

Phylogenetic analyses of trilobites from the Cambrian and Ordovician radiations

by

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Abstract

Trilobites are an ideal group used for phylogenetic studies due to their complex morphology and abundance in the Paleozoic fossil record. Because of this, trilobite phylogenetics has become an important component of understanding macroevolutionary patterns during key evolutionary radiations. Two radiations that this dissertation investigates are the Cambrian and Ordovician radiations. While both occur during the early Paleozoic, they present very different patterns. The Cambrian radiation was the sudden appearance of all major metazoan phyla, whereas in the Ordovician, those new beaplans were already in place and there was instead a great increase in diversity among those groups. Presented here are phylogenetic analyses of trilobites from those radiations to further our understanding of the evolutionary patterns occurring at those times.

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Introduction

Life on Earth has experienced a number of evolutionary radiations throughout its history, such as the sudden appearance of most major metazoan phyla in the Cambrian, the Cretaceous diversification of flowering plants, and rapid evolution of mammals in the early Cenozoic. These radiations have been attributed to various factors, including availability of niche space (Simpson, 1944), geological complexity (Abe and Lieberman, 2009), and developmental plasticity (Gould, 1989).

Recent studies of the Cambrian radiation have focused on rates of evolution and paleobiogeography using trilobites (Lieberman, 1997, 2001a, b, 2003). Because trilobites are so diverse and abundant, with broad geographic distributions and complex morphology (for character analysis), they are ideal for macroevolutionary studies. These macroevolutionary studies use phylogenetic analyses to test speciation rates and biogeographic patterns (Lieberman, 1997, 1999a, 2001a,b, 2003, 2005, Lieberman and Eldredge, 1996). Results have shown trilobite evolution during the Cambrian was influenced more by vicariance than by geodispersal, related to the tectonic events of the time and further that rates of speciation were high for Early Cambrian trilobites, though not statistically distinguishable from the rates prevailing at other times in the history of life (Lieberman 2001a).

The Ordovician is also an important time of evolutionary radiation. Whereas during the Cambrian there was the sudden appearance of major body plans with increased morphological disparity, the Ordovician radiation saw more of an increase in species and ecological diversity (Harper, 2006). Known as the Great Ordovician Biodiversification event, it occurred during an interval of about 25 Myr, spanning the mid to late Ordovician

(Harper, 2006); at this time there was a significant increase in biodiversity and biocomplexity. During this period, Laurentia, Baltica, and Avalonia were in close proximity at low latitudes. These paleobiogeographic relationships may have been important in the speciation of trilobites during the Ordovician, based on paleobiogeographic patterns of deiphonine trilobites (Congreve and Lieberman, 2010). Gondwana was still intact and occupied much of the southern hemisphere. The Ordovician ended with the first of the five mass extinctions known from the fossil record. Recent evidence suggests that this may have been the result of a gamma ray burst (Melott et al., 2004).

A key aspect for better understanding these evolutionary radiations is through the phylogenetic relationships among the taxa studied. The first chapter of this dissertation addresses the phylogenetic relationships of a group of enigmatic Ordovician cheirurid trilobites, the Eccoptochilinae. The Eccoptochilinae was identified as a subfamily by Lane (1971), comprising species within the genera *Areia* Barrande 1872, *Placoparina* Whittard 1940, *Eccoptochile* Hawle & Corda 1847, *Pseudosphaerexochus* Schmidt, 1881, *Skelipyx* Lane 1971. This study is the first attempt to unravel the relationships among the group using phylogenetic techniques while also assessing the monophyly of the group itself. Sixteen ingroup taxa plus the addition of seven sphaerexochine taxa were analyzed using parsimony analysis.

In the second chapter, the focus is trilobites of the Cambrian radiation, specifically descriptions of new species of Early Cambrian Olenelloidea. The new species included in this dissertation come from the Sekwi Formation of the Northwest Territories, Canada. The Sekwi Formation, located in the Mackenzie Mountains of the Northwest Territories, Canada, is between 715 and 770m thick and dates from the late

Early Cambrian (Fritz, 1972; Randell et al., 2005). The unit of interbedded carbonate, shale, and sandstone, consists mainly of weathering dolostone and limestone (Handfield, 1968). Previous studies of trilobites from the Sekwi Formation and related strata of the Selwyn Basin include descriptions of numerous species (Fritz, 1972, 1973, 1991, 1992, 1995). Recent work by Gapp et al. (2010) identified four additional trilobite species and incorporated the Sekwi Formation species, *Judomia absita*, into a higher-level phylogeny. Here I present seven new species of olenelloid trilobite belonging to six different genera: *Olenellus* Hall, 1862, *Mesonacis* Walcott, 1885, *Elliptocephala* Emmons, 1844, *Holmiella* Fritz, 1972, *Bristolia* Harrington, 1956, and *Mummaspis* Fritz, 1992. Also recovered were specimens of *Elliptocephala logani* Walcott, 1910 and *Holmiella preancora* Fritz, 1972 and some trilobites whose taxonomic identity could not be precisely determined yet seem to have affinities to previously described species of *Olenellus*, *Fritzenellus*, and *Bolbolenellus*.

In the final chapter, I explore different phylogenetic methods for estimating tree topology for clades with speciose taxa using morphological data. In the past, the number of morphological characters has limited traditional parsimony analysis for large clades and this was dealt with by combining smaller phylogenetic trees using data from a higher-level phylogeny. In this study, I have assembled a supermatrix of seventy-five species of Olenelloidea as well as four out-group taxa using eighty-eight morphological characters. This data was explored using two methods for assessing the phylogeny of this group. First parsimony was used, which has been the traditional method applied by paleontologists. Secondly a new method, developed with Mark Holder, was applied which uses maximum likelihood methods to arrive at a tree. In the past, maximum likelihood has only been used with molecular data, as it can handle large data sets, is less

sensitive to heterogeneous branch lengths, and at times can perform better than parsimony on some tree shapes. Our new method is designed to explore tree space for data of non-constant morphological characters, which has not been done previously using maximum likelihood.

This dissertation explores trilobite groups from two dramatic periods of diversification during the early Paleozoic. Through detailed phylogenetic analyses and systematic revisions for these groups, I have improved our understanding of evolutionary relationships among these taxa, furthering our knowledge of evolution during these key radiations.

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Chapter 1. Unraveling the Phylogenetic Relationships of the Eccoptochilinae, an Enigmatic Array of Ordovician Cheirurid Trilobites

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Abstract: The Cheiruridae are a diverse group of trilobites and several subfamilies within the clade have been the focus of recent phylogenetic studies. This paper focuses on the relationships of one of those subfamilies, the Ordovician Eccoptochilinae. We analyze sixteen species from six genera within the traditionally defined group, using the pilekiid *Anacheirurus frederici* as an outgroup. To assess the monophyly of the Eccoptochilinae seven sphaerexochine species, *Kawina arnoldi*, *Sphaerexochus arenosus*, *S. atacius*, *S. latifrons*, *S. mirus*, *S. parvus*, and *S. scabridus* were included in the analysis as well. The results of this analysis show that the genus *Eccoptochile* represents a paraphyletic grade and species traditionally assigned to *Parasphaerexochus* and *Skelipyx* plot within *Pseudosphaerexochus*. Also, representative species of Sphaerexochinae plot within the traditionally defined Eccoptochilinae, suggesting Eccoptochilinae itself is paraphyletic. To resolve this, we propose all species of *Pseudosphaerexochus* be placed within Sphaerexochinae and Eccoptochilinae be restricted to a monotypic *Eccoptochile clavigera*.

Introduction

The Cheiruridae Hawle and Corda 1847 [1] are a diverse trilobite group that first appears in the Early Ordovician and persists into the Devonian. Subfamilies within this group have been the subject of recent phylogenetic studies [2-4] and have been useful in studying macroevolutionary patterns associated with the Ordovician mass extinction [3]. Other groups of trilobites that persisted concurrently with the cheirurids, such as the aulacopleurids, have also been useful for phylogenetic analysis and the study of paleobiogeographic patterns [5-9].

Lane, [10] proposed the Eccoptochilinae as a group within the Cheiruridae, and this is only one of several subfamilial classifications proposed for the Cheiruridae [11-15]. Lane [10] contended that the cheirurids be split into seven subfamilies, noting the wide diversity of form within the Cyrtometopinae that Öpik [12] had used to group 14 different genera. Pärnaste [16] agreed with Lane's assessment of the Cyrtometopinae, redefining the group based on several apomorphies and removing taxa that represented transitional forms between other groups. The Eccoptochilinae was erected by Lane based on a lack of constriction in the thoracic pleurae (the character, which he used to remove these species from the Cyrtometopinae) as well as a prominent to effaced pitting along a transverse line across the thoracic segments (which added species from the Areiinae and a new genus, *Skelipyx* Lane, 1971 [10]). This new grouping included *Eccoptochile* Hawle and Corda, 1847 [1], *Placoparina* Whittard, 1940 [17], *Pseudosphaerexochus* Schmidt, 1881 [18], *Skelipyx*, and *Arieaspis* Pribyl and Vanek, 1964 [19].

Lane's assignment was not created within a phylogenetic framework, however, and others have speculated about the efficacy of the subfamily grouping. Pribyl *et al.* [20] disagreed with Lane's assessment of the group, arguing that Öpik's [12] original grouping of the Cyrtometopinae was valid and that Lane should not have synonymized *Stubblefeldia* with *Pseudosphaerexochus*.

Whittington [21], in an attempt to address the evolutionary history of the Cheiruridae, hypothesized a theoretical phylogeny for the group. In it, *Pseudosphaerexochus* was grouped with members of the Sphaerexochinae and *Eccoptochile* and *Ariea* are a part of a separate lineage. More recently there have been more analytical attempts to assess phylogeny within the Cheiruridae, evaluating individual subfamilies within the group. Studies of the Acanthoparyphinae, Deiphoninae, Sphaerexochinae [2-4] have revealed that much of the earlier understanding of the species relationships did not necessarily involve monophyletic groupings.

The purpose of this study is to resolve the phylogenetic relationships within the Eccoptochilinae, a key cheirurid subfamily needing examination in a phylogenetic framework, to test whether the clade is monophyletic and determine its position in relation to the Sphaerexochinae. Taxa analyzed include species classified by Lane [10] within the Eccoptochilinae. Further, six taxa from the Sphaerexochinae (*Sphaerexochus arenosus*, *S. atacius*, *S. latifrons*, *S. mirus*, *S. parvus*, *S. scabridus*, and *Kawina arnoldi*) were included to assess the monophyly and evolutionary position of the Eccoptochilinae with relation to the Sphaerexochinae.

Materials and Methodology

Phylogenetic Analysis. Morphological terminology follows Whittington [22]. Material was examined with permission at the University of Kansas Museum of Invertebrate Paleontology (KUMIP), Naturhistoriska Riksmuseet, Stockholm, Sweden (AR) the Yale University Peabody Museum of Natural History (YPM), the Museum of Comparative Zoology, Harvard University (MCZ), the VSEGEI in Saint Petersburg, Russia, and the Paleontological Museum of the University of Oslo, Norway (PMO). All material was either loaned or studied on site.

Taxa analyzed. Twenty-four taxa were analyzed in this phylogenetic analysis.

Anacheirurus frederici Salter, 1864 [23] was used as the outgroup as it has previously been suggested [21] that the early Ordovician Pilekiidae are basal to cheirurid subfamilies such as the Eccoptochilinae. Some taxa were excluded from this analysis due to the unavailability of specimens or photographic material or because the material available was poorly preserved or lacking too many characters necessary for the analysis. These species include *Eccoptochile guillieri*, *E. impedita*, *E. mariana*, *E. scrobiculata*, *E. vipera*, *Parasphaerexochus tuberculatus*, *Placoparina quadrata*, *Pseudosphaerexochus approximatus*, *P. bulbosus*, *P. dubius*, *P. juvenis*, *P. nullicauda*, *P. ovalis*, *P. parallelus*, *P. pater*, *P. ravni*, and *P. wolkae*. *Eccoptochile tumescens* was treated as *E. scuticauda*, following suggestions by Pribyl and Vanek [24] to synonymize the two species.

Specific taxa analyzed. (Relevant material examined is listed where appropriate. In instances where museum material was not examined, species were coded using photographs from scientific publications.) *Anacheirurus frederici*; *Areia bohémica*;

Placoparina sedgwickii; *Eccoptochile clavigera*; “*Eccoptochile*” *scuticauda*; “*E.*” *almaldensis*; “*E.*” *perlata*; *Pseudosphaerexochus ekphyma*; *P. tectus*; *P. densigranulatus* (PMO 9455, 94425, 94434, 100.378, 15.60); *P. zapata*; *P. octolobatus*; *P. laticeps*; *P. hemicranium* (VSEGEI 23/11059); *P. cancrura*; *P. roemeri* (VSEGEI 29/11059, 30/11059, 31/11059); *P. conformis* (VSEGEI 26/11059, 27/11059); *Kawina arnoldi*; “*Sphaerexochus*” *arenosus*; “*S.*” *atacius*; *S. latifrons*; *S. mirus* (AR 39276, 39477–39482, 39484–39486, 39553 a, b; MCZ 1325, 1328, 196479, 196484, 196498; YPM 6573, 183982 183984, 183998–194000; KUMIP 321539–321541); “*S.*” *parvus*; “*S.*” *scabridus*.

Characters. The characters used in phylogenetic analysis are listed below in appropriate order from anterior to posterior position on the organism. A complete character matrix is given in Table 1. Characters emphasize the dorsal exoskeleton of adult, holaspid stage, as ontogenetic information for most of these species is unavailable. Hypostomal characters were not included in this analysis as this information was absent for most taxa included. Any characters regarding size ranges were analyzed to show they were representative of discrete groupings and not continuous.

1. Anterior boarder (0) straight to weakly curved, (1) strongly curved
2. Anterior cephalic boarder visible in dorsal view (0) present, (1) absent [State 0 is represented in Fig. 1.1-3 and state 1 is represented in Fig. 1.4]
3. Proportion of the cephalon that is glabella (0) <50%, (1) >60%
4. Lateral glabellar margins (dorsal view); (0) parallel, (1) straight, expanding anteriorly, (2) curved [State 0 is represented in Fig. 1.1, state 1 is represented in Fig. 1.2, and state 2 is represented in Fig. 1.4]

5. Genae are (0) flat, (1) strongly tilted ventrally
6. S2 and S3 furrows (0) strongly incised, (1) weakly incised, (2) indistinct or absent
7. Anterior most position of the eye (0) abaxial to S3, (1) abaxial to S2
8. S1 (0) as distinct as S2 and S3, (1) more distinct than S2 and S3
9. S1 (lateral) (0) S-shaped; (1) U-shaped
10. SO (0) middle positioned anterior to rest of furrow, (1) straight [State 0 is represented in Fig. 1.3 and state 1 is represented in Fig 1.1]
11. SO (0) straight (1) concave posteriorly
12. S1 furrow (0) does not intersect SO, (1) intersects SO
13. Genal spines (0) present, (1) absent
14. Number of thoracic segments (0) 11, (1) 9, (2) 12, (3) 10
15. Pitting on thoracic segments (0) absent, (1) present
16. Number of pygidial paired spines; (0) 3, (1) 4
17. Pygidial pleurae (0) appear to be fused, (1) do not appear to be fused
18. Pygidial convexity (posterior) (0) nearly flat, (1) vaulted
19. Pygidial dimensions (0) width approx. equal to length, (1) width approx. twice length
20. First axial ring width (0) 1.5 times greater than width of interpleural field of first pygidial segment, (1) equal to or less than width of interpleural field of first pygidial segment.
21. Furrow on the proximal end of the first pleural spine (0) visible in dorsal view, (1) not visible in dorsal view

22. Orientation of distal ends of first pygidial spines (0) directed straight back, (1) directed abaxially
23. Second pygidial spine (0) strongly curved medially, (1) weakly curved medially or straight
24. Angle the pygidial lateral axial furrow along axial ring 1 and 2 makes with a sagittal line (0) sharp, (1) shallow
25. Distal pleural tips (0) subtriangular, (1) rounded, (2) flat
26. Distal ends of the inner pleural spines (0) gradually taper, (1) expand distally
27. Pleural spines (0) separate from each other distally, (1) terminate close to each other forming pygidial shield [State 0 is represented in Fig. 1.4 and state 1 is represented in Fig. 1.1]
28. Last pleural spines terminate (0) posterior to the second to last pleural spines, (1) anterior to middle pleural spines
29. Terminal axial piece (0) present, (1) absent [State 0 is represented in Fig. 1.3 and state 1 is represented in Fig. 1.4]
30. Last axial ring (0) partially fused, (1) ring not fused, (2) fused completely to terminal axial piece forming a notched shape anteriorly, (3) terminal axial piece absent
31. Lateral edges of terminal axial piece (1) strongly curved, (0) straight sided, (2) absent
32. Terminal axial piece (0) small (sagittal length is equal to or less than the sagittal length of first axial ring), (1) large (sagittal length is equal to or greater than twice the sagittal length of first axial ring), (2) absent

33. Terminal axial piece (sag); (0) short (length equal to width), (1) long (length at least twice as long as wide), (2) absent [Characters 32 and 33 represent two distinct characters and are independent from each other. Character 32 addresses relative overall size whereas character 33 focuses on the relative length of the terminal axial piece.]
34. Distal posterior end of the terminal axial piece (0) rounded, (1) pointed, (2) absent

Methods. The data were analyzed using TNT v1.1 [25]. A traditional search algorithm (TBR) with 10,000 replications, 1 random seed, and 100 trees saved per replication was used to determine the most parsimonious trees for the data matrix. All characters were unweighted and all multistate characters were treated as unordered as there were no obvious criteria for ordering them. To assess tree support, bootstrap and jackknife values were calculated in TNT. Bootstrap and jackknife tests were analyzed using 10,000 replicates and a traditional search (4 characters, 10 percent of the data, were removed during the jackknife test). The matrix data were compiled into Nexus files using Mesquite v.2.75 [26], and FigTree v.1.3.1 [27] was used to generate the tree figures.

