974
<i>Alokistocare idahoensis</i> Walcott, 1939	23	2	Middle Cambrian	Campbell, 1974
<i>Alokistocare packi</i> Resser, 1935	17	3	Middle Cambrian	Oldroyd, 1973
<i>Alokistocare piochensis</i> (Walcott, 1886)	19	3	Middle Cambrian	Palmer, 1954
<i>Alokistocare piochensis</i> (Walcott, 1886)	17	3	Middle Cambrian	Palmer, 1954
<i>Alokistocare piochensis</i> (Walcott, 1886)	19	4	Middle Cambrian	Palmer, 1954
<i>Alokistocare piochensis</i> (Walcott, 1886)	17	4	Middle Cambrian	Palmer, 1954
<i>Alokistocarella fieldensis</i> Rasetti, 1951	17	3	Middle Cambrian	Rasetti, 1951
<i>Altiocculus harrisi</i> (Robison, 1971)	32	2	Middle Cambrian	Robison, 1971
<i>Amecephalus agnesensis</i> (Walcott, 1912)	16	4	Middle Cambrian	Rasetti, 1951
<i>Amecephalus cleora</i> (Walcott, 1917)	16	4	Middle Cambrian	Rasetti, 1951
<i>Amecephalina? coosensis</i> Resser, 1938	10	9	Middle Cambrian	unpublished data
<i>Aphelaspis cantori</i> Jago, 1987	12	27	Upper Cambrian	Jago, 1987
<i>Aphelaspis haguei</i> (Hall & Whitfield, 1877)	12	4	Upper Cambrian	Palmer, 1965
<i>Aphelaspis haguei</i> (Hall & Whitfield, 1877)	13	4	Upper Cambrian	Palmer, 1965
<i>Aphelaspis subditus</i> Palmer, 1965	12	4	Upper Cambrian	Palmer, 1965
<i>Asaphiscus gregarius</i> Walcott, 1916	9	8	Middle Cambrian	Schwimmer, 1989
<i>Asaphiscus wheeleri</i> Meek, 1873	9	8	Middle Cambrian	Palmer, 1954
<i>Asaphiscus wheeleri</i> Meek, 1873	9	10	Middle Cambrian	Palmer, 1954
<i>Asaphiscus wheeleri</i> Meek, 1873	9	9	Middle Cambrian	Palmer, 1954
<i>Atops rupertensis</i> Jell, Jago & Gehling, 1992	25	4	Lower Cambrian	Jell et al., 1992
<i>Aulacodigma quasispinale</i> Öpik, 1967	8	4	Upper Cambrian	Öpik, 1967
<i>Bailiella griffiei</i> Courtessole, 1967	14	5	Middle Cambrian	Courtessole, 1973
<i>Bailiella levyi</i> (Munier-Chalmes & Bergerar, 1889)	14	5	Middle Cambrian	Courtessole, 1973
<i>Bailiella levyi</i> (Munier-Chalmes & Bergerar, 1889)	14	6	Middle Cambrian	Courtessole, 1973
<i>Bailiella seguieri</i> Courtessole, 1973	14	5	Middle Cambrian	Courtessole, 1973
<i>Blountia bristolensis</i> Resser, 1938	7	9	Upper Cambrian	Rasetti, 1965
<i>Bolaspidella halli</i> (Resser, 1938)	18	3	Middle Cambrian	unpublished data
<i>Bolaspidella housensis</i> (Walcott, 1886)	15	5	Middle Cambrian	Robison, 1964
<i>Bolaspidella wellsvillensis</i> (Lochman & Denson, 1944)	24	4	Middle Cambrian	Robison, 1971
<i>Bolaspis labrosa</i> (Walcott, 1916)	13	7	Middle Cambrian	Schwimmer, 1973
<i>Brachyaspidion microps</i> Robison, 1971	13	6	Middle Cambrian	Robison, 1971
<i>Bythicheilus typicum</i> Resser, 1939	14	2	Middle Cambrian	Campbell, 1974
<i>Bythicheilus typicum</i> Resser, 1939	13	2	Middle Cambrian	Campbell, 1974
<i>Carinamala</i> sp.	7	7	Upper Cambrian	Eby, 1981
<i>Cedaria minor</i> Walcott, 1916	7	8	Upper Cambrian	Bebee, 1990
<i>Cedaria minor</i> Walcott, 1916	7	5	Upper Cambrian	Whittington, 1992
<i>Cedaria prolifica</i> Walcott, 1924	12	7	Upper Cambrian	Robison, 1988

Appendix. Continued.

