Arthropod pattern theory and Cambrian trilobites

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Keywords: Arthropod pattern theory, Cambrian, trilobites, segment distributions

Abstract

An analysis of duplomere (= 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 duplomere 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 Bauplâné 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 opisthoothorax in some Olenellida. According to Harrington et al. (1959, p. 073), 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 suprageneric classification
Bijdragen tot de Dierkunde, 64 (4) – 1995

195

Bijdragen
tot
de
Dierkunde,
64
(4)
- 1995

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 trilobite 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-

**Fig. 1.** Distribution of duplomeres (= segments) of representatives of Oryctocephalidae (Corynexochida) relative to the fields and nodes predicted from APT.
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*; Cerarurus pleurexanthemus Green, 1832; Phacops sp.; Rhenops sp.; Cryptolithus tessellatus (Green, 1832); Agnostus pipiformis (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 "diverticula" caeca for each thoracic and/or pygidial segment in Redlichida (Redlichia and Centropleurida) and Ptychopariaida (Papyriaspis), which also supports a duplomere construction of these segments.

Counting the number of duplomeres (= segments) within the thorax is usually straightforward, each duplomere is well defined. Counting 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), *Polieilla* (pl. 11, figs. 2, 3), *Parmigianoides* (pl. 11, figs. 12, 18), and Zanacanthoides (pl. 11, fig. 19); and (3) in Ptychopariida the genera *Alokistocarelia*? (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. Oryctocarinnae show the thorax/pygidium boundary consistently at the end of node 2. Oryctocephalinae show the thorax/pygidium boundary in either nodes 2 or 3. Cheirurodinae 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 corynexichids, 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 ($G = 54.6 > \chi^2_{0.001}[17] = 40.8$, $p < 0.001$). Corynexichids 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 corynexichids fall within the nodes. If we assume an expected normal distribution around the mean of $14.2 \pm 2.6$, 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 1). 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 $19.7 \pm 4.1$, 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 duplomere in the thorax of olenellids, redlichiiids, corynexochids, and Ptychopariiids. 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 χ² column are p values.

| Taxa/Tagmata boundary | Node | No. of observed | No. of expected | % Change | G     | χ²0.001[1] |
|-----------------------|------|----------------|----------------|----------|-------|------------|
| Corynexochida         |      |                |                |          |       |            |
| Thorax/pygidium (x̄ = 14.2, s = 2.6, n = 80) |      |                |                |          |       |            |
| Node 2                | 35   | 20             | +75%           | 32.869   | <0.01 |            |
| 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 (x̄ = 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 (x̄ = 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 (x̄ = 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 different 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, redlichiiids, corynexochids, and ptychopariids. Six duplomeres are assumed in the cephalon. Arrows indicate mean values.
Table II. Macropleural spine duplomere location.

| Species                          | Thoracic | Pygidial |
|---------------------------------|----------|----------|
| **REDLICHIIDA**                 |          |          |
| Balcoracania bailyi Pocock, 1970| 15       |          |
| Balcoracania flindersii Pocock, 1970| 15      |          |
| Bathynotellus vermolaevi Lermontova, 1940 | 17 |          |
| Bathynotus holoptygia (Hall, 1859) | 17      |          |
| Despujosia rochi Neltner & Poctey, 1949 | 17 |          |
| Emuella daigarnoi Pocock, 1970  | 15       |          |
| Emuella polynea Pocock, 1970    | 15       |          |
| Resserops resserianus Richter & Richter, 1940 | 15 |          |
| Richterops falloti Hupé, 1953  | 17       |          |
| **OLENELLIDA**                  |          |          |
| Biceratops nevadensis Pack & Gayle, 1971 | 9       |          |
| Fallotaspis sp.                 |          |          |
| Fallotaspis typica Hupé, 1953   | 9        |          |
| Olenelloides armatus Peach, 1894| 9        |          |
| Olenellus bonnensis Resser & Howell, 1938 | 9 |          |
| Olenellus clarki (Resser, 1928) | 9        |          |
| Olenellus fremonti Walcott, 1910| 9        |          |
| Olenellus geogiensis Resser & Howell, 1938 | 9 |          |
| Olenellus getzi Dunbar, 1925    | 9        |          |
| Olenellus lapworthi Peach & Horne, 1892 | 9 |          |
| Olenellus reticulatus Peach, 1894| 9        |          |
| Olenellus roddyi Resser & Howell, 1938 | 9 |          |
| Olenellus similaris Resser & Howell, 1938 | 9 |          |
| Olenellus thompsoni (Hall, 1859) | 9        |          |
| Olenellus transitans (Walcott, 1910) | 9 |          |
| Olenellus vermontanus (Hall, 1859) | 9 |          |
| Olenellus yorkensis Resser & Howell, 1938 | 9 |          |
| **CORYNEXOCHIDA**               |          |          |
| Albertella bosworthi Walcott, 1908 | 10, 13  | 14       |
| Albertella nitida Resser, 1936  | 9, 13    | 14       |
| Anoria tontoensis (Walcott, 1916) | 11       |          |
| Bathyrurusca adaeus Walcott, 1916| 17       |          |
| Orystocephalus burgessensis Resser, 1938 | 17 |          |
| Orystocephalus reynoldsi Reed, 1899 | 17 |          |
| **PTYCHOPARIIDA**               |          |          |
| Damesella paronai (Airaghi, 1902) | 19       |          |
| Drepanura premensis Bergeron, 1899 | 20      |          |
| Irvingella nuneatonensis (Sharman, 1886) | 8  |          |
| Levisella brevifrons Rasetti, 1944 | 11      |          |
| Loganellus macropleurus Rasetti, 1944 | 11 |          |
| Proceratopyge rectispinatus      |          |          |