Results

Parsimony analysis recovered fourteen most parsimonious trees of length 119 steps with RI values of 0.556, and CI values (when uninformative characters are excluded) of 0.344. A strict consensus of these trees (Fig. 2.1) suggests that taxa traditionally assigned to *Eccoptochile* form a paraphyletic grade basal to *Pseudosphaerexochus* and the Sphaerexochinae. Also, *Parasphaerexochus zapata* and

the monotypic *Skelipyx cancrura* fall within *Pseudosphaerexochus*. *Areia* and *Placoparina* plot most basally among ingroup taxa.

“*Sphaerexochus*” *arenosus*, “*S.*” *atacius*, *S. latifrons*, *S. mirus*, “*S.*” *parvus*, *S. scabridus*, and *Kawina arnoldi*, the seven taxa chosen to represent the Sphaerexochinae do not resolve as a monophyletic clade. Based on this analysis, *S. mirus*, *S. latifrons*, and *S. scabridus* group together with the other four taxa creating a grade. The monophyly of this group has been discussed previously by Congreve and Lieberman [4], however these results suggest that the sphaerexochines may represent a paraphyletic grade within the traditionally defined Eccoptochilinae.

Discussion

Our analysis suggests that the traditional Eccoptochilinae is paraphyletic as the included sphaerexochine species resolved within the other ingroup taxa rather than as an independent lineage. Within the subfamily, the traditionally defined *Eccoptochile* forms a basal paraphyletic grade leading towards the sphaerexochines, and *Parasphaerexochus zapata*, *Skelipyx cancrura*, and various *Pseudosphaerexochus* species.

Pseudosphaerexochus sits up the tree and is paraphyletic due to the inclusion of *Parasphaerexochus* and *Skelipyx*.

To resolve the issues of paraphyly, *Eccoptochile clavigera* is assigned to a monotypic Eccoptochilinae and *Eccoptochile*. *Areia bohémica*, *Placoparina sedgwickii*, “*E.*” *scuticauda*, “*E.*” *perlata*, and “*E.*” *almaldensis* are removed from Eccoptochilinae and placed within “Eccoptochilinae” using quotation marks to indicate paraphyly *sensu* Wiley [28]. Further, “*E.*” *scuticauda*, “*E.*” *perlata*, and “*E.*” *almaldensis* are removed from *Eccoptochile* and placed within a paraphyletic “*Eccoptochile*.” In this, we are

conforming to standard phylogenetic practice by maintaining that all taxonomic definitions should be monophyletic [29].

Parasphaerexochus zapata and *Skelipyx cancrura* are herein included within *Pseudosphaerexochus* to make that genus monophyletic. In addition, *Pseudosphaerexochus* is removed from Eccoptochilinae and reassigned to Sphaerexochinae based on the phylogenetic position of the sphaerexochine taxa included in this analysis.

Regarding Lane's original character diagnosis for the group, lack of constriction in the thoracic pleurae appears to hold true for the Eccoptochilinae and the taxa grading towards it, and we also see some evidence for this among *Pseudosphaerexochus* as demonstrated by *P. octolobatus*, however much of the other taxa within the genus are missing thoracic data to make an assessment of this character's behavior. Also, it is interesting to note that the pitting along the thorax is present in all "Eccoptochilinae" and absent in all sphaerexochines (with the exception of *P. cancrura*).

The potential paraphyly within parts of *Sphaerexochus* is to be noted. Congreve and Lieberman [4] had shown that the genus was monophyletic when included in an analysis with species of *Kawina*. By including the Eccoptochilinae with representatives from this group, our analysis suggests that *Pseudosphaerexochus* is a derived sphaerexochine and thus parts of *Sphaerexochus* may not be a monophyletic clade as previously thought. We will not attempt to further revise the taxonomy for this genus as it is not the main focus of this paper and will require further detailed phylogenetic analysis, however it is interesting to note that the subgenus *S. (Sphaerexochus)* does resolve monophyletically, consistent with the results of Congreve and Lieberman [4].

Öpik's [12] treatment of these groups belonging to a larger Cyrtometopinae

appears to be invalid. Our placement of the Sphaerexochinae within Lane's Eccoptochilinae demonstrates this and provides support for his claims that the Cyrtometopinae had a great range in morphological variation.

Further, our study provides results contradictory to what Whittington [21] had hypothesized for cheirurid relationships. Whittington saw *Eccoptochile* and *Areia* as constituents of a lineage separate from *Kawina*, *Sphaerexochus*, and *Pseudosphaerexochus*. The analysis supports his hypothesis that *Areia* is basal to *Eccoptochile*, however our results suggest Sphaerexochinae derived from these trilobites. Our analysis also disagrees with his suggestion that *Kawina* and *Sphaerexochus* form a separate lineage from *Pseudosphaerexochus*, as our tree indicates that *Pseudosphaerexochus* is a more derived genus that evolves out of *Sphaerexochus*.

Systematic Paleontology

Family CHEIRURIDAE Hawle and Corda 1847 [1]

Subfamily ECCOPTOCHILINAE Lane 1971 [10]

Genus ECCOPTOCHILE Hawle and Corda 1847 [1]

Type species. *Eccoptochile clavigera* (Beyrich 1845) [30]

Diagnosis. Genae are flat. S2 and S3 are strongly incised and as distinct as S1. S1 furrow is S-shaped and does not penetrate SO. 12 thoracic segments with transverse rows of pitting. The pygidium is shield-like with a small terminal axial piece present.

Discussion. Because the phylogenetic analysis indicates the traditional *Eccoptochile* is paraphyletic, we redefine it as a monotypic taxon consisting of the type species *E. clavigera*. All other species originally placed within the genus *Eccoptochile* are placed within “*Eccoptochile*” *sensu* Wiley [28].

Subfamily SPHAEREXOCHININAE Öpik 1937 [12]

Genus PSEUDOSPHAEREXOCHUS Schmidt 1881 [18]

Type species. *Pseudosphaerexochus hemicranium* (Kutorga 1854) [31]

Other species. *P. cancrura* (Salter 1853 [32]), *P. conformis* (Angelin 1854 [33]), *P. densigranulatus* Nikolaisen 1965 [34], *P. ekphyma* Lane, 1971 [10], *P. laticeps* (Linnarsson 1866) [35], 1991, *P. octolobatus* (McCoy 1849 [36]), *P. roemeri* Schmidt 1881 [18], *P. tectus* Ingham, 1974 [37], *P. zapata* (Adrain and Fortey 1997 [38]).

Diagnosis. Glabella is wide, hides anterior cephalic boarder in dorsal view, with curved lateral margins. Genae are strongly tilted ventrally. The anterior most position of the eye is abaxial of S2. Pitting on the thoracic segment is absent and the first axial ring of the

pygidium is wide. The terminal axial piece is absent.

Discussion. To create a monophyletic genus, *Parasphaerexochus zapata* and *Skelipyx cancrura* are subsumed within *Pseudosphaerexochus*. These taxa share many characters with other members of *Pseudosphaerexochus* that support their placement within the genus. These include a U-shaped S1, a flat pygidium, pleural spines that separate from each other distally, and an absent terminal axial piece. Further, *Pseudosphaerexochus* is removed from Eccoptochilinae and placed within Sphaerexochinae.

Lane's diagnosis for the genus includes an inflated and ovate glabella with small cheeks and three pairs of lateral furrows, the posterior pair being most distinct. These characters are still valid for describing *Pseudosphaerexochus*, however they are also common among *Sphaerexochus* taxa as well. Lane also noted the short rounded terminal axial piece present in *Pseudosphaerexochus*. This analysis shows that this character was lost within the group with the exception of *P. ekphyma*, which plots more basally to the rest of the group and closer to *Sphaerexochus*. Further, Pribyl et al.'s [20] suggestion that there are two lineages within *Pseudosphaerexochus* based on two pygidial morphotypes does not hold true for our results.

In creating the genus *Skelipyx*, Lane distinguished it from *Pseudosphaerexochus* based on its rounder glabella, much of which is vertical or overhangs. We found the steepness of the lateral margins of the glabella to be very similar between the two genera and that degrees of roundness do not appear to be diagnosably distinct. Lane further notes the unique shape of the pygidium with the wide space between the posterior pair of spines. This character is indeed unique to this taxon, however due to its autapomorphic nature it is not included in this phylogenetic analysis. The placement of *Skelipyx* within

Pseudosphaerexochus is consistent with Pribyl et al. [20] who assumed *Skelipyx* was derived from that genus.

Evolutionary implications. It is interesting to note that, save for the one clade of trilobites belonging to the genus *Sphaerexochus*, all of the other species are restricted to the Ordovician. Furthermore, the early Ordovician species of *Kawina* and *Sphaerexochus* represent the only Laurentian forms, with nearly all other species of “Eccoptochilinae” originating in Avalonia, Bohemia, and Baltica. The topology of our analysis suggests that there may have been a dispersal event early on during the Ordovician that gave rise to the split between *Sphaerexochus* and *Pseudosphaerexochus*. In turn, these Laurentian forms would go on to diversify and dramatically expand their ranges during the Late Ordovician mass extinction [4], while all of the other “Eccoptochilinae” went entirely extinct. It is possible that dispersal to Laurentia may have been an important factor contributing to the group’s survival. A similar pattern of survivability can be found in the homalonotid trilobites during that time period; most old world homalonotid trilobites went extinction but the one clade that dispersed to Laurentia thrived [39].

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Figures.

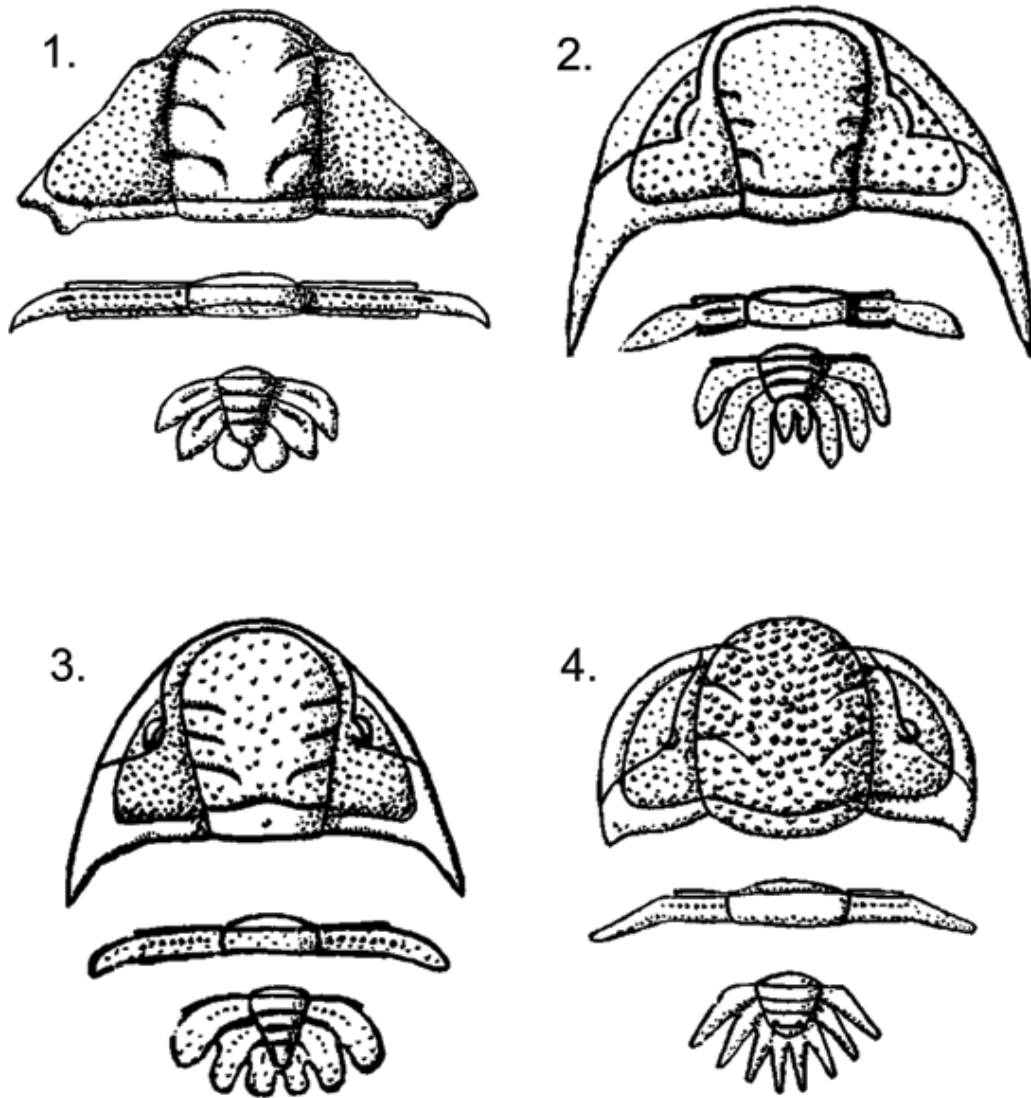


Figure 1. Line drawing of cranidium, thoracic segment, and pygidium of four species traditionally assigned to the Ectochoilinae. 1, *Placoparina sedgwickii*. 2, "Ectochoile" *scuticauda*. 3, *Ectochoile clavigera*. 4, *Pseudosphaerexochus hemicranium*. Modified from Treatise on Invertebrate Paleontology ©1959, courtesy of The Geological Society of America and The University of Kansas.