Taxa	Thorax	Pygidium	Age	Reference
<i>Chancia ebdome</i> Walcott, 1924	20	2	Middle Cambrian	Campbell, 1974
<i>Chancia palliseri</i> (Walcott, 1908)	23	5	Middle Cambrian	Rasetti, 1951
<i>Chancia palliseri</i> (Walcott, 1908)	20	5	Middle Cambrian	Rasetti, 1951
<i>Chancia palliseri</i> (Walcott, 1908)	21	5	Middle Cambrian	Rasetti, 1951
<i>Clappaspis typica</i> Deiss, 1939	13	4	Middle Cambrian	Schwimmer, 1973
<i>Conocoryphe brevifrons</i> (Thoral, 1946)	14	5	Middle Cambrian	Courtessole, 1973
<i>Conocoryphe fessalsensis</i> Courtessole, 1967	14	5	Middle Cambrian	Courtessole, 1973
<i>Conocoryphe fessalsensis</i> Courtessole, 1967	14	4	Middle Cambrian	Courtessole, 1973
<i>Conocoryphe heberti</i> Munier-Chalmes & Bergerar, 1889	14	5	Middle Cambrian	Courtessole, 1973
<i>Conocoryphe languedocensis</i> Thoral, 1946	14	4	Middle Cambrian	Courtessole, 1973
<i>Conocoryphe pseudooculata</i> Mantel, 1905	14	5	Middle Cambrian	Courtessole, 1973
<i>Conocoryphe pseudooculata</i> Mantel, 1905	14	4	Middle Cambrian	Courtessole, 1973
<i>Conocoryphe sulzeri</i> (Schlotheim, 1823)	14	5	Middle Cambrian	Whittington, 1992
<i>Coosia alethes</i> (Walcott, 1916)	12	4	Upper Cambrian	Rasetti, 1965
<i>Ctenocephalus bergeroni</i> Thoral, 1946	15	1?	Middle Cambrian	Courtessole, 1973
<i>Ctenocephalus bergeroni</i> Thoral, 1946	14	1?	Middle Cambrian	Courtessole, 1973
<i>Ctenocephalus coronatus</i> (Barrande, 1846)	15	5	Middle Cambrian	Horný & Bastl, 1970
<i>Densonella semele</i> (Walcott, 1916)	26	3?	Upper Cambrian	Bebee, 1990
<i>Densonella semele</i> (Walcott, 1916)	25	3?	Upper Cambrian	Bebee, 1990
<i>Densonella semele</i> (Walcott, 1916)	27	3?	Upper Cambrian	Bebee, 1990
<i>Dicanthopyge quadrata</i> Palmer, 1965	13	3	Upper Cambrian	Palmer, 1965
<i>Dunderbergia nitida</i> (Hall & Whitfield, 1877)	13	4	Upper Cambrian	Palmer, 1965
<i>Dunderbergia nitida</i> (Hall & Whitfield, 1877)	13	3	Upper Cambrian	Palmer, 1965
<i>Ehmania weedi</i> Resser, 1935	13	5	Middle Cambrian	Schwimmer, 1973
<i>Ehmania weedi</i> Resser, 1935	13	7	Middle Cambrian	Schwimmer, 1973