*Note: 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 redlichids 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 duplomeress (s = 3.3, n = 22), with a peak at 25 duplomeress. Redlichids have a mean termination location at 27.6 duplomeress (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 redlichids (n = 9), macropleural spines occurred in thoracic segments at duplomere 15 (n = 5) or 17 (n = 4). Corynexochids show three groups of duplomeress 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 duplomeress with macropleural spines, four fall within nodes and one each at duplomeress 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 duplomeress 19 (Elliptocephala), 20 (Bristolia, Callavia, and Olenellus),...
and 23 (Fallotaspis and Neuvadia). Duplomeres 19 and 20 fall within node 3, whereas duplomere 23 falls within field 4.

The Emuellidæ are multisegmented Redlichii�a, which can contain 46+ to 61 thoracic segments (Emulla and Balcorcania; Pocock, 1970). Pocock made a distinction between the pleuræ that are anterior of the macroleurous spine (duplomere 21, field 4) to those posterior of the spine based on their size, thus they could be interpreted as prothoracic and opisthoothoracic segments. However, the pleuræ posterior of the macroleurous spine are roughly the same shape as the pleuræ anterior of the spine. Excluding the macroleurous spine, the pleuræ gradually decrease in size from the first thoracic segment to the last. Thus, the posterior segments of the Emuellidæ probably do not represent an opisthoothorax.

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, Redlichiiда, 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 macroleurous 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 opisthotorax 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 duplomere 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 duplomere 15, which may represent an anterior shift from the predicted occurrence at duplomere 16. There is also a concentration of macropleural spines of corynexochids and redlichiids at duplomere 17 instead of the predicted duplomere 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., duplomere 17 then becomes duplomere 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 duplomere 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; Runneger & 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 (duplomere 6) in olenellids, redlichiids, corynexochids, and ptychopariids. The boundary between the thorax and pygidium is in field 4 (post duplomere 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 diplomeres 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.

Acknowledgements

My interest in trilobite segmentation has been spawned by several discussions with David K. Jacobs (Museum of Natural History, New York) and Frederick R. Schram (University of Amsterdam) on arthropod segmentation. I wish to thank Dave and Fred for these discussions. Fred Schram also reviewed an earlier version of this paper. I also wish to acknowledge the constructive comments provided by Nigel Hughes (Cincinnati Museum of Natural History) and two other anonymous reviewers.

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Received: 1 March 1994
Revised: 14 October 1994