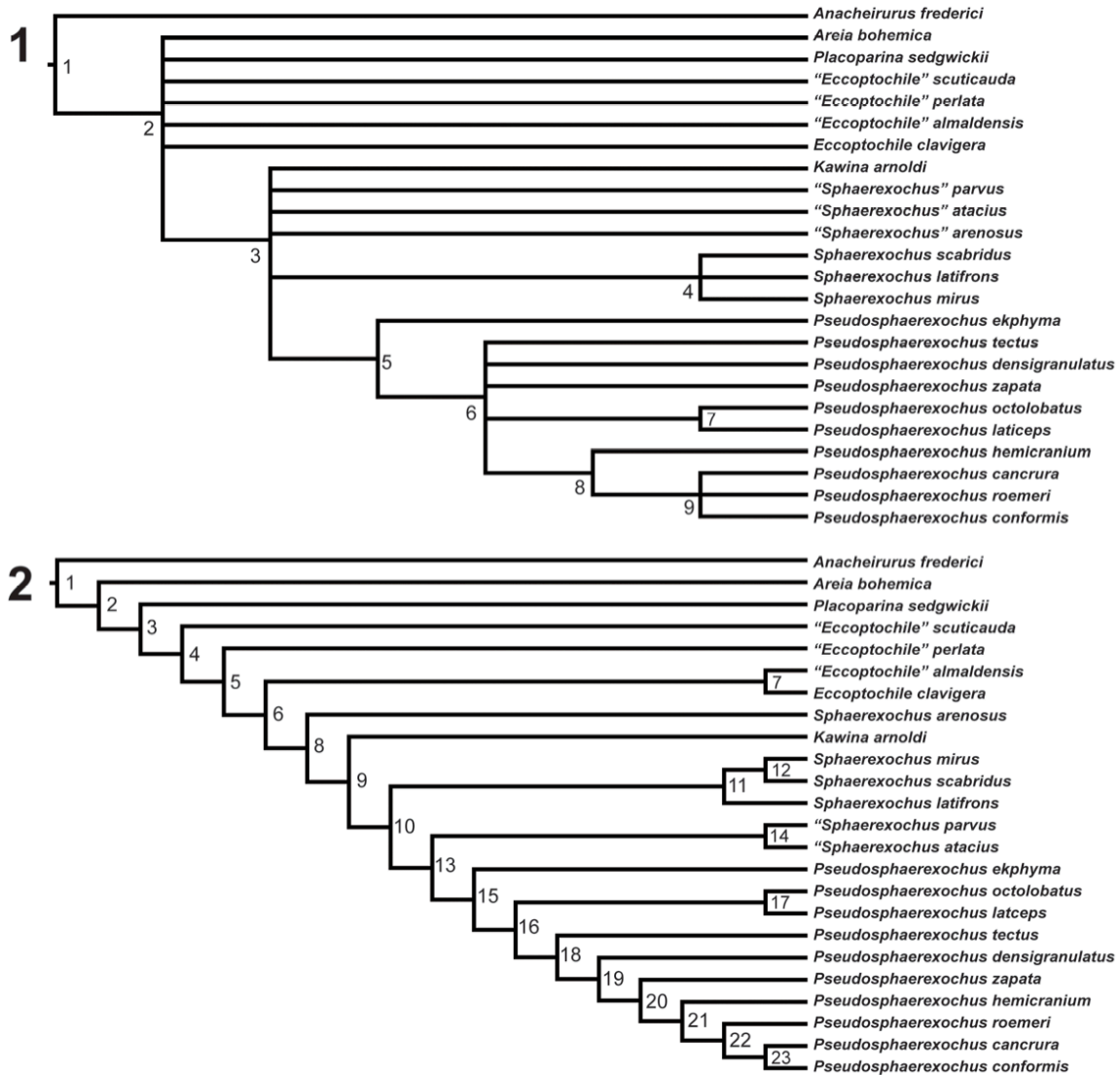


Figure 2. A strict consensus and one of fourteen most parsimonious trees. 1, Results from parsimony analysis showing strict consensus of fourteen most parsimonious trees of length 119 steps. Tree graphics generated using FigTree v.1.3.1 [26] with genera labeled and paraphyletic genus identified using quotations following Wiley [27]. The following nodes of the tree were supported by the following jackknife confidence values (see text for jackknife procedure utilized): Node 2 = 100; Node 3 = 78; Node 4 = 92; Node 5 = 49; Node 6 = 30; Node 7 = 30; Node 8 = 42; Node 9 = 56. The following nodes of the tree

were supported by the following bootstrap confidence values (see text for bootstrapping procedure utilized): Node 2 = 100; Node 3 = 29; Node 4 = 57; Node 6 = 7; Node 7 = 2; Node 8 = 8; Node 9 = 18.; 2, One of fourteen most parsimonious trees of length 119 steps. Most parsimonious character state reconstructions are: *Node 1*:14[0,1,2]; 15[0,1]; 19[0,1]; 20[0,1]; 24[0,1]; 26[0,1]; 28[0,1]; 30[0,1]; 32[0,1]. *Node 2*:19(1); 20(1); 26(1); 30(1); 32(1). *Node 3*:1(1); 14(2); 31(1); 34(1). *Node 4*:4(1); 8(1). *Node 5*:13(1); 23(1). *Node 6*:25(1); 28(0); 30(2). *Node 8*:2(1); 3(1); 4(2); 5(1); 7(1); 10(1); 15(0); 18(1); 20(0); 21(1). *Node 9*:27(1). *Node 10*:6[0,2]; 12[0,1]; 31(0); 34(0). *Node 11*:6(2); 12(1); 14(3); 33(1). *Node 13*:16(1); 30(0); 32(0). *Node 14*:6(2); 10(0). *Node 15*:9(1); 11(1); 12(1); 18(0); 23(0); 25(0); 27(0). *Node 16*:29(1); 30(3); 31(2); 32(2); 33(2); 34(2). *Node 17*:14(0). *Node 18*:26(0). *Node 19*:11(0), 25(1). *Node 20*:13[0,1]; 23(1). *Node 21*:6(1); 10(0); 12(0). *Node 22*:11(1); 17[0,1]; 19[0,1]. *Node 23*:9(0); 13(0); 21(0); Parentheses denote unambiguous optimizations and brackets denote ambiguity.

Table 1 Character state distributions for taxa used in phylogenetic analysis. Characters and character states are as listed in the text. Missing data are indicated by “?”. Character numbers are listed at the top of the table. Character states listed as “X” are polymorphic, where “X” = (0&1).

	1	2	3	4	5	6	7	8	9	0	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	2	2	3	3	3	3	3		
<i>Anacheirus frederici</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Areia bohemica</i>	0	0	0	0	0	0	0	0	0	X	0	0	?	1	1	0	0	0	1	1	0	0	0	1	0	1	0	0	0	1	0	1	0	1	1	0			
<i>Placoparina sedgwickii</i>	1	0	0	0	0	0	0	0	0	0	1	0	0	2	1	0	0	0	1	1	0	0	0	1	0	1	1	1	0	1	1	1	0	1	1	0	1		
<i>"Eccoptychile" scuticauda</i>	1	0	0	1	0	0	0	1	0	1	0	0	0	3	1	1	0	0	1	1	0	0	0	0	0	1	0	1	1	3	2	2	2	2	2	2			
<i>"E." almaldensis</i>	1	0	0	1	0	0	0	1	1	X	0	0	1	2	1	0	0	0	1	1	0	0	1	0	1	1	0	0	0	2	1	1	1	1	1	1			
<i>"E." perlata</i>	1	0	0	1	0	0	0	1	0	0	0	0	1	2	1	0	0	0	1	1	0	0	1	1	0	0	1	0	0	1	0	X	0	1	1	0	0	1	
<i>E. clavigera</i>	1	0	0	1	0	0	0	1	0	0	0	0	1	2	1	0	0	0	1	1	0	0	0	1	1	0	0	0	1	1	X	0	0	2	0	0	0	1	
<i>Kawina arnoldi</i>	0	1	1	2	1	0	1	0	0	1	0	0	1	2	0	0	0	1	1	0	1	0	1	0	1	0	2	1	1	0	0	1	1	1	0	1	0	1	
<i>"Sphaerexochus" atacius</i>	1	1	1	2	1	2	1	1	0	0	0	0	1	?	0	0	0	1	1	0	1	1	0	1	1	1	0	1	1	1	0	0	0	0	0	0	0	0	
<i>"S." parvus</i>	1	1	1	2	1	2	1	1	0	0	0	X	1	?	0	0	0	1	1	0	1	0	1	0	1	0	2	1	1	0	0	0	0	0	0	0	0	0	
<i>"S." arenosus</i>	1	1	1	2	1	1	1	1	0	1	0	0	1	?	0	0	0	1	1	0	1	0	1	0	1	0	1	0	0	0	0	2	1	1	0	1	0	1	
<i>S. latifrons</i>	1	1	1	2	1	2	1	1	0	1	0	1	1	3	0	0	0	1	1	0	1	0	1	0	1	0	1	1	1	0	0	2	0	1	1	0	1	0	
<i>S. scabridus</i>	1	1	1	2	1	2	0	1	0	1	0	1	1	?	0	0	0	1	1	0	1	0	1	0	1	0	1	1	1	0	0	2	0	1	1	0	1	0	
<i>S. mirus</i>	1	1	1	2	1	2	1	1	1	1	0	1	1	3	0	0	0	1	1	0	1	1	0	1	1	1	1	1	1	1	0	0	2	0	1	1	0	1	0
<i>Pseudosphaerexochus ekphyma</i>	1	1	1	2	1	0	1	1	1	1	1	1	1	?	0	0	0	0	1	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>P. tectus</i>	1	1	1	2	1	0	1	1	1	1	1	1	1	?	0	1	0	0	1	0	1	0	1	0	0	0	0	0	0	1	1	3	2	2	2	2	2	2	2
<i>P. densigranulatus</i>	1	1	1	2	1	0	1	1	1	1	0	1	1	?	0	1	1	0	1	0	0	0	0	0	1	1	0	0	0	1	3	2	2	2	2	2	2	2	2
<i>P. zapata</i>	1	1	1	2	1	0	0	1	1	1	0	1	0	?	0	0	0	0	1	0	1	0	1	0	1	0	1	0	0	1	1	3	2	2	2	2	2	2	2
<i>P. octolobatus</i>	1	1	1	2	1	0	1	1	1	1	1	X	1	0	0	1	0	0	1	0	0	1	0	1	0	1	0	0	0	1	0	0	1	3	2	2	2	2	2
<i>P. laticeps</i>	1	1	1	2	1	2	1	1	1	0	X	0	1	0	0	1	0	0	1	0	0	1	0	1	0	1	0	0	0	1	1	0	1	3	2	2	2	2	2
<i>P. hemicranium</i>	1	1	1	2	1	1	1	1	1	0	0	0	1	2	0	1	0	0	1	0	0	1	0	1	0	1	0	1	0	1	0	1	3	2	2	2	2	2	2
<i>P. cancrura</i>	1	1	1	2	1	1	1	1	0	0	1	0	0	?	1	1	0	0	1	0	0	1	0	0	1	1	0	1	0	0	0	1	3	2	2	2	2	2	2
<i>P. roemeri</i>	1	1	1	2	1	1	1	1	1	0	1	0	?	?	0	1	1	0	0	0	1	0	1	0	1	0	1	0	0	0	1	3	2	2	2	2	2	2	2
<i>P. conformis</i>	1	1	1	2	1	1	1	1	0	0	X	0	0	?	0	1	1	0	0	0	0	0	0	0	1	0	1	1	0	1	1	3	2	2	2	2	2	2	2

Chapter 2. New Olenelloid trilobites from the Northwest Territories, Canada

In review at *Zootaxa* as: Gapp, I.W. & B.S. Lieberman “New Olenelloid trilobites from the Northwest Territories, Canada”

Abstract

The Olenelloidea are a superfamily of Early Cambrian trilobites, which have been the subject of several phylogenetic analyses and also used to address macroevolutionary questions regarding the nature and timing of the Cambrian radiation. The Sekwi Formation of the Mackenzie Mountains, Northwest Territories, Canada, has yielded numerous species from this clade, and here we present new information that expands on the diversity known from this biogeographically and biostratigraphically important region. In particular, we describe seven new species, (*Olenellus baileyi*, *Mesonacis wileyi*, *Elliptocephala jaredi*, *Holmiella taurus*, *H. domackae*, *Mummaspis rodriguezdelgadoe*, and *Bristolia colberti*). Also recovered are specimens of *Elliptocephala logani*, specimens that shared affinities with *Olenellus clarki*, *O. getzi*, *O. fowleri*, and *Frizolenellus hanseni*, and one partial specimen, which appears to be a new species of *Bolbolenellus*. Results of this paper further our understanding of this diverse group of Early Cambrian trilobites.

Introduction

The Olenelloidea Walcott, 1890 are a diverse superfamily of Early Cambrian trilobites referable to the suborder Olenellina Walcott, 1890 and have been the focus of

much attention in the study of evolutionary tempo and mode during the Cambrian radiation (Fortey *et al.* 1996; Lieberman 1999, 2001, 2003). The purpose of this study is to present new species and additional material of previously described species in order to expand our understanding of the diversity and history of the group. The new material comes from the Sekwi Formation, Mackenzie Mountains, Northwest Territories, Canada. This formation has yielded a diverse array of Early Cambrian trilobites (Fritz 1972; Abe *et al.* 2010; Gapp *et al.* 2011) as well as a well preserved chancelloriid fauna (Randell *et al.* 2005). The unit is relatively thick, representing 715 to 750m of interbedded carbonate, shale, and sandstone, comprising mainly weathered limestone and dolostone, deposited during the *Fallotaspis*, *Nevadella*, and *Olenellus* trilobite zones (Fritz 1972, 1973; Randell *et al.* 2005; Dilliard *et al.* 2007, 2010).

This paper presents seven new species of olenelloid trilobite belonging to six different genera: *Olenellus* Hall, 1862, *Mesonacis* Walcott, 1885, *Elliptocephala* Emmons, 1844, *Holmiella* Fritz, 1972, *Bristolia* Harrington, 1956, and *Mummaspis* Fritz, 1992. Also recovered were specimens of *Elliptocephala logani* Walcott, 1910 and *Holmiella preancora* Fritz, 1972 and some trilobites whose taxonomic identity could not be precisely determined yet seem to have affinities to previously described species of *Olenellus*, *Fritzenellus*, and *Bolbolenellus*.

The specimens presented in this study are represented as internal and external moulds with some in relief (see Hughes 1995 and Paterson *et al.* 2007 for more detailed studies regarding Early Cambrian trilobite taphonomy). Some material was collected *in situ* and other material was collected in float. Specimens were prepared manually, by air abrasion, and vibratool. For photographic purposes, specimens were blackened using process black, then coated with ammonium chloride. Casts were made of external moulds

using latex for figuring (these are noted in figure descriptions). Sections given for the Sekwi Formation under “occurrences” refer to those used in Dilliard *et al.* 2007, Abe *et al.* (2010), and Gapp *et al.* (2011).

Systematics

Repositories. Specimens are housed in the Prince of Wales Northern Heritage Centre, Yellowknife, Northwest Territories, Canada (PWNHC) and the University of Kansas Natural History Museum and Biodiversity Institute, Division of Invertebrate Paleontology (KUMIP).

Order Redlichiida Richter, 1933

Suborder Olenellina Walcott, 1890

Superfamily Olenelloidea Walcott 1890

Family Olenellidae Walcott 1890

Subfamily Olenellinae Walcott 1890

Genus Olenellus Hall 1862

Type species. *Olenus thompsoni* Hall 1859

***Olenellus baileyi* sp. nov.**

(Fig. 1.3, 1.6)

Type material. Holotype PWNHC-2013.XXXX. Paratype KUMIP 355554. *Olenellus* zone, Early Cambrian, Sekwi Formation, Mackenzie Mountains, Northwest Territories, Canada, Section 4 in float.

Etymology. In honour of Hamilton college geologist David G. Bailey, who had an important influence on the professional development of IWG.

Diagnosis. Narrow prelabellar field is present with a visible plectrum; ocular lobe terminates posteriorly opposite SO; prominent furrow across entire margin of ocular lobe; furrow present across posterior part of LO; extraocular area is wide.