<i>Ehmania weedi</i> Resser, 1935	13	6	Middle Cambrian	Schwimmer, 1973
<i>Ehmaniella burgessensis</i> Rasetti, 1951	13	6	Middle Cambrian	Rasetti, 1951
" <i>Ehmaniella</i> " <i>nodulosa</i> (Deiss, 1939)	15	5	Middle Cambrian	Schwimmer, 1973
" <i>Ehmaniella</i> " <i>nodulosa</i> (Deiss, 1939)	14	4	Middle Cambrian	Campbell, 1974
<i>Ehmaniella waptaensis</i> Rasetti, 1951	13	4	Middle Cambrian	Rasetti, 1951
<i>Elrathia alagype</i> Robison, 1964	15	4	Middle Cambrian	Robison, 1964
<i>Elrathia antiquata</i> (Salter, 1859)	13	7	Middle Cambrian	Schwimmer, 1989
<i>Elrathia antiquata</i> (Salter, 1859)	14	7	Middle Cambrian	Schwimmer, 1989
<i>Elrathia kingii</i> (Meek, 1970)	13	5	Middle Cambrian	Palmer, 1954
<i>Elrathia marjumi</i> Robison, 1964	12	6	Middle Cambrian	Robison, 1964
<i>Elrathia omega</i> Robison, 1988	14	6	Upper Cambrian	Robison, 1988
<i>Elrathia permulta</i> (Walcott, 1918)	14	4	Middle Cambrian	Rasetti, 1951
<i>Elrathia</i> sp.	13	7	Middle Cambrian	White, 1973
<i>Elrathiella walcotti</i> (Resser, 1938)	14	5	Middle Cambrian	unpublished data
<i>Elrathina antiqua</i> Palmer, 1979	15	2	Middle Cambrian	Palmer & Halley, 1979
<i>Elrathina antiqua</i> Palmer, 1979	16	1	Middle Cambrian	Palmer & Halley, 1979
<i>Elrathina antiqua</i> Palmer, 1979	16	2	Middle Cambrian	Palmer & Halley, 1979
<i>Elrathina antiqua</i> Palmer, 1979	15	1	Middle Cambrian	Palmer & Halley, 1979
<i>Elrathina brevifrons</i> Rasetti, 1951	19	2	Middle Cambrian	Rasetti, 1951
<i>Elrathina brevifrons</i> Rasetti, 1951	18	2	Middle Cambrian	Rasetti, 1951
<i>Elrathina</i> cf. <i>E. parallela</i> Rasetti, 1951	17	2	Middle Cambrian	White, 1973
<i>Elrathina cordillerae</i> (Rominger, 1887)	18	3	Middle Cambrian	Rasetti, 1951
<i>Elrathina cordillerae</i> (Rominger, 1887)	19	3	Middle Cambrian	Rasetti, 1951
<i>Elrathina cordillerae</i> (Rominger, 1887)	17	2	Middle Cambrian	Rasetti, 1951
<i>Elrathina cordillerae</i> (Rominger, 1887)	18	2	Middle Cambrian	Rasetti, 1951
<i>Elrathina fecunda</i> Deiss, 1939	18	2	Middle Cambrian	Schwimmer, 1973
<i>Elrathina parallela</i> Rasetti, 1951	17	2	Middle Cambrian	Rasetti, 1951

Appendix. Continued.