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

| Taxa                                      | Thorax | Pygidium | Age         | Reference            |
|-------------------------------------------|--------|----------|-------------|----------------------|
| REDLICHIIDA                               |        |          |             |                      |
| Acadoparadoxides sacheri (Barrande, 1852) | 20     | 37       | Middle Cambrian | Horný & Bastl, 1970 |
| Balcoracania baiyi Pocock, 1970           | 53     | 47       | Lower Cambrian | Pocock, 1970         |
| Balcoracania flindersi Pocock, 1970       | 61     | ?        | Lower Cambrian | Pocock, 1970         |
| Bathynotellus yermolaevi Lermontova, 1940| 13     | 5?       | Middle Cambrian | Harrington et al., 1959 |
| Bathynotus holopyga (Hall, 1859)          | 13     | 3       | Lower Cambrian | Harrington et al., 1959 |
| Bergerronellia asiaticus Lermontova, 1940 | 15     | 1       | Lower Cambrian | Harrington et al., 1959 |
| Despuijolsia rochii Neltner & Poctey, 1949| 14     | 4?      | Lower Cambrian | Harrington et al., 1959 |
| Dolerolenus zoppii (Meneghini, 1882)      | 15     | 2       | Middle Cambrian | Harrington et al., 1959 |
| Eccparadoxides brachyrachis Linnarsson, 1883| 18     | 2       | Middle Cambrian | Courtoisole, 1973    |
| Eccparadoxides pusillus (Barrande, 1846)  | 16     | 3?      | Middle Cambrian | Horný & Bastl, 1970  |
| Eccparadoxides rouvillii Miquel, 1905      | 20     | 3       | Middle Cambrian | Courtoisole, 1973    |
| Edelsteinaspis ornata Lermontova, 1940    | 15     | 6       | Middle Cambrian | Suworova, 1964       |
| Ellipsoccephalus hoffi (Schlotheim, 1823)  | 12     | 3       | Middle Cambrian | Whittington, 1992    |
| Ellipsoccephalus gripi (Kautsky, 1945)    | 14     | 1       | Lower Cambrian | Harrington et al., 1959 |
| Emuella dalgarnoi Pocock, 1970            | 56     | 5?      | Lower Cambrian | Pocock, 1970         |
| Emuella polymea Pocock, 1970              | 46+    | ?       | Lower Cambrian | Pocock, 1970         |
| Galahetes fulcrosus Ópik, 1975            | 13     | 6       | Middle Cambrian | McNamara, 1981       |
| Gigantopygus bondoni Hupé, 1953           | 15     | 3       | Lower Cambrian | Harrington et al., 1959 |
| Hicksina elvensis (Vogdes, 1925)          | 19     | 2       | Lower Cambrian | Harrington et al., 1959 |
| Hindermyeria insecta (Richter & Richter, 1940) | 14     | 1       | Lower Cambrian | Harrington et al., 1959 |
| Lermontovia dzevanowskii Suworova, 1956   | 23     | 1       | Lower Cambrian | Harrington et al., 1959 |
| Longianda termieri Hupé, 1953             | 15     | 4       | Lower Cambrian | Harrington et al., 1959 |
| Paradoxides carens (Barrande, 1852)       | 18     | 37      | Middle Cambrian | Horný & Bastl, 1970  |
| Paradoxides davidis Salter, 1863          | 20     | 3       | Middle Cambrian | Whittington, 1992    |
| Paradoxides gracilis (Boeck, 1838)        | 20     | 3       | Middle Cambrian | Whittington, 1992    |
| Paradoxides hicksi Salter, 1866           | 22     | 2       | Middle Cambrian | Morris & Fortey, 1985 |
| Paradoxides paradoxissimus (Wahlenberg, 1821) | 21     | 4       | Middle Cambrian | Harrington et al., 1959 |
| Redlichia chinensis Walcott, 1905          | 16     | 2       | Lower Cambrian | Harrington et al., 1959 |
| Redlichia mansayi Resser & Endo, 1937     | 15     | 17      | Middle Cambrian | Whittington, 1992    |
| Resserops resserianus Richter & Richter, 1940 | 12     | 7       | Lower Cambrian | Harrington et al., 1959 |
| Richterops falloti Hupé, 1953             | 14     | 7       | Lower Cambrian | Harrington et al., 1959 |
| Xystridua saintsmitthi (Chapman, 1929)    | 13     | 4       | Middle Cambrian | Harrington et al., 1959 |
| Xystridua altera Ópik, 1975               | 13     | 7       | Middle Cambrian | McNamara, 1981       |
| Xystridua carteri Ópik, 1975              | 13     | 4       | Middle Cambrian | McNamara, 1981       |
| Xystridua templetonensis (Chapman, 1929)  | 13     | 6?      | Middle Cambrian | McNamara, 1981       |
| Yunnanocephalus yunnanensis (Mansuy, 1912)| 14     | 1       | Lower Cambrian | Harrington et al., 1959 |

OLENELLIDA

| Taxa                                      | Thorax | Pygidium | Age         | Reference            |
|-------------------------------------------|--------|----------|-------------|----------------------|
| Biceratops nevadensis Pack & Gayle, 1971  | 18     | 17       | Lower Cambrian | Whittington, 1992    |
| Bondonella typica Hupé, 1953              | 17     | 2        | Lower Cambrian | Harrington et al., 1959 |
| Callavia broeggera (Walcott, 1890)        | 18     | 1        | Lower Cambrian | Harrington et al., 1959 |
### Appendix. Continued.