Description. Anterior border narrow, length (sag.) 0.5 times length (sag.) of LO, developed as a flattened ledge; anterior border furrow present; prelabellar field present, approximately 15% length (sag.) of L4; plectrum is visible; anterolateral margins of L4 angled posteriorly at approximately 40 degrees; anteroglabellar furrow and parafrontal band present; length (sag.) L4 approximately equal to combined length of LO and L1; S3 convex anteriorly, not conjoined adaxially; L3 length (sag.) equal to length (sag.) LO, lateral margins abaxial to lateral margins of L2; L2 and L3 do not merge abaxially; S2 convex anteriorly, is not conjoined adaxially; length (sag.) L2 equal to length LO; S1 convex anteriorly, creates 40 degree angle with transverse line, conjoined adaxially; lateral margins of LO convex slightly abaxially, furrow across posterior portion on LO

Discussion. This specimen most closely resembles *Olenellus agellus* Resser and Howell 1938, a species also discussed in Lieberman (1999). Shared characteristics include: a plectrum and short preglabellar field are present; the lateral margins of L4 are abaxial to the lateral margins of LO; S2 is not conjoined adaxially; the ocular lobes have a prominent furrow across the entire margin; and the extraocular area is wide and gently convex. Some important differences between the two species include: in *O. baileyi* the lateral margins of L2 are subparallel, such that they do not bulge laterally relative to L1, unlike *O. agellus* where they are diverging anteriorly; the posterior margin of the ocular lobes extend back to the abaxial tips of SO in *O. baileyi*, rather than to the adaxial part of the abaxial margin of LO; and in *O. baileyi* L2 and L3 do not conjoin abaxially.

?*Olenellus fowleri* Palmer, 1998

(Fig. 2.3)

Olenellus (Olenellus?) fowleri PALMER, 1998, p. 669, figs. 5.5, 10.1-10.6; see for complete synonymy.

Material examined. KUMIP 355555 from *Olenellus* zone, Early Cambrian, Sekwi Formation, Northwest Territories, Canada, Section 2 in float.

Description. The addition of the new specimen figured here does not warrant a redescription of the species as only a partial thorax is present. At least six prothoracic segments and thirty-six opistothoracic segments are visible in this specimen. The end of a spine found most abaxially to the right on the specimen is likely part of a macropleural

T3 spine. The length of the prothoracic segments are long, some are longer than the length of the entire opistothorax.

Discussion. Assigning this specimen to *Nephrolenellus* (a genus known for having greater than 22 segments in the opistothorax) is ruled out because the prothorax pleural spines are much longer in this specimen than in species of *Nephrolenellus* (and have the condition typical of *O. fowleri*). Also, this specimen is much larger than is common for other *Nephrolenellus* species, which are known for having the cephalon generally 12mm or shorter (sag.) (Palmer 1998).

As Palmer (1998) noted, the thorax of *O. robsonensis* Burling, 1916 is very similar to that of *O. fowleri*. The main difference that he observed in thoracic characters was a lack of granules on either pleural spines or the axial spine of T15 in *O. fowleri*, and by the lack of axial nodes in *O. robsonensis*. Unfortunately the preservation of this specimen is too poor to observe these details, especially since T15 is not visible.

However, the single specimen of *O. robsonensis* appears to lack the long T3 spines (see Lieberman 1999) that are present in specimens of *O. fowleri*. Thus, the small part of the very large spine (present in the upper right part of Fig. 2.3) that we interpret as part of T3 is evidence for questionably assigning this specimen to *O. fowleri* (as opposed to *O. robsonensis*).

Olenellus fowleri has been recovered previously from the Pioche Formation, Nevada (Palmer 1957; 1998), the Grapevine Mountains, California (Palmer in Palmer & Halley 1979).

***Olenellus* sp. aff. *getzi* Dunbar 1952**

(Fig. 2.1, 2.2)

?*Olenellus* sp. 1 FRITZ, 1991, p. 16, pl. 2, figs. 7, 8.

Material examined. KUMIP 355557 and PWNHC-2013.XXXX

Discussion. These specimens most closely resemble *O. getzi*. Key diagnostic features that they share include: broadly convex anterior cephalic border; the absence of a preglabellar field; S2 and S1 are not conjoined adaxially; and the ocular lobe has a prominent furrow that is present across the entire margin. Fritz (1991) and Whittington (1989) both noted strong similarities between *O. getzi* and *O. thompsoni* (Hall 1859), and this close relationship was further supported by phylogenetic evidence (Lieberman 1999). The specimens presented here can be distinguished from *O. thompsoni* based on characters identified by Lieberman (1999) that include: lateral margins of L4 directly anterior of lateral margins of LO; the lateral margins of L2 do not bulge laterally relative to L1; the posterior margins of the ocular lobes extend back to the abaxial tips of SO; and the anterior margins of T3 are deflected anteriorly relative to a transverse line. However, these specimens do not exactly match the characteristics of *O. getzi*. For instance, in the specimens illustrated herein S3 is conjoined adaxially. Because the material available is too incomplete to merit description of a new species, we only treat these two specimens as having affinities with *O. getzi*.

Olenellus sp. 1 in Fritz (1991), represent early ontogenetic stages yet they shares several characters with *O. sp. aff. getzi*. These include the lack of a preglabellar area, S3 strongly convex and conjoined adaxially, S2 not conjoined adaxially, and an extraocular

area that is gently convex. Due to these similarities, we suggest that Fritz's (1991) specimens may be an early ontogenetic stage for the species identified here.

Occurrence. Sekwi Formation, Mackenzie Mountains, Northwest Territories, Canada, Section 2, 260-280m above the base of section, and also questionably from Illtyd Formation, Wernecke Mountains, Yukon Territory, Canada (Unit 3) (see Fritz 1991).

***Olenellus* sp. aff. *clarki* (Resser 1928)**

(Fig. 3.3, 3.4)

Olenellus clarki LIEBERMAN, 1999, p. 21, figs. 3.2, 3.5; see for complete synonymy.

Material examined. KUMIP 355556 and PWNHC-2013.XXXX.

Discussion. Despite being incompletely preserved specimens, it is possible to identify similarities these two cephalons share consistent with *O. clarki*. These include the plectrum and preglabellar field being present, the narrow cephalic border, the lateral margins of L2 diverging anteriorly, a prominent furrow is present on the ocular lobe, and the extraocular area is prominently flattened.

Occurrence. Canada, Northwest Territories, Sekwi Formation, Section 4, 430-720m above the base of section.

Subfamily Mesonacinae Walcott 1890

Genus Mesonacis Walcott 1885

Type species. *Olenus vermontanus* Hall 1859

Mesonacis wileyi sp. nov.

(Fig. 4.1-4.4)

Type material. Holotype KUMIP 355550. Paratypes KUMIP 355551 and PWNHC-2013.XXXX-XXXX. Sekwi Formation, Mackenzie Mountains, Northwest Territories, Canada, Section 4, 430-435m above the base of section; Section 3, 700-800m above the base of the section.

Etymology. In honour of Edward O. Wiley, University of Kansas, for his fundamental contributions to the field of phylogenetics.

Diagnosis. L4 does not contact anterior cephalic border furrow; width of extraocular area approximately equal to width (tr.) of glabella at L1; posterior border between LO and intergenal angle parallel to a transverse line; intergenal angle 45 to 50 degrees relative to a transverse line; genal spines terminate posteriorly opposite of T4.

Description. Anterior cephalic border developed as a raised ridge, length (sag.) directly anterior of L4 is approximately 0.5 times length (sag.) LO; small area present between anterior border furrow and L4; anterolateral margin of L4 directed posteriorly at approximately 45 degrees; L4 length (sag.) equal to the combined length (sag.) of LO and L1; ocular furrow present; ocular lobes extend back to SO; S3 convex anteriorly,

conjoined adaxially; abaxial margins of L2 adaxial of abaxial margins of L3; S1 and SO both conjoined adaxially; L1 length (sag.) approximately length (sag.) of LO; abaxial margins of L1 adaxial to abaxial margins of LO; posterior margin of LO convex posteriorly; extraocular area wide, with prominent anastomosing ridges; posterior border between intergenal angle and LO is parallel to a transverse line; intergenal angle deflected anteriorly at 45 to 50 degrees; genal spine narrow, developed opposite L1 or S1, extends back to T5 or T6; prothorax consists of 10(?) segments and opistothorax about 5 or 6; pleural spines long and directed posteriorly; T3 is macropleural with spines extending posterior of pygidium; axial spine is present, approximately the length (sag.) of the thorax.

Discussion. This species is assigned to *Mesonacis* due to the presence of several character states including: the anterolateral margins of L4 are not prominently separated from the extraocular area by a furrow; the lateral margins of each prosomal thoracic axial ring converge when proceeding from anterior to posterior. Further, this species can be distinguished from species of *Olenellus* based on several character states including: the transverse profile of the ocular lobe is convex dorsally; the intergenal angle is directed anteriorly 45 degrees relative to a transverse line; and the thoracic pleural spines on all segments but the third are relatively narrow (tr.) compared to those of *Olenellus*. Lastly, this species is assigned to *Mesonacis*, rather than *Bristolia* based on several character states including: the lateral margins of L2, when proceeding anteriorly, do not bulge relative to LO; the surface of the interocular area does not slope evenly from the tip of the ocular lobe to the glabella; the width of the interocular area is approximately equal to the width of the ocular lobe at its midlength; and the posterior margin of the thoracic pleural furrow on the third segment is directed evenly posterolaterally.

The new species described here is distinct from previously known species of *Mesonacis*. For example, *M. vermontanus* (Hall 1859) has shorter thoracic spines and genal spines and possesses a much longer (sag.) thorax. *Mesonacis fremonti* (Walcott 1910) possesses a genal angle further posterior than that of *M. wileyi* **sp. nov.**, a posterior border directed posteriorly between LO and the intergenal angle, and a prominent intergenal ridge. *Mesonacis bonnensis* (Resser and Howell 1938) has a narrower extraocular area and a prominent intergenal ridge. *Mesonacis eagerensis* (Best 1952) possesses a narrower extraocular area and narrower pleural lobes. *Mesonacis hamoculus* (Cowie & McNamara 1978) has a prominent occipital spine and a narrower (tr.) posterior border between LO and the intergenal angle, which is directed slightly posteriorly.

Mesonacis cylindricus (Palmer in Parmer & Halley 1979), which Lieberman (1999) determined phylogenetically to be a more derived species within the genus, appears to be most similar to *M. wileyi*. Similarities include: the extraocular area is wider than the width of the glabella (tr.); L4 does not contact the anterior cephalic border furrow; the adaxial and abaxial tips of S2 are on a transverse line; the lateral border of L2 diverges anteriorly; SO is conjoined adaxially (although this is not observed in the smallest specimen of *M. wileyi* which represents an earlier ontogenetic stage); and the intergenal angle is 45 to 50 degrees relative to a transverse line. Some key differences between the species observed include: the posterior margin of the ocular lobe is opposite SO in *M. wileyi* and opposite the adaxial part of L1 in *M. cylindricus*; S2 in *M. wileyi* is less faintly incised adaxially; the adaxial part of the cephalic border between the lateral margins of LO and the intergenal angle parallels a transverse line rather than being directed posteriorly (though again this is not observed in the smallest specimen of *M.*

wileyi); and lastly the direction of the ocular lobes of *M. wileyi* do not form as large an angle to a sagittal line as those in *M. cylindricus*.

Family “Wanneriidae” Hupé 1953

Genus *Elliptocephala* Emmons 1844

Type species. *Elliptocephala asaphoides* Emmons 1844

***Elliptocephala jaredi* sp. nov.**

(Fig. 1.1, 1.2, 1.4, 1.5)

Type material. Holotype KUMIP 355534. Paratypes KUMIP 355535-355544 and PWNHC-2013.XXXX-XXXX.

Etymology. In honor of Jared Lieberman, son of BSL.

Diagnosis. L4 contacts anterior cephalic margin; L4 approximately 1.5 times combined length of LO and L1; glabellar furrows not conjoined; S3 strongly convex; ocular lobes terminate posteriorly opposite SO; posterior cephalic margin parallel to a transverse line.

Description. Anterior cephalic margin forms smooth, semi-circular arc; length of anterior cephalic border is short to moderately long (length = 0.5-1 times length [sag.] of

LO); L4 contacts the anterior glabellar furrow; anterior margins of the frontal lobes at each side of the midline deflected posteriorly at roughly 40 degree angle relative to a transverse line; length (sag.) of L4 long, equal to 1.5 times length of LO and L1 adaxially; L4 does not expand prominently dorsally; lateral margins of L4 proximal to lateral margins of LO; ocular lobes contact frontal lobe at posterolateral margins of frontal lobe; ocular furrow present; line from posterior tip of the ocular lobe to junction of posterior margin of lobe with glabella forms 10-20 degree angle with sagittal line; posterior tips of the ocular lobes developed opposite SO; anterodistal margins of L3 formed by ocular lobes; SO, S1, and S2 are convex, S3 very convex; none of the axial furrows are conjoined adaxially; L2 and L3 do not merge abaxially; lateral lobes present on LO; extraocular area approximately two-thirds width of glabella, gently convex; polygonal fracturing visible on some cephalae; posterior cephalic border parallel with transverse line or directed slightly posteriorly; intergenal spine and intergenal angle not present; genal spines directed posteriorly approximately 10 degrees relative to a sagittal line, extend back approximately three thoracic segments.

Discussion. This species is assigned to the genus *Elliptocephala* on the basis of character states such as: the length of L4 (sag.) is approximately 1.5 times the length (sag.) of LO and L1; the anterior margins of the frontal lobe at each side of the midline deflects posteriorly at approximately a 40 degree relative to a transverse line; L2 and L3 do not merge abaxially; the abaxial margins of L2 diverge anteriorly; S2 is convex anteriorly; the ocular lobe has a prominent ocular furrow; the line from the posterior tip of the ocular lobe to the junction of the lobe with the glabella forms a 10 to 20 degree angle with the sagittal line; the anterodistal margins of L3 are formed by the ocular lobes; and polygonal fracturing is visible on cephalae.

Elliptocephala jaredi shares many similarities with *Wanneria walcottana* (Wanner 1901). This includes the fact that none of the glabellar furrows are conjoined adaxially, S3 is strongly convex, there are an absence of anastomosing ridges on the extraocular area, the frontal lobe contacts the anterior cephalic border, and the abaxial margins of the glabella at L1 relative to LO are constricted. Differences include the fact that the ocular lobes extend further posteriorly in *E. jaredi*, as well as the presence of lateral lobes, shorter genal spines, and the length of L4 relative to LO and L1 is longer in *E. jaredi*. Due to the similarities between *E. jaredi* and *W. walcottana*, it is likely that *E. jaredi* is positioned basally within *Elliptocephala*, however further phylogenetic investigation is needed to test this.

Occurrence. Sekwi Formation, Mackenzie Mountains, Northwest Territories, Canada, Section 2, 260-395m above the base of section, Section 3, 700-800m above the base of the section, and Section 4, in float).

***Elliptocephala logani* Walcott 1910**

(Fig. 5.1-4)

Elliptocephala logani WALCOTT, 1910, p. 333, pl. 41, figs. 5, 6; LIEBERMAN, 1999, p. 61, fig. 12.5, see for complete synonymy.

Material examined. KUMIP 355558-355560 and PWNHC-2013.XXXX.

Occurrence. Canada: Northwest Territories, the type section of the Sekwi Formation (Hanfield 1968), 0.2 mi SE of June Lake, 1668 ft to 1937 ft above the base of the formation, middle *Olenellus* zone following Fritz (1972), S end of the Sekwi Range;

Northwest Territories, Section 3, 700-800m above the base, and Section 4 in float, Mackenzie Mountains; Yukon Territory, the Iltyd Formation, Fritz's (1991) Unit 3, *Olenellus* zone, Wernecke Mountains; Newfoundland, the Forteau Formation, *Olenellus* Zone, L'Anse au Loup, straits of Belle Isle, Labrador.