Taxa	Thorax	Pygidium	Age	Reference
<i>Elrathina parallela</i> Rasetti, 1951	18	2	Middle Cambrian	Rasetti, 1951
<i>Elrathina spencei</i> (Resser, 1939)	17	2	Middle Cambrian	Campbell, 1974
<i>Eoptychoparia piochensis</i> Palmer, 1979	15	?	Middle Cambrian	Palmer & Halley, 1979
<i>Germaropyge germari</i> (Barrande, 1852)	14	2	Middle Cambrian	Horný & Bastl, 1970
<i>Gloria nefanda</i> Yegorova & Savitskiy, 1968	14	2	Upper Cambrian	Yegorova & Savitskiy, 1968
<i>Glossocorpus typus</i> Deiss, 1939	12	5	Middle Cambrian	Schwimmer, 1973
<i>Glyphaspis calenus</i> (Walcott, 1916)	9	6	Middle Cambrian	Schwimmer, 1973
<i>Glyphaspis capella</i> (Walcott, 1916)	9	9	Middle Cambrian	Schwimmer, 1973
<i>Glyphaspis parkensis</i> Rasetti, 1951	10	7	Middle Cambrian	Rasetti, 1951
<i>Glyphaspis?</i> sp.	8	7	Middle Cambrian	Schwimmer, 1973
<i>Glyphopeltis primus</i> Deiss, 1939	12	6	Middle Cambrian	Schwimmer, 1973
<i>Hatangia scita</i> Yegorova & Savitskiy, 1968	15	4	Upper Cambrian	Yegorova & Savitskiy, 1968
<i>Irinia arcuata</i> Yegorova & Savitskiy, 1968	13	3	Upper Cambrian	Yegorova & Savitskiy, 1968
<i>Irvingella nuneatonensis</i> (Sharman, 1886)	12	4	Upper Cambrian	Rushton, 1967
<i>Jenkinsonia varga</i> Robison, 1971	13	2	Middle Cambrian	Robison, 1971
<i>Jenkinsonia varga</i> Robison, 1971	12	2	Middle Cambrian	Robison, 1971
<i>Jenkinsonia varga</i> Robison, 1971	14	2	Middle Cambrian	Robison, 1971
<i>Kingstonia</i> sp.	4	8	Upper Cambrian	Eby, 1981
<i>Kochina americana</i> (Walcott, 1912)	17	3	Middle Cambrian	Rasetti, 1951
<i>Kuraspis praecox</i> Nazarou, 1973	12	2?	Upper Cambrian	Nazarov, 1973
<i>Leiocoryphe brevis</i> (Raymond, 1924)	8	2	Upper Cambrian	Ludvigsen et al., 1989
<i>Leiocoryphe gemma</i> Clark, 1924	8	2	Upper Cambrian	Ludvigsen et al., 1989
<i>Levisella brevifrons</i> Rasetti, 1944	11	5	Upper Cambrian	Ludvigsen et al., 1989
<i>Loganellus logani</i> (Devine, 1863)	12	6	Upper Cambrian	Ludvigsen et al., 1989
<i>Matania quadrata</i> Robison, 1988	10	5	Upper Cambrian	Robison, 1988
<i>Meneviella venulosa</i> (Salter, 1872)	26	?	Middle Cambrian	Morris & Fortey, 1985
<i>Meteoraspis dis</i> (Walcott, 1916)	13	4	Upper Cambrian	Bebee, 1990
<i>Mexicella stator</i> (Walcott, 1916)	20	4	Middle Cambrian	Rasetti, 1951
<i>Michaspis librata</i> Yegorova & Savitskiy, 1968	12	6	Upper Cambrian	Yegorova & Savitskiy, 1968
<i>Mindycrusta mindycrusta</i> Öpik, 1967	7	9	Upper Cambrian	Öpik, 1967
<i>Modocia anglica</i> Rushton, 1978	13	4	Upper Cambrian	Rushton, 1978
<i>Modocia brevispina</i> Robison, 1964	13	5	Middle Cambrian	Robison, 1964
<i>Modocia laevinucha</i> Robison, 1964	13	5	Middle Cambrian	Robison, 1971
<i>Modocia masoni</i> (Resser, 1938)	13	5	Middle Cambrian	unpublished data
<i>Modocia</i> sp.	12	5	Upper Cambrian	Bebee, 1990