| Taxa                        | Thorax | Pygidium | Age          | Reference                      |
|-----------------------------|--------|----------|--------------|--------------------------------|
| Daguinaspis ambrogii Hupé & Abadie, 1950 | 17     | 1        | Lower Cambrian | Harrington et al., 1959       |
| Ellipsocephala asaphoides Emmons, 1844    | 18     | 1        | Lower Cambrian | Harrington et al., 1959       |
| Fallotaspis sp.               | 15     |          | Lower Cambrian | Nelson, 1977                   |
| Fallotaspis typica Hupé, 1953   | 21     | 1        | Lower Cambrian | Harrington et al., 1959       |
| Holmia kjerulfii (Linnarsson, 1871) | 16     | 2        | Lower Cambrian | Whittington, 1992             |
| Holmia lapponica Ahlberg & Bergström, 1982 | 15     | 2        | Lower Cambrian | Ahlberg & Bergström, 1982     |
| Holmia rowei Resser & Howell, 1938 | 17     | 1        | Lower Cambrian | Resser & Howell, 1938         |
| Holmiella sp.                 | 18     |          | Lower Cambrian | Nelson, 1977                   |
| Judomia rossea Jell & Repina, 1992  | 17     | 1        | Lower Cambrian | Jell & Repina, 1992           |
| Kjerulfia lata Kiar, 1917      | 18     | 1        | Lower Cambrian | Harrington et al., 1959       |
| Neltneria jaqueti (Nelter & Poctey, 1950) | 17     | 3?       | Lower Cambrian | Harrington et al., 1959       |
| Neopholenellus multinodus (Palmer, 1979) | 17     |          | Lower Cambrian | Palmer & Halley, 1979         |
| Nevadella sp.                 | 24     |          | Lower Cambrian | Nelson, 1977                   |
| Nevadia sp.                   | 15     |          | Lower Cambrian | Nelson, 1977                   |
| Nevadia weeksi Walcott, 1910  | 21     | 1        | Lower Cambrian | Whittington, 1992             |
| Olenelloides armatus Peach, 1894 | 8      | 1?       | Lower Cambrian | Harrington et al., 1959       |
| Olenellus bonnensis Resser & Howell, 1938 | 18     | ?        | Lower Cambrian | Resser & Howell, 1938         |
| Olenellus clarki (Resser, 1928)  | 14     |          | Lower Cambrian | Nelson, 1977                   |
| Olenellus fremonti Walcott, 1910 | 14     |          | Lower Cambrian | Nelson, 1977                   |
| Olenellus geogiensis Resser & Howell, 1938 | 25     | 1        | Lower Cambrian | Resser & Howell, 1938         |
| Olenellus getzi Dunbar, 1925   | 18     | 1        | Lower Cambrian | Resser & Howell, 1938         |
| Olenellus lapworthi Peach & Horne, 1982 | 14     | ?        | Lower Cambrian | Cowie & McNamara, 1978        |
| Olenellus reticulatus Peach, 1894 | 14     | ?        | Lower Cambrian | Cowie & McNamara, 1978        |
| Olenellus roddyi Resser & Howell, 1938 | 19     | 1?       | Lower Cambrian | Resser & Howell, 1938         |
| Olenellus similis Resser & Howell, 1938 | 18     |          | Lower Cambrian | Resser & Howell, 1938         |
| Olenellus sp.                 | 14     |          | Lower Cambrian | Nelson, 1977                   |
| Olenellus thompsoni (Hall, 1859) | 19     | 1        | Lower Cambrian | Resser & Howell, 1938         |
| Olenellus thompsoni (Hall, 1859) | 18     | 1        | Lower Cambrian | Resser & Howell, 1938         |
| Olenellus transitans (Walcott, 1910) | 15+    |          | Lower Cambrian | Whittington, 1992             |
| Olenellus vermontanus (Hall, 1859) | 25     | 1        | Lower Cambrian | Resser & Howell, 1938         |
| Olenellus yorkensis Resser & Howell, 1938 | 20     | 1        | Lower Cambrian | Resser & Howell, 1938         |
| Wanneria walcottanus (Wanner, 1910) | 17     | 1        | Lower Cambrian | Harrington et al., 1959       |

**Corynexochida**

| Taxa                        | Thorax | Pygidium | Age          | Reference                      |
|-----------------------------|--------|----------|--------------|--------------------------------|
| Abakania usitata Repina, 1973 | 7      | 2        | Lower Cambrian | Poletaeva, 1973                |
| Albertella bosworthy Walcott, 1908 | 7      | 6        | Middle Cambrian | Rasetti, 1951                 |
| Albertella helena Walcott, 1908 | 7      | 5        | Middle Cambrian | Schwimmer, 1973                |
| Albertella microps Rasetti, 1951 | 7      | 4        | Middle Cambrian | Rasetti, 1951                 |
| Albertella nitida Resser, 1936 | 7      | 5        | Middle Cambrian | Rasetti, 1951                 |
| Anoria baton (Walcott, 1916)  | 7      | 6        | Middle Cambrian | Schwimmer, 1973                |
| Anoria baton (Walcott, 1916)  | 8      | 6        | Middle Cambrian | Schwimmer, 1973                |
| Athabaska bithus (Walcott, 1916) | 8      | 6        | Middle Cambrian | Campbell, 1974                |
| Athabaska howelli (Walcott, 1886) | 8      | 4        | Middle Cambrian | Palmer, 1954                   |
| Athabaska wataschensis (Resser, 1939) | 8      | 5        | Middle Cambrian | Campbell, 1974                |
| Bathyuriscus adaeus Walcott, 1916 | 8      | 7        | Middle Cambrian | Rasetti, 1951                 |
| Bathyuriscus brighamensis Resser, 1939 | 9      | 5        | Middle Cambrian | Campbell, 1974                |
| Bathyuriscus brighamensis Resser, 1939 | 9      | 6        | Middle Cambrian | Campbell, 1974                |
| Bathyuriscus fimbriatus Robison, 1964 | 8      | 7        | Middle Cambrian | Robison, 1971                  |
| Bathyuriscus fimbriatus Robison, 1964 | 8      | 8        | Middle Cambrian | Robison, 1971                  |
| Bathyuriscus haydeni (Meek, 1873) | 9      | 6        | Middle Cambrian | Schwimmer, 1973                |
| Bathyuriscus rotundatus (Rominger, 1887) | 9      | 6        | Middle Cambrian | Rasetti, 1951                 |
| Bathyuriscus rotundatus (Rominger, 1887) | 9      | 5        | Middle Cambrian | Rasetti, 1951                 |
### Appendix. Continued.