Family Holmiidae Hupé 1953

Subfamily Holmiinae Hupé 1953

Genus Holmiella Fritz 1972

Type species. *Holmiella preancora* Fritz 1972

Holmiella taurus sp. nov.

(Fig. 6.1-6.4)

Type material. Holotype KUMIP 355545. Paratypes KUMIP 355546-355547 and PWNHC 2013.XXXX-XXXX.

Etymology. The name *taurus* was chosen because the large genal spines resemble the horns of a bull.

Diagnosis. Anterior constriction of cephalic border between intergenal spine and genal spine, where border meets genal spine; strongly incised S3; short ocular lobes

(terminate opposite S1); anterior most part of genal spine is anterior of L4; anterior cephalic margin is approximately parallel to a sagittal line; the posterolateral margin of L4 is constricted to subparallel anteriorly.

Description. Anterior cephalic margin relatively straight, extending to genal spines, parallel to the transverse line, developed as a flattened ledge; anterior cephalic border directly anterior of L4 length approximately equal to length L3 and expands greatly abaxially; genal spine where attached subparallel to transverse line and then further abaxial deflected back strongly, directed slightly inward, posterior of the posterior cephalic border; length (sag.) of L4 approximately equal to combined length (sag.) of L1, L2, and L3; anterior margin of L4 semicircular in shape; lateral margins of L4 abaxial of lateral margins of LO; anterior margin of ocular lobe separated from L4 by a furrow; S3 convex anteriorly; lateral margin of L3 convex abaxially; length (sag.) of L3 equal to length of L2; S2 convex anteriorly; lateral margin of L2 convex abaxially; S1 convex anteriorly; length (sag.) of L1 is approximately 1.5 times the length of L2; lateral margins of L1 adaxial of lateral margins of LO; length (sag.) of LO is approximately length (sag.) L2 and L3; small occipital spine present; small spines present on posterior border angled abaxially.

Discussion. This species differs from other species of *Holmiella* by characters such as the anterior cephalic margin being nearly parallel to a transverse line, short ocular lobes that terminate posteriorly at S1, the posterolateral margin of L4 is constricted to subparallel to a sagittal line, and the cephalic border between the intergenal spine and genal spine constricting anteriorly. Like *H. domackae* **sp. nov.**, the genal spines are prominently directed posteriorly, however the ends of the genal spines in *H. taurus* are directed more adaxially.

Occurrence: Sekwi Formation, Mackenzie Mountains, Northwest Territories, Canada, Section 14, in float.

***Holmiella domackae* sp. nov.**

(Fig. 7.1-7.3)

Type material. Holotype: PWNHC 2013.XXXX; paratype: KUMIP 355548-355549

Etymology: In honour of Hamilton College paleontologist Cindy Domack, who had an important influence on the professional development of IWG.

Diagnosis. Cephalic border between intergenal spine and genal spine diverges anteriorly; genal spines have a sinuous shape; the posterolateral margins of L4 diverge anteriorly.

Description. Anterior border abaxial of sagittal line at an angle approximately 25 degrees to transverse line; length (sag.) anterior cephalic border directly anterior L4 approximately 0.5 length of L3, developed as a flattened shelf; anterior portion of genal spines attached to cephalon at point directly abaxial midpoint of L4 along a sagittal line; genal spine deflected back rapidly and slightly outward creating an S-shape; length (sag.) L4 approximately equal to length (sag.) of LO and L1; lateral margins of L4 abaxial lateral margins of LO; S3 convex anteriorly; ocular lobe separated from glabella by furrow; line created by anterior and posterior position of ocular lobe creates an angle with sagittal line of approximately 0-10 degrees; posterior ends of ocular lobes extend back to adaxial part of L1; width of ocular lobe at adaxial point about 60-70% length (sag.) of L1; width (tr.) of extraocular area approximately 55-65% interocular area; S3 gently

convex and does not conjoin adaxially; S2 gently convex and not conjoined adaxially; S1 gently convex and not conjoined adaxially; L1, L2, and L3 are approximately equal in length (sag.); lateral margins of L2, L3, and L4 constricted posteriorly; width (tr.) of LO approximately equal to width of L3, length (sag.) approximately 1.5 times length (sag.) of L1; small spine on posterior margin of LO; intergenal spines positioned directly abaxial of occipital spine; posterior border between LO and intergenal spine directed back posteriorly abaxially.

Discussion. This species can be distinguished from *H. falcata* and *H. preancora* by its much wider genal spines, which are directed abaxially before being directed posteriorly, and have a slightly sinuous shape. The posterior cephalic border between the intergenal spine and the genal spine diverges anteriorly in *H. domackae* unlike in other species of *Holmiella*, which are parallel to subparallel. Lastly, the posterolateral margin of L4 diverges anteriorly unlike *H. taurus* **sp. nov.**

Occurrence. Sekwi Formation, Mackenzie Mountains, Northwest Territories, Canada, Section 2, in float, Section 3, 700-800m above the base of section, Section 14 in float.

Family “Laudoniidae” Harrington 1959

Subfamily “Laudoniinae” Harrington 1959

Genus *Mummaspis* Fritz 1992

Type species. *Wanneria occidens* Walcott 1913

***Mummaspis rodriguezdelgadoe* sp. nov.**

(Fig. 8.1-8.6)

Type material. Holotype PWNHC-2013.XXXX. Paratypes KUMIP 355525-355533 and PWNHC-2013.XXXX-XXXX.

Etymology. In honour of Alejandra Rodriguez Delgado, who has helped inspire IWG throughout the course of this study.

Diagnosis. Species shares character states used to describe *Mummaspis* by Lieberman (1999) with the exception of its presence of a parafrontal band. Various diagnostic characters of *Mummaspis* present include ocular lobes separated from L3 by the S3 furrow and extending back posteriorly to LO, the ocular furrow terminates posteriorly at SO, prominent anastomosing ridges are present on the extraocular area, lateral furrows are present on LO, and the posterior border of LO is convex posteriorly.

Description. Anterior border narrow (sag.), approx. 0.5 times length of LO; L4 contacts anterior border furrow and length (sag.) approx. length (sag.) of LO and L1; parafrontal band present; anterior margin of L4 at each side of the midline deflected posteriorly at roughly 40 degree angle; ocular furrow present; preocular furrow on frontal lobe directed inward and forward from glabellar margin; ocular lobes contact frontal lobe at posterolateral margin of frontal lobe and extend posteriorly to LO, separated from extraocular area by prominent shelf; width (tr.) of interocular area approx. equal to the width (tr.) of the ocular lobe; lateral margins of L4 directly anterior to lateral margins of LO; anterodistal margin of L3 formed by ocular lobes; course of S3 jaggedly convex and

conjoined adaxially; L2 and L3 do not merge abaxially; S2 polymorphic, conjoined adaxially or not conjoined; S2 convex anteriorly; SO and S1 not conjoined adaxially, convex anteriorly; lateral lobes on LO present; axial part of LO smooth, without spine or node present; prominent anastomosing ridges with ocular line and genal ridge present on extraocular area; width (tr.) of extraocular area from abaxial tip of ocular lobe to position of anterior border furrow opposite L1 approx. 50% width (tr.) of glabella at L1; genal spine directed posteriorly about 80-90% to transverse line; length (sag.) of genal spines approximately equal to the length (sag.) of the first 2-3 thoracic segments; genal spine angle developed opposite LO; intergenal angle not prominently developed.

Discussion. This species has been assigned to *Mummaspis* due to its possession of key characters such as: the anterior cephalic border between the frontal lobe and genal spine angle having a length (sag.) equal to the length (sag.) of LO; the anterior border is prominently separated from extraocular area by a furrow; the preocular furrow is directed inward and forward from the glabellar margin; S3 is jaggedly convex and conjoined adaxially; lateral lobes on LO are present; the posterior margin of LO is convex; and the intergenal angle roughly parallels a transverse line.

Mummaspis rodriguezdelgadoae can be distinguished from other species of *Mummaspis* based on characters identified by Lieberman (1999). For example, *M. occidens* (Walcott 1913) has a wider (tr.) L4 with a furrow more strongly incised along the anterior border, a longer occipital spine, and glabellar furrows that are more steeply angled (especially SO and S1). *Mummaspis truncatooculatus* (Fritz 1992) has a greater constriction of the glabella at L1 and L2, more prominent intergenal ridges, L3 is conjoined with the ocular lobe, shorter ocular lobes, and a more strongly incised preocular furrow. *Mummaspis oblioooculatus* Fritz 1992 possesses an anterior border

that is flatter and angled further posteriorly directly abaxial of S3, L2 and L3 are conjoined abaxially, and S3 is more jaggedly convex. *Mummaspis muralensis* (Fritz 1992) appears to be most similar to *M. rodriguezdelgadoe* and they share commonalities such as prominent anastomosing ridges and they also show evidence of polygonal fracturing on some of the cephalon. However, the species are diagnosably distinct. For example, *M. muralensis* has a more prominent intergenal ridge, wider (tr.) ocular lobes, and there is a greater constriction in the width of the glabella anteriorly from LO to L2.

Occurrence. Sekwi Formation, Mackenzie Mountains, Northwest Territories, Canada, Section 1, in float, Section 2, 350-375m above the base of section and in float.

Family “Laudoniidae” Harrington 1956

Subfamily “Laudoniinae” Harrington 1956

Genus *Fritzolenellus* Lieberman Lieberman 1998

Type species. *Olenellus truemani* Walcott 1913

***Fritzolenellus* sp. aff. *hanseni* (Poulsen 1932)**

(Fig. 3.1)

Paedeumias hanseni POULSEN 1932

Olenellus lapworthi COWIE & MCNAMARA 1978

Olenellus hanseni STEIN 2008 Fig. 8B, 8C

Material Examined. KUMIP 355562-355563.

Discussion. This species shares the following characters with *O. hanseni*, which is known from the Ella Island Formation of North-East Greenland: the anterior cephalic margin is narrow (sag.) and developed as a raised ridge; an anterior glabellar furrow present; the anterolateral margins of the glabella deflect posteriorly at approximately at 40 degrees; L4 length (sag.) equal to combined length (sag.) of LO, L1, and L2; the ocular lobe terminates posteriorly at SO; a prominent ocular furrow extends the length of the ocular lobe; the extraocular area is approximately the width (tr.) of the glabella at L2; S3 is strongly convex and conjoined adaxially; L2 and L3 merge abaxially; S2 is convex anteriorly and conjoined adaxially; L1 is straight and not conjoined adaxially; the lateral margins of LO and L1 are straight and parallel to a sagittal line; SO is slightly convex posteriorly, and not conjoined adaxially; posterior margin of LO convex posteriorly; the posterior border between LO and the intergenal angle is parallel to a transverse line; the intergenal angle is approximately 30-40 degrees; and the genal spines are relatively long (exsag.). Cowie & McNamara (1978) suggested *O. hanseni* was very similar to *Fritzolenellus lapworthi* (Peach and Horne 1892), with the primary differences involving the length of the ocular lobes. Stein (2008) reiterated this suggestion, and also recognized the absence of a parafrontal band and the presence of a plectrum when compared with *F. lapworthi*. These features are also observed in the specimens presented here. Due to the quality of preservation and the limited material, we are only tentatively assigning these specimens to *F. hanseni*.

Occurrence. Canada, Northwest Territories, Sekwi Formation, Section 4, 430-435m above the base of section.

Family Biceratopsidae Pack & Gayle 1971

Subfamily Bristolinae Harrington 1956

Genus Bristolia Harrington 1956

Type species. *Mesonacis bristolensis* Resser 1928

***Bristolia colberti* sp. nov.**

(Fig. 2.4)

Type material. Holotype KUMIP 355552. Paratypes KUMIP 355553 and PWNHC 2013.XXXX-XXXX.

Etymology. In honour of American actor and comedian Stephen T. Colbert.

Description. Anterior cephalic border directly anterior of ocular lobes directed posteriorly 5-10 degrees, length (sag.) approximately 0.6 times length LO; anterior border furrow present; L4 contacts anterior border furrow; length (sag.) of L4 is approximately the combined length (sag.) of LO, LI, and L2; posterior half of L4 constricts to width 0.6 times that of widest part of L4; furrow present where ocular lobes contact L4; ocular furrow present; ocular lobes wide, approximately width (tr.) extraocular area, extending

posteriorly to L1; width of interocular area approximately 0.5 times the width (tr.) of ocular lobe; S3 convex anteriorly, conjoined adaxially; abaxial margins of L3 extend further adaxially than L2; L2 and L3 do not merge abaxially; S2 convex anteriorly, conjoined adaxially; L1 straight, not conjoined adaxially; abaxial margins of L1 directly anterior of LO; SO slightly convex posteriorly, not conjoined adaxially; posterior border of LO slightly convex posteriorly; posterior border between LO and intergenal angle straight, parallel to a transverse line; posterior border between genal angle and intergenal angle is deflected anteriorly approximately 70 degrees at intergenal angle; intergenal angle developed midway between genal angle and ocular lobe; intergenal swelling present; genal angle developed adaxial of anterior margin of ocular lobe; genal spines deflected posteriorly at approximately 45 degrees with an average width equal to the length (sag.) of LO.

Discussion. This specimen is assigned to the genus *Bristolia* based on a number of characters that it shares with other species within the genus. These include: a short (sag.) anterior cephalic border, prominently separated from the extraocular area by a furrow; the frontal lobe contacts the anterior border furrow; the ocular lobe contacts L4 at the postero-lateral border; faint neutral depression across entire region where ocular lobe hits frontal lobe (present in most *Bristolia* except for *B. anteros* Palmer in Palmer & Halley 1979 and *B. sp.* [Fritz 1972]); S3 is the same depth laterally as adaxially; lateral margins of L2 are constricted compared to the rest of the glabella; posterior edge of ocular lobe opposite adaxial part of margin of L1; long genal spines are present; a faint intergenal ridge is observed; extraocular area is flattened; and as with other species of *Bristolia*, this specimen has a prominent intergenal angle flexing anteriorly and genal spines that are positioned further anteriorly on the cephalon.

Unlike other species of *Bristolia*, this specimen has a prominent ocular furrow. Also the ratio of the width (sag.) of L3 to L2 is greater than in other species and the lateral furrows of LO and L1 are not as constricted anteriorly. Lastly, the width of the ocular lobe (measured perpendicular to the lobe axis at its midpoint) is equal to the width of the extraocular area abaxial to L2, whereas other species have narrower ocular lobes and wider ocular areas (sag.).

Occurrence. Sekwi Formation, Mackenzie Mountains, Northwest Territories, Canada, Section 4, 430-435m above the base of section.

Subfamily Biceratopsinae Pack & Gayle 1971

Genus Bolbolenellus Palmer & Repina 1993

Type species. *Olenellus euryparia* Palmer in Palmer & Halley 1979

***Bolbolenellus* sp.**

(Fig. 3.2, 3.5)

Material examined. KUMIP 355561

Discussion. Fritz (1972) suggested his *Olenellus* sp. 4 was similar to *B. altifrontatus* (Fritz 1972). This specimen was compared to both species and it appears to be more similar to *B. altifrontatus*. It does differ however from *B. altifrontatus* in having somewhat more prominently incised S1-S3, but this might be attributable to the fact that

the specimen medially is somewhat weathered. As we only have a single incompletely preserved specimen, we are treating it as *B. sp.*

Occurrence. Sekwi Formation, Mackenzie Mountains, Northwest Territories, Canada, Section 4, 710-720m above the base of section.

Acknowledgements

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Figures.