<i>Modocia typicalis</i> (Resser, 1938)	14	5	Middle Cambrian	Robison, 1964
New genus & new species	9	?	Upper Cambrian	Bebee, 1990
New genus & new species	10	9	Upper Cambrian	Bebee, 1990
<i>Norwoodella saffordi</i> (Walcott, 1916)	9	4	Upper Cambrian	Rasetti, 1965
<i>Norwoodia</i> sp.	9	3	Upper Cambrian	Bebee, 1990
<i>Olenaspella separata</i> Palmer, 1965	13	5	Upper Cambrian	Palmer, 1965
<i>Orgmaspis billingsi</i> Ludvigsen, Westrop & Kindle, 1989	11	5	Upper Cambrian	Ludvigsen et al., 1989
<i>Orloviella poletaevae</i> Romanenko, 1988	13	3	Middle Cambrian	Romanenko, 1988
<i>Pachyaspis gallagari</i> Fritz, 1968	16	2	Middle Cambrian	Palmer & Halley, 1979
<i>Pachyaspis gallagari</i> Fritz, 1968	16	1	Middle Cambrian	Palmer & Halley, 1979
<i>Parabolina monstruosa</i> Pokrovskaya, 1966	12	4	Upper Cambrian	Ergaliev, 1980
<i>Parabolinites (?) caesa</i> (Lake, 1913)	15	4	Upper Cambrian	Morris & Fortey, 1985
<i>Parabolinites (?) longispinus</i> (Belt, 1868)	14	3	Upper Cambrian	Morris & Fortey, 1985
<i>Parehmania princeps</i> Deiss, 1939	12	5	Middle Cambrian	Schwimmer, 1973
<i>Parehmania princeps</i> Deiss, 1939	13	5	Middle Cambrian	Schwimmer, 1973
<i>Pareuloma aculeatum</i> Webby, Qizheng & Mills, 1988	15	5	Upper Cambrian	Webby et al., 1988
<i>Plethopeltis armatus</i> (Billings, 1860)	10	2	Upper Cambrian	Ludvigsen et al., 1989

Appendix. Continued.

Taxa	Thorax	Pygidium	Age	Reference
<i>Plethopeltis pulveris</i> Ludvigsen, Westrop & Kindle, 1989	10	3	Upper Cambrian	Ludvigsen et al., 1989
<i>Plethopeltis pulveris</i> Ludvigsen, Westrop & Kindle, 1989	10	2	Upper Cambrian	Ludvigsen et al., 1989
<i>Proasaphiscus rigidus</i> Yegorova & Savitskiy, 1968	14	4	Upper Cambrian	Yegorova & Savitskiy, 1968
<i>Probilacunaspis prolatus</i> Ergaliev, 1980	13	3	Lower Cambrian	Ergaliev, 1980
<i>Proceratopyge gordonensis</i> Jago, 1987	9	8	Upper Cambrian	Jago, 1987
<i>Proceratopyge occella</i> Webby, Qizheng & Mills, 1988	9	10	Upper Cambrian	Webby et al., 1988
<i>Proceratopyge rectispinatus</i> (Troedsson, 1937)	9	7	Upper Cambrian	Palmer, 1968
<i>Proceratopyge rectispinatus</i> (Troedsson, 1937)	9	8	Upper Cambrian	Palmer, 1968
<i>Proceratopyge</i> sp.	9	6	Upper Cambrian	Jago, 1987
<i>Proehmaniella basilica</i> (Resser, 1945)	13	4	Middle Cambrian	Sundberg, 1994
<i>Proehmaniella basilica</i> (Resser, 1945)	14	4	Middle Cambrian	Sundberg, 1994
<i>Proteuloma debila</i> Ergaliev, 1980	12	3	Lower Cambrian	Ergaliev, 1980
"Protolenid" sp.	7	9	Lower Cambrian	Nelson, 1977
<i>Pseudoyuepingia lata</i> Webby, Qizheng & Mills, 1988	9	8	Upper Cambrian	Webby et al., 1988
<i>Pseudoyuepingia white</i> Webby, Qizheng & Mills, 1988	8	4?	Upper Cambrian	Webby et al., 1992
<i>Ptychoparid</i> sp.	11	7	Lower Cambrian	Nelson, 1977