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

| Taxa                          | Thorax | Pygidium | Age           | Reference         |
|-------------------------------|--------|----------|---------------|-------------------|
| Vanuxemella nortia Walcott, 1916 | 5      | 6        | Middle Cambrian | Rasetti, 1951    |
| Wenkchemnia spinicollis Rasetti, 1951 | 9      | 5        | Middle Cambrian | Rasetti, 1951    |
| Wenkchemnia walcotti Rasetti, 1951 | 9      | 4        | Middle Cambrian | Rasetti, 1951    |
| Zacanthoides ctenus Walcott, 1917 | 9      | 5        | Middle Cambrian | Schwimmer, 1973  |
| Zacanthoides ctenus Walcott, 1917 | 9      | 4        | Middle Cambrian | Schwimmer, 1973  |
| Zacanthoides divegens Rasetti, 1951 | 9      | 4        | Middle Cambrian | Rasetti, 1951    |
| Zacanthoides idahoensis Walcott, 1908 | 8      | 6        | Middle Cambrian | Campbell, 1974   |
| Zacanthoides planifrons Rasetti, 1951 | 9      | 4        | Middle Cambrian | Rasetti, 1951    |
| Zacanthoides rogersi Resser, 1942 | 9      | 4        | Middle Cambrian | Rasetti, 1951    |
| Zacanthoides typicalis (Walcott, 1886) | 9      | 4        | Middle Cambrian | Palmer, 1954     |

**PTYCHOPARIIDA**

| Agraulos ceticephalus (Barrande, 1846) | 16     | 2        | Middle Cambrian | Horný & Bastl, 1970 |
| Agraulos longicephalus (Hicks, 1872) | 16     | 3        | Middle Cambrian | Courtissole, 1973  |
| Alotikostarididae idahoensis Walcott, 1939 | 24     | 2        | Middle Cambrian | Campbell, 1974    |
| Alotikostarididae idahoensis Walcott, 1939 | 23     | 2        | Middle Cambrian | Campbell, 1974    |
| Alotikostarididae packi Resser, 1935                | 17     | 3        | Middle Cambrian | Oldroyd, 1973     |
| Alotikostarididae packi Resser, 1935                 | 19     | 3        | Middle Cambrian | Palmer, 1954      |
| Alotikostarididae packi Resser, 1935              | 17     | 3        | Middle Cambrian | Palmer, 1954      |
| Alotikostarididae packi Resser, 1935                | 19     | 4        | Middle Cambrian | Palmer, 1954      |
| Alotikostarididae packi Resser, 1935              | 17     | 4        | Middle Cambrian | Palmer, 1954      |
| Alotikostarididae packi Resser, 1935                | 17     | 3        | Middle Cambrian | Rasetti, 1951     |
| Alotikostarididae harrisi (Robison, 1971)           | 32     | 2        | Middle Cambrian | Robison, 1971     |
| Amecephalus agnesensis (Walcott, 1912)             | 16     | 4        | Middle Cambrian | Rasetti, 1951     |
| Amecephalus cleora (Walcott, 1917)                 | 16     | 4        | Middle Cambrian | Rasetti, 1951     |
| Amecephalus? coosensis Resser, 1938                | 10     | 9        | Middle Cambrian | unpublished data  |
| Aphelaspis cantori Jago, 1987                      | 12     | 2?       | Upper Cambrian  | Jago, 1987        |
| Aphelaspis hagaei (Hall & Whitfield, 1877)         | 12     | 4        | Upper Cambrian  | Palmer, 1965      |
| Aphelaspis hagaei (Hall & Whitfield, 1877)         | 13     | 4        | Upper Cambrian  | Palmer, 1965      |
| Aphelaspis subditus Palmer, 1965                   | 12     | 4        | Upper Cambrian  | Palmer, 1965      |
| Asaphiscus gregarius Walcott, 1916                 | 9      | 8        | Middle Cambrian | Schwimmer, 1989   |
| Asaphiscus wheeleri Meek, 1973                    | 9      | 8        | Middle Cambrian | Palmer, 1954      |
| Asaphiscus wheeleri Meek, 1973                    | 9      | 10       | Middle Cambrian | Palmer, 1954      |
| Asaphiscus wheeleri Meek, 1973                    | 9      | 9        | Middle Cambrian | Palmer, 1954      |
| Atops rupertensis Jell, Jago & Gehling, 1992       | 25     | 4        | Lower Cambrian  | Jell et al., 1992 |
| Aulaocodigma quasipinate Opié, 1967               | 8      | 4        | Upper Cambrian  | Opié, 1967        |
| Bailiaella griffi Courtesse, 1967                  | 14     | 5        | Middle Cambrian | Courtissole, 1973 |
| Bailiaella levei (Munier-Chalmes & Berger, 1889)    | 14     | 5        | Middle Cambrian | Courtissole, 1973 |
| Bailiaella levei (Munier-Chalmes & Berger, 1889)    | 14     | 6        | Middle Cambrian | Courtissole, 1973 |
| Bailiaella seguieri Courtesse, 1973                | 14     | 5        | Middle Cambrian | Courtissole, 1973 |
| Blountia brolertensis Resser, 1938                 | 7      | 9        | Upper Cambrian  | Rasetti, 1965     |
| Bolaspidella halli (Resser, 1938)                  | 18     | 3        | Middle Cambrian | unpublished data  |
| Bolaspidella houssensis (Walcott, 1886)            | 15     | 5        | Middle Cambrian | Robison, 1964     |
| Bolaspidella wellsvillensis (Lochman & Densos, 1944) | 24     | 4        | Middle Cambrian | Robison, 1971     |
| Bolaspis labrosa (Walcott, 1916)                   | 13     | 7        | Middle Cambrian | Schwimmer, 1973   |
| Brachyaspidion microps Robison, 1971               | 13     | 6        | Middle Cambrian | Robison, 1971     |
| Bythieclis typicum Resser, 1939                    | 14     | 2        | Middle Cambrian | Campbell, 1974    |
| Bythieclis typicum Resser, 1939                    | 13     | 2        | Middle Cambrian | Campbell, 1974    |
| Carinamala sp.                                    | 7      | 7        | Upper Cambrian  | Eby, 1981         |
| Cedaria minor Walcott, 1916                        | 7      | 8        | Upper Cambrian  | Bebee, 1990       |
| Cedaria minor Walcott, 1916                        | 7      | 5        | Upper Cambrian  | Whittington, 1992 |
| Cedaria prolifica Walcott, 1924                    | 12     | 7        | Upper Cambrian  | Robison, 1988     |
Appendix. Continued.