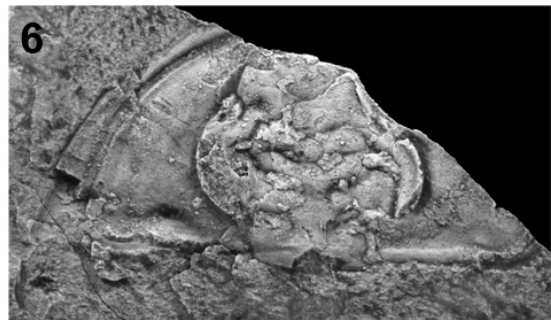
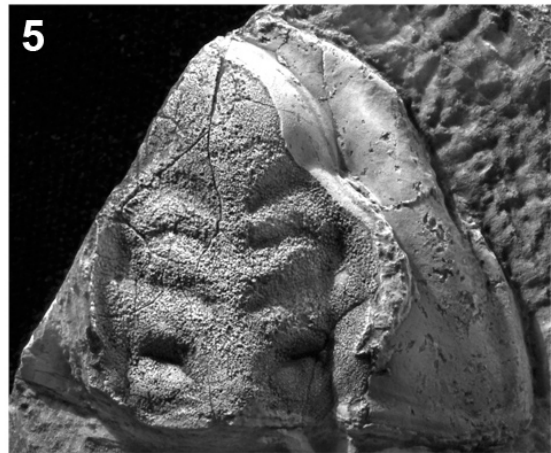
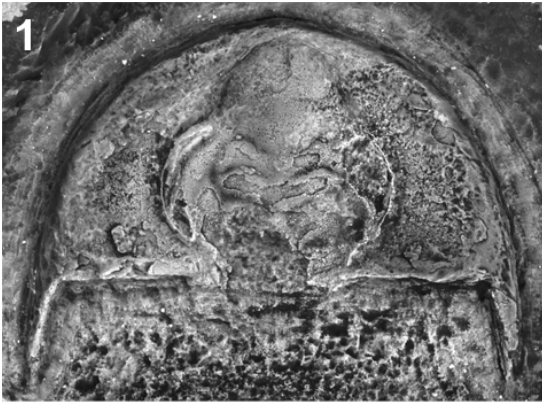


Figure 1. – 1-2, 4-5: *Elliptocephala jaredi* sp. nov.; 3, 6: *Olenellus baileyi* sp. nov.

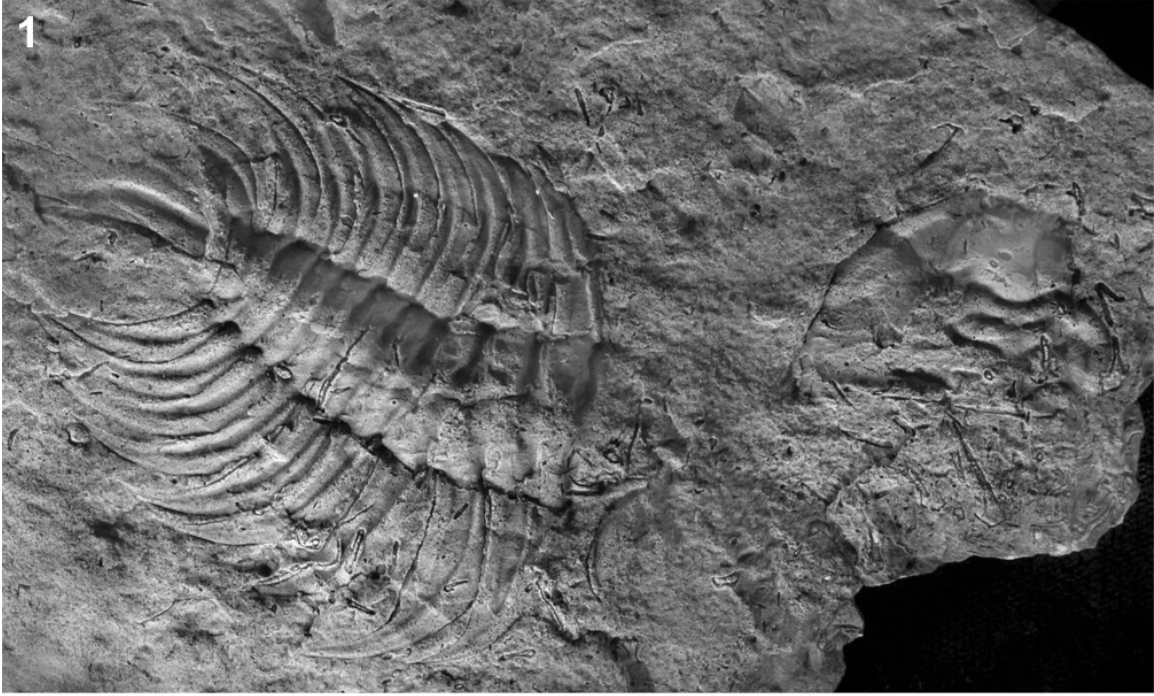


Figure 2. – 1, 2: *Olenellus getzi* sp. aff. *getzi*; 3: ?*Olenellus fowleri*; 4: *Bristolia colberti* sp. nov.

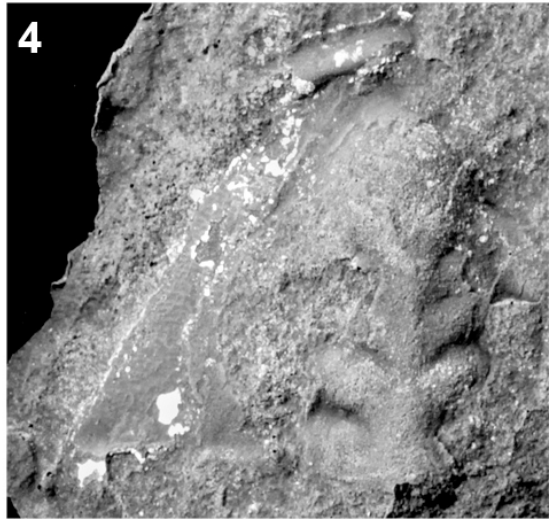
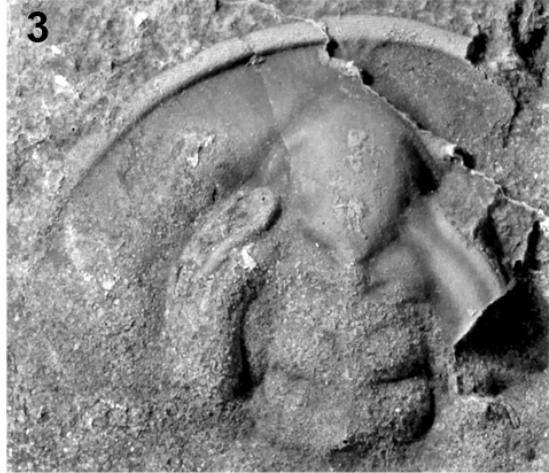
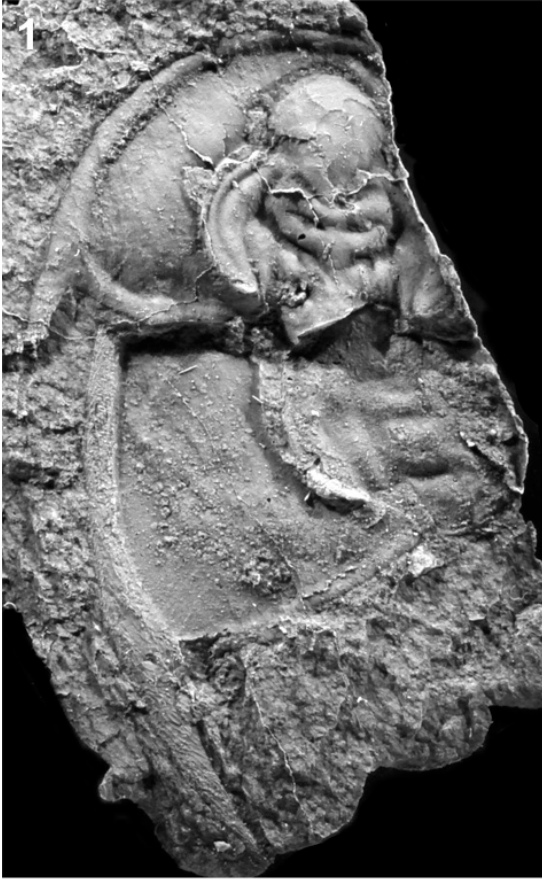


Figure 3. – 1: *Fritzolenellus* sp. aff. *hanseni*; 2, 5: *Bolbolenellus* sp.; 3-4: *Olenellus* sp. aff. *clarki*.

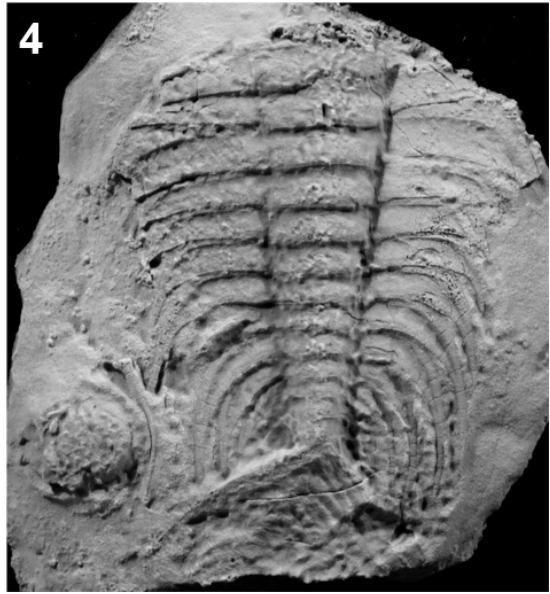
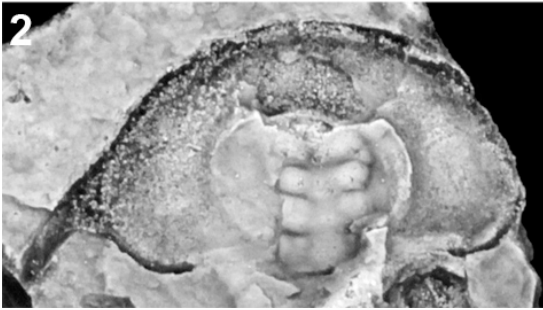
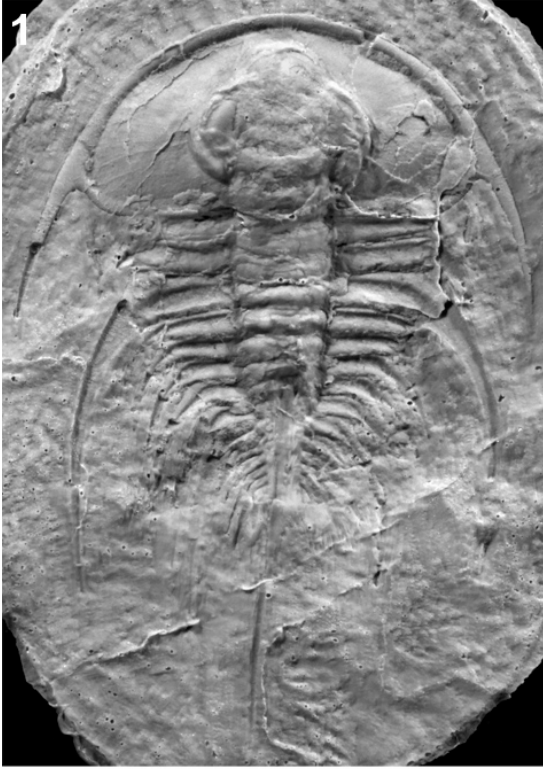


Figure 4. – 1-4: *Mesonacis wileyi* sp. nov.

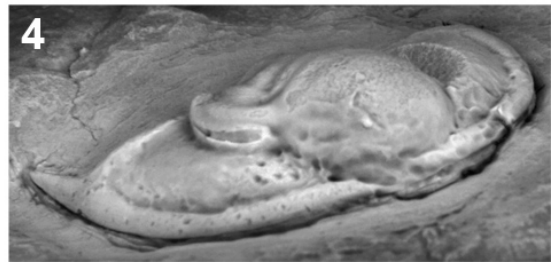


Figure 5. – 1-4: *Elliptocephala logani*.

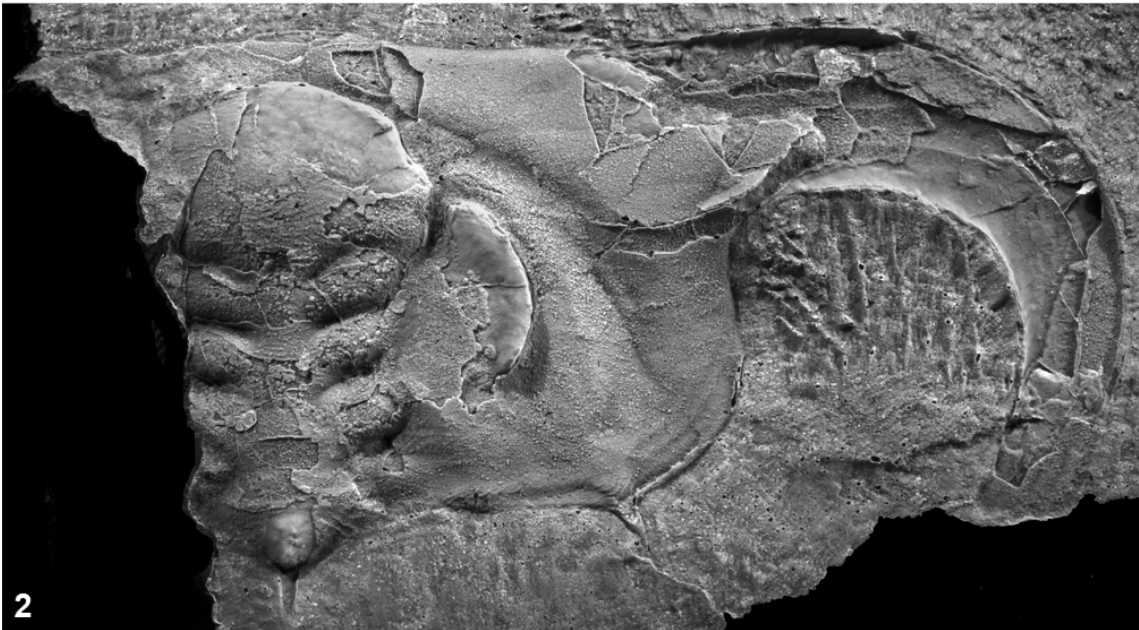


Figure 6. – 1-4: *Holmiella taurus* sp nov.



Figure 7. – 1-3: *Holmiella domackae* sp. nov.

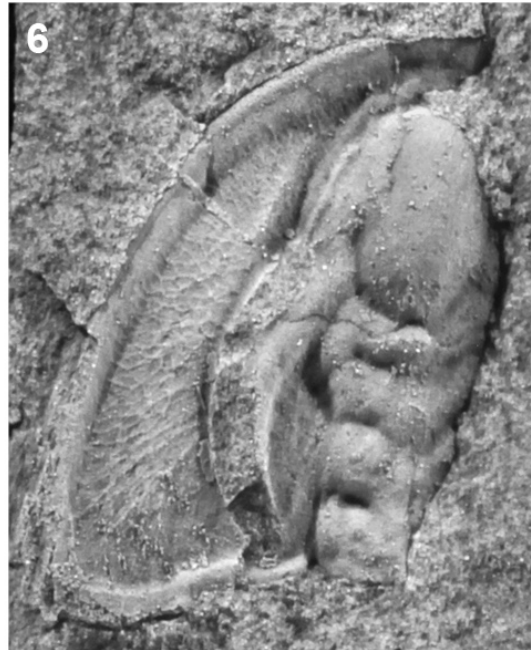
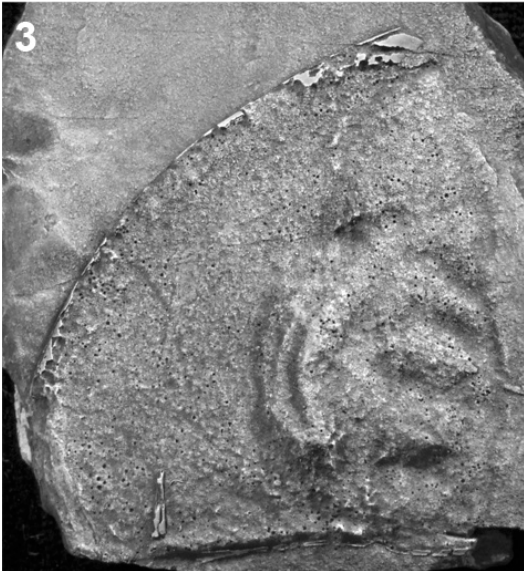
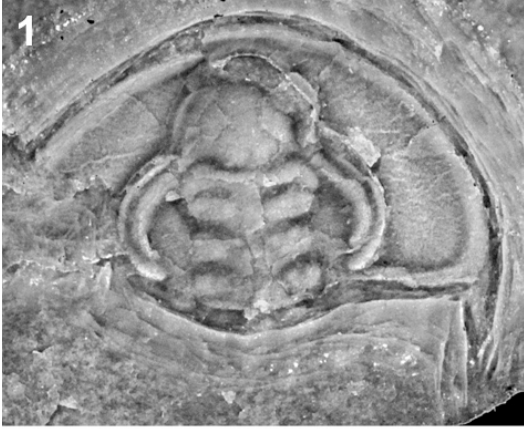


Figure 8. – 1-6: *Mummaspis rodriguezdelgadoe* sp. nov.