<i>Pseudoyuepingia vanensis</i> Jago, 1987	9	7	Upper Cambrian	Jago, 1987
<i>Ptychoparia striata</i> (Emmrich, 1839)	14	6	Middle Cambrian	Horný & Bastl, 1970
<i>Ptychoparia striata</i> (Emmrich, 1839)	14	5	Middle Cambrian	Whittington, 1992
<i>Rhyssometopus rostrifinis</i> Öpik, 1967	9	5	Upper Cambrian	Öpik, 1967
<i>Sao hirsuta</i> Barrande, 1846	17	2	Middle Cambrian	Whittington, 1992
<i>Saukia acuta</i> Ulrich & Resser	12	6	Upper Cambrian	Whittington, 1992
<i>Semicyclocephalus flexilis</i> Yegorova	13	3	Upper Cambrian	Yegorova & Savitskiy, 1968
<i>Skreiaspis brianensis</i> Courtessole, 1973	13	3	Middle Cambrian	Courtessole, 1973
<i>Skreiaspis brianensis</i> Courtessole, 1973	12	2	Middle Cambrian	Courtessole, 1973
<i>Skreiaspis brianensis</i> Courtessole, 1973	13	2	Middle Cambrian	Courtessole, 1973
<i>Solenopleuropsis rouayrouxi</i> (Munier-Chalmes & Bergerar, 1889)	16	2	Middle Cambrian	Courtessole, 1973
<i>Spencella</i> sp.	11	2	Middle Cambrian	White, 1973
<i>Spencia typicalis</i> Resser, 1939	16	3	Middle Cambrian	Campbell, 1974
<i>Stella demissa</i> Yegorova & Savitskiy, 1968	12	4	Upper Cambrian	Yegorova & Savitskiy, 1968
<i>Stella flabellata</i> Yegorova & Savitskiy, 1968	12	5	Upper Cambrian	Yegorova & Savitskiy, 1968
<i>Suludella solita</i> Yegorova & Savitskiy, 1968	13	3	Upper Cambrian	Yegorova & Savitskiy, 1968
<i>Syspacephalus gregarius</i> Rasetti, 1951	14	3	Middle Cambrian	Rasetti, 1951
<i>Syspacephalus laevigatus</i> Rasetti, 1951	13	3	Middle Cambrian	Rasetti, 1951
<i>Syspacephalus longus</i> Palmer, 1979	16	2	Middle Cambrian	Palmer & Halley, 1979
<i>Syspacephalus longus</i> Palmer, 1979	15	2	Middle Cambrian	Palmer & Halley, 1979
<i>Syspacephalus perola</i> (Walcott, 1917)	15	?	Middle Cambrian	Rasetti, 1951
<i>Taenicephalops kyrshabactensis</i> Ergaliev, 1980	12	4	Lower Cambrian	Ergaliev, 1980
<i>Tricrepecephalus coria</i> Walcott, 1916	12	4	Upper Cambrian	Bebee, 1990
<i>Tricrepecephalus texanus</i> (Shumard, 1861)	11	4	Upper Cambrian	Whittington, 1992
<i>Tropidopyge laevis</i> Ergaliev, 1980	9	6	Lower Cambrian	Ergaliev, 1980
<i>Ujungaspis picta</i> Yegorova & Savitskiy, 1968	13	2	Upper Cambrian	Yegorova & Savitskiy, 1968
<i>Utaspi marjumensis</i> (Resser, 1935)	15	7	Middle Cambrian	Robison, 1964
<i>Utaspi marjumensis</i> (Resser, 1935)	15	8	Middle Cambrian	Robison, 1964
<i>Wandellella compta</i> Robison, 1988	11	5	Upper Cambrian	Robison, 1988
<i>Wandellella compta</i> Robison, 1988	11	7	Upper Cambrian	Robison, 1988
<i>Wandellella compta</i> Robison, 1988	11	6	Upper Cambrian	Robison, 1988
<i>Wandellella compta</i> Robison, 1988	11	4	Upper Cambrian	Robison, 1988
<i>Weeksina unispina</i> Walcott, 1916	10	5	Upper Cambrian	Bebee, 1990
"Weeksina" <i>granulatus</i> (Walcott, 1916)	10	6	Upper Cambrian	Bebee, 1990