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

| Taxa                      | Thorax | Pygidium | Age           | Reference               |
|---------------------------|--------|----------|---------------|-------------------------|
| Elrathina parelela Rasetti, 1951 | 18     | 2        | Middle Cambrian | Rasetti, 1951          |
| Elrathina spencei (Resser, 1939) | 17     | 2        | Middle Cambrian | Campbell, 1974         |
| Eoptychoparia piochensis Palmer, 1979 | 15     | 7        | Middle Cambrian | Palmer & Halley, 1979  |
| Eogmaropus gerrami (Barrande, 1852) | 14     | 2        | Middle Cambrian | Horný & Bastl, 1970    |
| Gloria nefanda Yegorova & Savitskiy, 1968 | 14     | 2        | Upper Cambrian | Yegorova & Savitskiy, 1968 |
| Glossocorphus typus Deiss, 1939 | 12     | 5        | Middle Cambrian | Schwimmer, 1973        |
| Glyphaspis calenus (Walcott, 1916) | 9      | 6        | Middle Cambrian | Schwimmer, 1973        |
| Glyphaspis capella (Walcott, 1916) | 9      | 9        | Middle Cambrian | Schwimmer, 1973        |
| Glyphaspis parkensis Rasetti, 1951 | 10     | 7        | Middle Cambrian | Rasetti, 1951          |
| Glyphaspis? sp. | 8      | 7        | Middle Cambrian | Schwimmer, 1973        |
| Glyphopeltis primus Deiss, 1939 | 12     | 6        | Middle Cambrian | Schwimmer, 1973        |
| Hatangia scita Yegorova & Savitskiy, 1968 | 15     | 4        | Upper Cambrian | Yegorova & Savitskiy, 1968 |
| Irinia arcuata Yegorova & Savitskiy, 1968 | 13     | 3        | Upper Cambrian | Yegorova & Savitskiy, 1968 |
| Irvingella nuneatonensis (Sharman, 1886) | 12     | 4        | Upper Cambrian | Rushon, 1967           |
| Jenkinstonia varga Robison, 1971 | 13     | 2        | Middle Cambrian | Robison, 1971          |
| Jenkinstonia varga Robison, 1971 | 12     | 2        | Middle Cambrian | Robison, 1971          |
| Jenkinstonia varga Robison, 1971 | 14     | 2        | Middle Cambrian | Robison, 1971          |
| Kingstonia sp. | 4      | 8        | Upper Cambrian | Eby, 1981              |
| Kochina americana (Walcott, 1912) | 17     | 3        | Middle Cambrian | Rasetti, 1951          |
| Kuriaspis praeox Nazarov, 1973 | 12     | 2?       | Upper Cambrian | Nazarov, 1973          |
| Leiacoryphe brevis (Raymond, 1924) | 8      | 2        | Upper Cambrian | Ludwig et al., 1989    |
| Leiacoryphe gema Clark, 1924 | 8      | 2        | Upper Cambrian | Ludwig et al., 1989    |
| Levisella brevifrons Rasetti, 1944 | 11     | 5        | Upper Cambrian | Ludwig et al., 1989    |
| Loganelius logani (Devine, 1863) | 12     | 6        | Upper Cambrian | Ludwig et al., 1989    |
| Matania quadrata Robison, 1988 | 10     | 5        | Upper Cambrian | Robison, 1988          |
| Meneviella venulosa (Salter, 1872) | 26     | ?        | Middle Cambrian | Morris & Forey, 1985   |
| Meteoraspis dis (Walcott, 1916) | 13     | 4        | Upper Cambrian | Bebee, 1990            |
| Mexicella stator (Walcott, 1916) | 20     | 4        | Middle Cambrian | Rasetti, 1951          |
| Michaspis librata Yegorova & Savitskiy, 1968 | 12     | 6        | Upper Cambrian | Yegorova & Savitskiy, 1968 |
| Mindcrusta mindcrusta Öpik, 1967 | 7      | 9        | Upper Cambrian | Öpik, 1967             |
| Modocia anglica Rushton, 1978 | 13     | 4        | Upper Cambrian | Rushton, 1978          |
| Modocia brevispina Robison, 1964 | 13     | 5        | Middle Cambrian | Robison, 1964          |
| Modocia laevinucha Robison, 1964 | 13     | 5        | Middle Cambrian | Robison, 1971          |
| Modocia masoni (Resser, 1938) | 13     | 5        | Middle Cambrian | unpublished data       |
| Modocia sp. | 12     | 5        | Upper Cambrian | Bebee, 1990            |
| Modocia typicalis (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            |
| Norwoodella saffordi (Walcott, 1916) | 9      | 4        | Upper Cambrian | Rasetti, 1965          |
| Norwoodia sp. | 9      | 3        | Upper Cambrian | Bebee, 1990            |
| Olenaspella separata Palmer, 1965 | 13     | 5        | Upper Cambrian | Palmer, 1965           |
| Orgmaspis billingsi Ludwigsen, Westrop & Kindle, 1989 | 11     | 5        | Upper Cambrian | Ludwig et al., 1989    |
| Orloviella poletaeav Romanenko, 1988 | 13     | 3        | Middle Cambrian | Romanenko, 1988        |
| Pachyaspis gallagari Fritz, 1968 | 16     | 2        | Middle Cambrian | Palm & Halley, 1979    |
| Pachyaspis gallagari Fritz, 1968 | 16     | 1        | Middle Cambrian | Palm & Halley, 1979    |
| Parabolina monstruosa Pokrovskaya, 1966 | 12     | 4        | Upper Cambrian | Ergaliev, 1980         |
| Parabolini (?) caesa (Lake, 1913) | 15     | 4        | Upper Cambrian | Morris & Forey, 1985   |
| Parabolini (?) longispinus (Belt, 1868) | 14     | 3        | Upper Cambrian | Morris & Forey, 1985   |
| Parehmania princeps Deiss, 1939 | 12     | 5        | Middle Cambrian | Schwimmer, 1973        |
| Parehmania princeps Deiss, 1939 | 13     | 5        | Middle Cambrian | Schwimmer, 1973        |
| Pareuoloma aculeatum Webby, Qizheng & Mills, 1988 | 15     | 5        | Upper Cambrian | Webby et al., 1988     |
| Plethopeltis armatus (Billings, 1860) | 10     | 2        | Upper Cambrian | Ludwig et al., 1989    |
### Appendix. Continued.