Chapter 3. Exploring new techniques to assess the phylogenies of large trilobite clades using morphological data: A case study using the Olenelloidea

Introduction

The Olenelloidea Walcott 1890 are a diverse superfamily of trilobites from the Early Cambrian. Because of their complex morphology with discrete character states, they have been ideal candidates for phylogenetic analysis (Lieberman 1998, 1999). This, combined with their global distribution, has made them a popular taxonomic group to address macroevolutionary questions including disparity and constraint (Smith & Lieberman 1999), the tempo of speciation (Lieberman 2001, 2003a), and the role of geological change in motivating evolution (Lieberman 2003b; Meert & Lieberman 2002, 2004).

To estimate phylogenetic relationships, paleontologists have traditionally relied on parsimony analysis (of course using morphological data). This method searches for the tree/trees with the fewest number of evolutionary changes (i.e. the most parsimonious solution). While parsimony analysis has been a successful means of assessing tree topology, there are some complications that have been known to occur under this method. For example, the accuracy of tree estimation is limited by sampling error. Also, phylogenetic analyses of large groups become limited when the number of taxa exceeds the number of characters. This has been dealt with in the past by creating smaller phylogenies for taxa within the group, and then reassembling them together in a super-tree based on higher-level phylogenetic information. Parsimony tree estimation can also

be limited by missing data. This is particularly an issue for paleontologists who may be dealing with partial specimens or organisms where only hard parts are preserved.

An alternative method to parsimony is maximum likelihood (ML) analysis. As with parsimony, it uses discrete characters and is a model based optimality criterion. In some instances, maximum likelihood may be preferred over parsimony for estimating tree topology. For example, it has been shown that parsimony performs poorly on some tree shapes and maximum likelihood is less sensitive to heterogeneous branch lengths (Felsenstein 2004). Additional benefits of ML include allowing us to analyze larger data sets and possibly combining fossil taxa with extant taxa (Ronquist *et al.* 2012).

At first glance it may seem as though we can easily substitute parsimony methods for maximum likelihood by converting morphological character states of 0's and 1's to molecular A's and T's, and process the data in RAxML using a Jukes and Cantor (1969) model to estimate the likeliest tree. This would, however, be a naïve approach as it neglects several important differences regarding the method of data collection between morphological and molecular analyses. For example, typically only variable characters are sampled with morphological data (Lewis 2001). This is due to the fact that when describing new species or comparing amongst taxa, constant characters are not useful and are therefore excluded. Further, this information is uninformative for parsimony analysis, another reason that it is not used or collected. For this same reason, autapomorphies are often excluded as well (Allman *et al.* 2010). Failure to account for this lack of data can result in extremely long branch lengths under ML, hindering the results of the analysis.

In this chapter I explore two techniques to assess tree topology in olenelloid trilobites. Whereas previous studies used parsimony methods to examine smaller clades and then created supertrees based on higher-level phylogenies (e.g. Lieberman 1999), I

have created a large data set of olenelloid trilobites, combining taxa and characters from multiple analyses, coding and recoding where necessary, to create one single matrix to be analyzed using parsimony and ML techniques. The ML analysis implemented here (in its preliminary stages of development) utilizes the Mkv model, as described by Lewis (2001), to correct for the variability of characters.

Taxa included

Seventy-nine taxa were analyzed in this phylogenetic analysis. *Nevadia weeksi* Walcott 1910, *Daguinaspis ambroggii* Hupé & Abadie 1950, *Neltneria jacqueti* (Neltner & Poctey 1949), *Judomia tera* Larazenko 1960, *Cambroinyoella wallacei* Lieberman 2001, and *Gabriellus* sp Lieberman 2001 were used as outgroup taxa, based on previous analyses by (Lieberman 1998). Ingroup taxa used were *Olenellus thompsoni* (Hall 1859), *O. transitans* (Walcott 1910), *O. romensis* Resser & Howell 1938, *O. agellus* Resser & Howell 1938, *O. rodnyi* Resser & Howell 1938, *O. clarki* (Resser 1928), *O. nevadensis* (Walcott 1910), *O. parvofrontatus* Fritz 1991, *O. robsonensis* Burling 1916, *O. getzi* Dunbar 1925, *O. crassimarginatus* Walcott 1910, *O. baileyi* Gapp *in review*, *O. granulatus* (Palmer 1964), *Mesonacis vermontanus* (Hall 1859), *M. bonnensis* Resser & Howell 1938, *M. fremonti* (Walcott 1910), *M. eagerensis* (Best 1952), *M. wileyi* Gapp *in review*, *Mesolenellus hyperborean* (Poulsen 1974), *M. svalbardensis* (Kielan 1960), *Wanneria walcottana* (Wanner 1901), *Elliptocephala asaphoides* Emmons 1844, *E. logani* (Walcott 1910), *E. sequomalus* (Fritz 1972), *E. walcotti* Lieberman 1999, *E. bicensis* (Walcott 1910), *E. laxocules* (Fritz 1972), *E. paraoculus* (Fritz 1972), *E. parvifrons* (Fritz 1972), *E. lundgreni* (Moberg 1892), *E. jaredi* Gapp *in review*, *Holmia*.

Kjerulfi (Linnarsson 1871), *H. lapponica* Ahlberg & Bergström 1983, *H. palpebra* (Ahlberg 1984), *Kjerulfia lata* Kiaer 1917, *Esmeraldina rowei* (Walcott 1910), *Laudonia bispinata* Harrington 1956, *Fremontella halli* (Walcott 1910), *Lochmanolenellus mexicana* (Lochman in Cooper et al. 1952), *Nephrolenellus multinodus* (Palmer in Palmer & Halley 1979), *Peachella iddingsi* (Walcott 1884), *Biceratops nevadensis* Pack & Gayle 1971, *Holmiella falcata* Fritz 1972, *H. preancora* Fritz 1972, *H. domackae* Gapp in review, *H. taurus* Gapp in review, *Baltobergstroemia mobergi* Bergström 1973, *Schmidtiellus mickwitzi torelli* (Moberg 1899), *S. reetae* Bergström 1973, *Palmettaspis consorta* (Fritz 1995), *P. parallela* Fritz 1995, *P. lidensis* (Fritz 1995), *P. cometes* (Fritz 1995), *Fritzolenellus truemani* (Walcott 1913), *F. lapworthi* (Peach & Horne 1892), *F. reticulatus* (Peach 1894), *Mummaspis occidens* (Walcott 1913), *M. truncatooculatus* (Fritz 1992), *M. obliosooculatus* Fritz 1992, *M. macer* (Walcott 1913), *M. muralensis* Fritz 1992, *Mummaspis rodriguezdelgadoe* Gapp in review, *Laudonia amputate* Fritz 1992, *Bristolia bristolensis* (Resser 1928), *B. insolens* (Resser 1928), *B. anteros* (Palmer in Palmer & Halley 1979), *B. mohavensis* (Hazzard & Crickmay 1933), *B. harringtoni* Lieberman 1999, *B. fragilis* Palmer in Palmer and Halley 1979, *B. colberti* Gapp in review, *Nephrolenellus jasperensis* Lieberman 1999, *Bolbolenellus euryparia* Palmer in Palmer & Halley 1979, *B. sphaerulosus* (Fritz 1991).

Characters.

The characters used in phylogenetic analysis are listed below roughly in approximate order from anterior to posterior position on the organism. A complete character matrix is given in Table 1. Characters emphasize the dorsal exoskeleton of the adult, holaspid stage, as ontogenetic information for many of these species is unavailable.

Hypostomal characters were not included in this analysis as this information was absent for most taxa included. In certain instances where additional discussion was necessary it is provided under the individual characters.

- 1) Length (exsag.) anterior cephalic border near but not directly anterior to frontal lobe (0) very short, length (exsag.) less than or equal to one-half length (sag.) of LO (1) moderately long, length (exsag.) equal to length (sag.) of LO (2) very long, length (exsag.) equal to 1.5 times length (sag.) of LO.
- 2) Anterior cephalic border developed as (0) flattened ledge (1) rounded ridge.
- 3) Anterior border (0) prominently separated from extraocular area by furrow (1) not prominently separated from extraocular area by furrow.
- 4) Plectrum (0) present (1) absent.
- 5) Frontal lobe of glabella (0) does not contact anterior border furrow (1) contacts anterior border furrow. Equivalent to presence or absence of preglabellar field.
- 6) Anterior part of glabella (0) prominently separated from anterior extraocular area or preglabellar area by furrow (1) not prominently separated from anterior extraocular area or preglabellar area by furrow. This character does not refer to the anterior border furrow, but rather to a distinct furrow present at the anterolateral margins of L4 in some taxa. For instance, it is present in *Lochmanolenellus mexicana*, where the

furrows are prominently visible at the anterolateral comers of L4 at its point of contact with the extraocular area.

7) Prominent parafrontal band (0) visible in dorsal view (1) not visible in dorsal view.

8) Anterior margins of frontal lobe at each side of midline deflected posteriorly at (0) roughly 40 degree angle relative to transverse line (1) roughly 10-20 degree angle relative to transverse line.

9) Length (sag.) of L4 (0) moderately long, equal to the length of LO and L1 (1) long, equal to 1.5 times length of LO and L1 medially (2) short, equal to length of LO medially.

10) L4 (0) does not expand prominently dorsally (1) expands dorsally.

11) Lateral margins of L4 (0) proximal to lateral margins of LO (1) distal to lateral margins of LO (2) directly anterior to lateral margins of LO.

12) Ocular lobes contact frontal lobe (0) at posterolateral margins of frontal lobe only (1) at antero and posterolateral margins of frontal lobe.

13) Preocular furrow on frontal lobe (0) directed inward and backward from glabellar margin (1) transverse (2) directed inward and forward from glabellar margin (3) not visible.

- 14) Abrupt dorsal notch like truncation of ocular lobes at margins of L4 (0) absent (1) present.
- 15) Ocular lobes (0) gradually decrease dorso-ventral elevation between axial furrows and mid-point of ocular lobes (1) of constant dorso-ventral elevation between axial furrows and mid-point of ocular lobes.
- 16) Ocular lobe (0) separated from extraocular area by prominent shelf and/or furrow (1) smoothly merges into extraocular area. This shelf is particularly evident in Fritz's (1972, pl. 14, figs. 9, 10) illustration of *Elliptocephala logani* in lateral view.
- 17) Posterolateral margins of L4 (0) convergent anteriorly (1) divergent anteriorly (2) subparallel.
- 18) Region of anterior part of ocular lobe between putative visual surfaces and L4 (0) narrow (tr.) (1) broad (tr.), one-third width of glabella at L1. State 1 is typical of redlichiine taxa, and is also found in *Daguinaspis ambroggi* and one olenelloid, *Nephrolenellus multinodus* (Palmer in Palmer and Halley, 1979).
- 19) Ocular furrow (0) prominent (1) not prominent.

20) Line from posterior tip of ocular lobe to junction of posterior margin of lobe with glabella (0) forms 10-20 degree angle with sagittal line (1) parallel to sagittal line (2) forms 45-degree angle with sagittal line. Taxa scored as 18(1) always have 20(2), but taxa scored as 18(0) have either state 0 or 1 for character 20. Therefore, these characters were treated as distinct.

21) Transverse profile of ocular lobes (0) convex dorsally (1) flattened dorsally. This character is unlikely to be taphonomic as shale preserved taxa are known with both states.

22) Surface of interocular area (0) slopes evenly from tip of ocular lobe to glabella (1) developed as flattened shelf (2) arched. This character is unlikely to be taphonomic as shale preserved taxa are known with all states.

23) Posterior tips of ocular lobes developed opposite (0) SO (1) medial part of distal margin of LO (2) medial part of distal margin of LI (3) medial part of distal margin of L2 (4) opposite S2 (5) opposite S1.

24) Width (tr.) of interocular area (0) approximately equal to at least width of ocular lobe (1) about half width of ocular lobe at its midlength. Taxa scored as 18(1) always have 24(0), but taxa scored as 18(0) can have 24(0) or 24(1). Thus, these characters were coded as distinct.

- 25) Anterodistal margins of L3 formed by (0) axial furrows (1) ocular lobes.
- 26) Distal margin of L3 (0) straight (1) convex outward.
- 27) Course of S3 (0) straight (1) gently convex (2) jaggedly convex or carat shape (3) not prominently incised. The approach used to formulate characters 27-29, 31, 33, and 34 is discussed in greater detail above in the section entitled parsimony analysis.
- 28) S3 (0) conjoined medially (1) not conjoined medially (2) not prominently incised medially.
- 29) Middle sector of S3 (0) linear (1) convex anteriorly (2) not prominently incised.
- 30) Transverse convexity of LI, L2, and L3 (0) gently convex (1) strongly convex. This character is unlikely to be taphonomic because shale preserved taxa are known to have both character states.
- 31) Line between ends of S2 (0) directed inward and posteriorly at roughly 45-degree angle to transverse line (1) transverse (2) not prominently incised.

32) L2 and L3 (0) do not merge distally (1) merge distally.

33) S2 (0) conjoined medially (1) not conjoined medially (2) not prominently incised.

This character is polymorphic in *Elliptocephala asaphoides* Emmons, 1844, *Holmia kjerulfi* (Linnarsson, 1871), *Fritzenellus truemani*, *Mummaspis occidentis* (Walcott, 1913), and *Laudonia bispinata* Harrington, 1956.

34) S2 (0) straight (1) convex anteriorly (2) not prominently incised.

35) Distal margins of L2 when proceeding anteriorly (0) converging (1) diverging (2) subparallel.

36) S1 (0) conjoined medially (1) not conjoined medially.

37) Distal sector of SO (0) straight (1) convex anteriorly (2) sinuous. This character is polymorphic in *L. bispinata*.

38) SO (0) not conjoined medially (1) conjoined medially.

39) Distal sector of SO with (0) proximal end well posterior to distal end (1) proximal and distal ends on transverse line. This character is polymorphic in *L. bispinata*.

40) Axial part of LO (0) smooth (1) with node present (2) with spine present. The precise distinction between node and spine was not quantified. The distinction is well illustrated by means of an example. *Mummaspis occidens* has a spine, and *Bristolia bristolensis* (Resser, 1928) has a node.

41) Posterior margin of LO (0) roughly transverse (1) convex posteriorly.

42) Lateral lobes on LO (0) absent (1) present.

43) Glabellar furrows (0) some moderately to strongly incised (1) all weakly incised.

44) Extraocular area (0) flattened (1) prominently vaulted (2) gently convex.

45) Prominent anastomosing ridges (0) present on extraocular area (1) absent on extraocular area (2) extraocular area narrow, ridges not resolvable. The approach used to formulate characters 45-51 is discussed in greater detail above in the section entitled parsimony analysis.