| Taxa                                           | Thorax | Pygidium | Age             | Reference                        |
|------------------------------------------------|--------|----------|-----------------|----------------------------------|
| **Plethopeltis pulveris** Ludvigsen, Westrop & Kindle, 1989 | 10     | 3        | Upper Cambrian  | Ludvigsen et al., 1989          |
| **Plethopeltis pulveris** Ludvigsen, Westrop & Kindle, 1989 | 10     | 2        | Upper Cambrian  | Ludvigsen et al., 1989          |
| **Proasaphicus rigidus** Yegorova & Savitskii, 1968            | 14     | 4        | Upper Cambrian  | Yegorova & Savitskii, 1968       |
| **Problacunaspis prolatus** Ergaliev, 1980                    | 13     | 3        | Lower Cambrian  | Ergaliev, 1980                   |
| **Proceratopgyne gordonensis** Jago, 1987                    | 9      | 8        | Upper Cambrian  | Jago, 1987                       |
| **Proceratopgyne occellata** Webby, Qizheng & Mills, 1988    | 9      | 10       | Upper Cambrian  | Webby et al., 1988               |
| **Proceratopgyne rectispinatis** (Troedsson, 1937)           | 9      | 7        | Upper Cambrian  | Palmer, 1968                     |
| **Proceratopgyne rectispinatis** (Troedsson, 1937)           | 9      | 8        | Upper Cambrian  | Palmer, 1968                     |
| **Proceratopgyne sp.**                                       | 9      | 6        | Upper Cambrian  | Jago, 1987                       |
| **Proehmaniella basilica** (Resser, 1945)                    | 13     | 4        | Middle Cambrian | Sundberg, 1994                   |
| **Proehmaniella basilica** (Resser, 1945)                    | 14     | 4        | Middle Cambrian | Sundberg, 1994                   |
| **Proteuloma debila** Ergaliev, 1980                         | 12     | 3        | Lower Cambrian  | Ergaliev, 1980                   |
| "Protolenid" sp.                                             | 7      | 9        | Lower Cambrian  | Nelson, 1977                     |
| **Pseudooyeunigma lata** Webby, Qizheng & Mills, 1988        | 9      | 8        | Upper Cambrian  | Webby et al., 1988               |
| **Pseudooyeunigma white** Webby, Qizheng & Mills, 1988       | 8      | 2?       | Upper Cambrian  | Webby et al., 1988               |
| **Pytychoparid sp.**                                         | 11     | 7        | Lower Cambrian  | Nelson, 1977                     |
| **Pseudooyeunigma vanensis** Jago, 1987                      | 9      | 7        | Upper Cambrian  | Jago, 1987                       |
| **Psytychoparia striata** (Emmrich, 1839)                     | 14     | 6        | Middle Cambrian | Horný & Bastl, 1970              |
| **Psytychoparia striata** (Emmrich, 1839)                     | 14     | 5        | Middle Cambrian | Whittington, 1992                |
| **Rhyssometopus rostrifinis** Ópik, 1967                     | 9      | 5        | Upper Cambrian  | Ópik, 1967                       |
| **Sao hisuta** Barrande, 1846                                | 12     | 2        | Middle Cambrian | Whittington, 1992                |
| **Saukia acuta** Ulrich & Resser                            | 12     | 6        | Upper Cambrian  | Whittington, 1992                |
| **Semicyclocephalus flexilis** Yegorova                      | 13     | 3        | Upper Cambrian  | Yegorova & Savitskii, 1968       |
| **Skreiaspis brianensis** Courttesoole, 1973                 | 13     | 3        | Middle Cambrian | Courttesoole, 1973               |
| **Skreiaspis brianensis** Courttesoole, 1973                 | 12     | 2        | Middle Cambrian | Courttesoole, 1973               |
| **Skreiaspis brianensis** Courttesoole, 1973                 | 13     | 2        | Middle Cambrian | Courttesoole, 1973               |
| **Solenopleuropsis rouayrouxi** (Munier-Chalmes & Berger, 1889) | 16     | 2        | Middle Cambrian | Courttesoole, 1973               |
| **Spencella sp.**                                            | 11     | 2        | Middle Cambrian | White, 1973                      |
| **Spencella typcalis** Resser, 1939                         | 16     | 3        | Middle Cambrian | Campbell, 1974                   |
| **Stella demissa** Yegorova & Savitskii, 1968                | 12     | 4        | Upper Cambrian  | Yegorova & Savitskii, 1968       |
| **Stella flabelata** Yegorova & Savitskii, 1968              | 12     | 5        | Upper Cambrian  | Yegorova & Savitskii, 1968       |
| **Suludella solita** Yegorova & Savitskii, 1968              | 13     | 3        | Upper Cambrian  | Yegorova & Savitskii, 1968       |
| **Syspacephalus gregarius** Rasetti, 1951                    | 14     | 3        | Middle Cambrian | Rasetti, 1951                    |
| **Syspacephalus laevigatus** Rasetti, 1951                   | 13     | 3        | Middle Cambrian | Rasetti, 1951                    |
| **Syspacephalus longus** Palmer, 1979                       | 16     | 2        | Middle Cambrian | Palmer & Halley, 1979            |
| **Syspacephalus longus** Palmer, 1979                       | 15     | 2        | Middle Cambrian | Palmer & Halley, 1979            |
| **Syspacephalus peralta** (Walcott, 1917)                    | 15     | 7        | Middle Cambrian | Rasetti, 1951                    |
| **Taenicephalops kyrshabactensis** Ergaliev, 1980            | 12     | 4        | Lower Cambrian  | Ergaliev, 1980                    |
| **Triceripechaleus coria** Walcott, 1916                     | 12     | 4        | Upper Cambrian  | Bebee, 1990                      |
| **Triceripechaleus texanus** (Shumard, 1861)                 | 11     | 4        | Upper Cambrian  | Whittington, 1992                |
| **Tropidogyne laevis** Ergaliev, 1980                        | 9      | 6        | Lower Cambrian  | Ergaliev, 1980                    |
| **Uljungaspis picta** Yegorova & Savitskii, 1968             | 13     | 2        | Upper Cambrian  | Yegorova & Savitskii, 1968       |
| **Utiaspis marjumensis** (Resser, 1935)                      | 15     | 7        | Middle Cambrian | Robison, 1964                    |
| **Utiaspis marjumensis** (Resser, 1935)                      | 15     | 8        | Middle Cambrian | Robison, 1964                    |
| **Wandelvilla compta** Robison, 1988                         | 11     | 5        | Upper Cambrian  | Robison, 1988                    |
| **Wandelvilla compta** Robison, 1988                         | 11     | 7        | Upper Cambrian  | Robison, 1988                    |
| **Wandelvilla compta** Robison, 1988                         | 11     | 6        | Upper Cambrian  | Robison, 1988                    |
| **Wandelvilla compta** Robison, 1988                         | 11     | 4        | Upper Cambrian  | Robison, 1988                    |
| **Weeksina unispina** Walcott, 1916                          | 10     | 5        | Upper Cambrian  | Bebee, 1990                      |
| "Weeksina" granulatus** (Walcott, 1916)                      | 10     | 6        | Upper Cambrian  | Bebee, 1990                      |