46) Anterior ocular line (0) visible (1) not visible (2) extraocular area narrow, line not resolvable.

- 47) Genal ridge (0) prominently developed (1) not visible (2) extraocular area narrow, ridge not resolvable.
- 48) Intergenal ridge (0) visible as trace (1) not visible (2) developed as prominently expanded ridge.
- 49) Width of extraocular region from distal tip of ocular lobe to position of anterior border furrow opposite L1 (0) broad, width (tr.) greater than or equal to 75 percent of the width of the glabella at L1 (1) narrow, width (tr.) 40 to 50 percent of the width of the glabella at L1 (2) very narrow, width (tr.) less than or equal to 15 to 20 percent of the width of the glabella at L1.
- 50) Orientation of genal spine near where it contacts cephalic border relative to sagittal line (0) directed posterolaterally at roughly 10-20 degree angle (1) directed posterolaterally at roughly 35-45 degree angle (2) directed posterolaterally at roughly 65-80 degree angle (3) genal spine not well developed or absent.
- 51) Length (exsag.) of genal spine (0) equal to length (sag.) of first two thoracic segments (1) equal to length (sag.) of first four to five thoracic segments (2) equal to length (sag.) of at least eight thoracic segments (3) genal spine not well developed or absent.

52) Genal spine angle developed opposite medial part of (0) distal margin of LO (1) distal margin of L1 (2) frontal lobe (3) distal margin of L3 (4) first thoracic segment (5) distal margin of L2. This character is polymorphic in *H. preancora* and *B. bristolensis*. It describes the relative placement or advancement sensu Harrington (1956) of the genal spines.

53) Intergenal angle developed (0) adjacent to or directly behind genal spine (1) posterior of lateral margins of ocular lobes (2) posterior to point half way between ocular lobes and genal spine (3) intergenal angle not prominently developed.

54) Intergenal spine (0) not developed (1) represented by distinct dorsal swelling or node (2) small pointed spine (3) well developed spine (4) represented by faint, posteriorly directed swelling.

55) Intergenal angle relative to a transverse line (0) deflected at roughly -10 to 10 degree angle (1) directed anteriorly at roughly 45-degree angle (2) directed anteriorly at roughly 60-70 degree angle (3) directed anteriorly at roughly 80-90 degree angle.

56) Medial part of posterior border between intergenal angle and LO (0) transverse (1) flexes posteriorly

- 57) Distal margins of glabella at L1 relative to LO (0) constricting (1) displaced par laterally.
- 58) Medial and distal tips of S3 (0) as forward (1) distal tip further forward than medial tip.
- 59) Ornament on occipital lobe (0) posterior of midline of LO (1) anterior of midline of LO.
- 60) S1 (0) convex (1) transverse.
- 61) Medial margins of genal spine (0) deflect posteriorly (1) loop anteriorly before deflecting posteriorly.
- 62) Tagmosis of thorax (0) broken up into pro- and opisthothorax (1) not prominently divided up into pro- and opisthothorax.
- 63) Anterior margin of third thoracic pleural segment, before flexing strongly posteriorly (0) parallel to a transverse line or very weakly directed posteriorly (1) directed anteriorly.
- 64) Third thoracic segment (0) normal (1) macropleural.

- 65) Pleural spine of third thoracic segment (0) normal, same length as other segments (1) projects posteriorly 6-8 thoracic segments (2) projects further posteriorly than length of entire prothorax (3) projects posteriorly 3- 4 thoracic segments.
- 66) Anterior margin of thoracic pleural furrow on third segment when proceeding from proximal to distal edge (0) directed weakly posteriorly, before flexing strongly posteriorly (1) parallels a transverse line, before flexing strongly posteriorly.
- 67) Posterior margin of thoracic pleural furrow on third thoracic segment (0) directed evenly posterolaterally (1) adaxial part directed strongly posteriorly, distal part parallel to a transverse line or weakly flexing anterolaterally (2) adaxial part parallel to a transverse line, distal part deflected weakly anterolaterally (3) adaxial part parallel to a transverse line, lateral part deflected weakly posteriorly.
- 68) Thoracic pleural spines on segments 5-8 (0) developed as broad sweeping projections extending back six to eight thoracic segments (1) developed as short projections extending two thoracic segments back (2) do not sweep significantly back (3) developed as broad sweeping projections extending four segments back.
- 69) Prothoracic axial rings (0) without lateral furrows, so form uniform rectangular or trapezoidal blocks (1) with two prominent anterolateral lobes. This character bears superficial similarity to character 42, but in some taxa these lobes are present on LO

but absent from the thoracic axial rings and vice versa, so these characters were treated as distinct.

- 70) Lateral margins of prothoracic axial rings (0) sub-parallel (1) converging when proceeding from anterior to posterior or first diverging, then converging, when proceeding from anterior to posterior.
- 71) Single nodes on median portion of thoracic axial rings (0) present (1) absent. Some species of the genus *Olenellus* Hall, 1862 may differ in terms of the number of axial rings that bear nodes, but to code this as a separate character in this analysis would not be phylogenetically informative because it is a phenomenon restricted to a very narrow group of species.
- 72) Thoracic pleural furrows (0) only extend width of inner pleural region (1) extend onto spines (2) extend only half width of inner pleural region.
- 73) Boundary between thoracic pleural furrow and anterior band (0) sharp (1) gradational.
- 74) Length (exsag.) of thoracic pleural furrows at medial (tr.) part of thoracic segment relative to length at distal part of segment (0) equal to 1-1.3 times length of pleural furrows on distal part of segment (1) equal to 1.9-2.0 times length of pleural furrows on distal part of segment.

75) Length (exsag.) of thoracic pleural furrows (excluding T3) at medial part of segment relative to length (exsag.) of posterior band of pleural segment (0) long, greater than or equal to 1.5 times the length of the posterior band (1) short, equal to the length of the posterior band (2) very short, equal to half the length of the posterior band.

76) Tips of thoracic pleural segments (0) distally in roughly same dorsoventral plane as medially (1) flex strongly ventrally laterally. State 1 is confined to *Peachella iddingsi* (Walcott, 1884) and *Biceratops nevadensis* Pack & Gayle, 1971. It refers to the strong ventral curvature of the distal tips of the thoracic pleurae seen in these taxa. Other taxa that co-occur with these species do not show this prominent distal curvature of the pleurae and therefore this character is not taphonomic.

77) Width of thoracic pleural spines T5-T8 at spine midlength (0) more than two-thirds length (exsag.) of medial part of inner pleural region (1) less than half length (exsag.) of medial part of inner pleural region.

78) Prominent spine on 15th thoracic axial ring (0) absent (1) present.

79) Spine on 15th thoracic segment (0) absent (1) length (sag.) of whole prothorax (2) short, length (sag.) of five thoracic segments (3) very short, length (sag.) of two thoracic segments. Characters 73 and 74 were treated as distinct because 1) there was no clear criterion to order the character states of 74; 2) it was posited that the actual possession of a spine should be treated as evidence of descent rather than allowing the transition between spine absent and very long spine to be equivalent in terms of the

number of steps to the transition between spine length (sag.) of five thoracic segments and spine length (sag.) of whole prothorax; and 3) there is one taxon which clearly bears a spine, but the length of the spine can not be determined, and character 73 allows this information to be captured. Removal of either character has no effect on tree topology.

80) Base of spine on 15th thoracic segment (0) absent (1) nearly as wide (tr.) as axis of segment (2) less than half width (tr.) of axis of segment.

81) Segments of opisthothorax or posterior to T15 (0) with prominent pleurae (1) with pleurae very reduced or absent.

82) Pleurae of opisthothoracic segments or segments posterior to T15 (0) same orientation as pleurae of prothoracic segments (1) orientation contrasts with that of prothoracic segments (2) barely developed.

83) Pygidium (0) relatively narrow, length (sag.) 1.5 times width (tr.) (1) relatively broad, length (sag.) equal to width (tr.) (2) very broad, two times as wide (tr.) as long (sag.).

84) Posterior margin of pygidium (0) transverse or weakly convex (1) bifurcated with median notch.

85) Ratio of width (tr.) of T7 to width (tr.) of T3 (excluding pleural spines) equal to (0) 0.50 to 0.64 (1) 0.70 to 0.75.

86) Width (tr.) of axis relative to width of pleural segment for T3 excluding spine (0)
60%-70% (1) 100%-105%.

87) Thoracic pleural spines of T1 to T4 (0) sweep back 4 segments (1) sweep back 2
segments (2) sweep back 1 or no segments.

88) Lateral margins of prothoracic pleural spines inclined at angle relative to sagittal line
(0) 10° to 20° (1) 40° to 50°

Parsimony Analysis

Methods.

The data were analyzed using PAUP v.4.0b10 (Swofford 2003). A heuristic search with 1000 replications using a tree-bisection-reconnection branch-swapping algorithm to determine the most parsimonious trees for the data matrix was employed (this is standard protocol for the analysis of large data sets). All characters were unweighted and all multistate characters were treated as unordered as there are no obvious criteria for ordering them. To assess tree support, bootstrap values were calculated in PAUP. Bootstrap tests were analyzed using 10,000 replicates and a traditional search. The matrix data were compiled into Nexus files using Mesquite v.2.75 (Madison & Madison 2011).

Results.

Parsimony analysis recovered six most parsimonious trees of length 1,141 steps

with RI values of 0.458, and CI values (when uninformative characters are excluded) of 0.1280. A strict consensus of these trees (Fig. 1) reveals monophyletic groupings of several taxa, consistent with assignments by Lieberman (1999). These include the genera *Palmettaspis*, *Holmiella*, and *Nephrolenellus*. Other genera that had previously been identified as monophyletic, however, did not plot so as such, for instance, *Bristolia* and *Elliptocephala*, which both are represented as paraphyletic grades. Further, *Olenellus* mostly plots as a derived clade with *Mesolenellus* and *Mesonacis*, however with some representatives, such as *O. romensis*, *O. granulatus*, and *O. baileyi*, not plotting with the rest.

ML Analysis

Methods.

The data were analyzed using GARLI 2.01.1084 (Zwickl 2006). The Mkv model (Lewis, 2001) was implemented to correct for the variability of characters. Bootstrap tests were run to assess the robustness of the clades returned by the analysis.

Results.

Maximum likelihood analysis recovered a most likely tree (Fig. 2) with a score of -4693.3309 and tree length of 36.501. The tree recovered shows few, if any similarities to topologies found by previous studies of the Olenelloidea or the aforementioned parsimony analysis of the group. A 50% majority-rule consensus of 200 trees recovered in the bootstrap analysis was uninformative for assessing the robustness of any clades.

Discussion

This is the first parsimony analysis of the Olenelloidea to consider the entire group in a single analysis, and a number of patterns seen in the parsimony analysis are congruent with results of previous studies. For example, *Elliptocephala* and *Wanneria* both share a close relationship, but as was shown by Lieberman (1998), it is not a sister relationship. There are also similarities among the holmiids. Just as Lieberman's (1999) analysis of the Holmiidae suggested a monophyletic grouping of *Esmeraldina* and *Holmiella*, with a sister relationship to *Palmettaspis*, the same pattern is observed here, even with the addition of two recently described species of *Holmiella*. Plotting just up the tree from these is a monophyletic grouping of the other holmiid taxa (to the exclusion of *Holmia kjerulfi*). It should be mentioned that initial attempts at analyzing this data with even more taxa were less successful (produced very limited resolution). However, these attempts included taxa with very incomplete data. Therefore, the following incomplete taxa were pruned from the analysis: *Bolbolenellus altifrontatus*, *Bolbolenellus hermani*, *Bolbolenellus groenlandicus*, *Olenelloides armatus*, *Baltobergstroemia sulcata*, *Baltobergstroemia* sp., *Schmidtellus* sp., *Mesonacis hamoculus*, and *Mesonacis cylindricus*.

Incongruences between this parsimony analysis and previous analyses are also worth mentioning. For example, we observe a derived clade of species of *Olenellus*, *Mesonacis*, and *Mesolenellus*. Lieberman (1999) by contrast had also suggested that these genera were closely related, yet each genus was deemed monophyletic, perhaps partly because of the supertree approach used. Historically there has been discussion regarding the relations of these groups with Resser (1929) and Whittington (1989) both having trouble distinguishing differences between *Olenellus* and *Mesonacis*. In the parsimony analysis presented here characters that cause the species of these three genera to group

into a single clade (though not necessarily in all taxa) include: the anterior cephalic border is developed as a flattened ledge, the anterior part of the glabella is not prominently separated from the anterior extraocular area or preglabellar field by a furrow, and a prominent parafrontal band is not visible in dorsal view. Therefore, it would be worthwhile to consider each of these characters in greater detail to see whether a single clade topology or three separate clades is ultimately preferred.

It is also worth noting that the clade of *Olenellus*, *Mesonacis*, and *Mesolenellus* appears to be more derived than shown by previous analysis (Lieberman 1998). This is interesting given that these taxa occur later stratigraphically compared to the holmiids, and now set up the tree relative to other holmiids. Characters that influenced this more derived phylogenetic position for these three genera include: the prominent parafrontal band not visible in dorsal view, the length (sag.) of L4 is equal to 1.5 times length of LO and L1 medially, L2 and L3 merge distally, the medial part of the posterior border between the interregal angle and LO is transverse. On the other hand, characters such as the distal margin of L3 straight, the spine present on the axial part of LO, and the width of the extraocular region from the distal tip of the ocular lobe to a position of the anterior border furrow opposite L1 is narrow with a width (tr.) 40 to 50 percent of the width of the glabella at L1 have resulted in the holmiids plotting more basally.

As was noted above, a paraphyletic grade of two more restricted holmiid monophyletic groups was revealed in this analysis with the exception of *Holmia kjerulfi* (ostensibly what should be the representative of a monophyletic Holmiidae). Lieberman (1999) had found this species to plot very basally within the family. Our analysis shows the Baltic *H. kjerulfi* plots sister to Laurentian *Wanneria walcottana*, a species shown by Lieberman (1998) to share a close relationship with the holmiids. Within this analysis,

characters that appear to pull *H. kjerulfi* up the tree with *W. walcottana* include, but are not limited to, a prominent parafrontal band not visible in dorsal view, the ocular lobe smoothly merges into the extraocular area, a node is present on the axial part of LO, a genal ridge is prominently developed, and the width of the extraocular region from the distal tip of the ocular lobe to a position at the anterior border furrow opposite L1 is broad with a width (tr.) greater than or equal to 75 percent of the width of the glabella at L1. Future analyses will explore the resiliency of these results. In particular, the relative positions of *H. kjerulfi*, the remainder of the holmiids, and genera such as *Olenellus*, *Mesonacis*, and *Mesolenellus*, especially in a ML framework.

At this point we see little congruence between the parsimony and ML trees, however this new technique used for maximum likelihood is still in its infancy and thus we would not emphasize the results from the ML analysis but consider these a work in progress. One of the issues is that still a prodigious amount of time is needed to search tree space. To diminish this time, all characters were reduced to a maximum of three character states, which meant there were several characters whose states were combined for this study. This could be partly responsible for the difference between the parsimony and ML analyses. In the future, new algorithms will be developed to better consider a larger scope of multistate characters and we can explore the extent to which this is causing the divergence between the ML and parsimony results. Another concern with the ML result is that the tree branch lengths produced from the ML analysis are suspiciously long, which is an indication that the variable-only version of the ascertainment bias (Mkv) may not be sufficient for these data and models that factor in other considerations will also need to be explored. For instance, in the future the Mkv *pars-inf* method that recognizes that only parsimony informative characters have been used in the analysis

could be employed. Still, the expanded character matrix presented here, along with the results from the parsimony analysis (and the early ML analysis) will serve as a framework to build on as scientists work to develop more efficient and accurate ML approaches to morphological character analysis. These will be very beneficial to the evolutionary biology and paleontology communities as they will expand the variety and types of character data that can be considered in phylogenetic studies.

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Figures

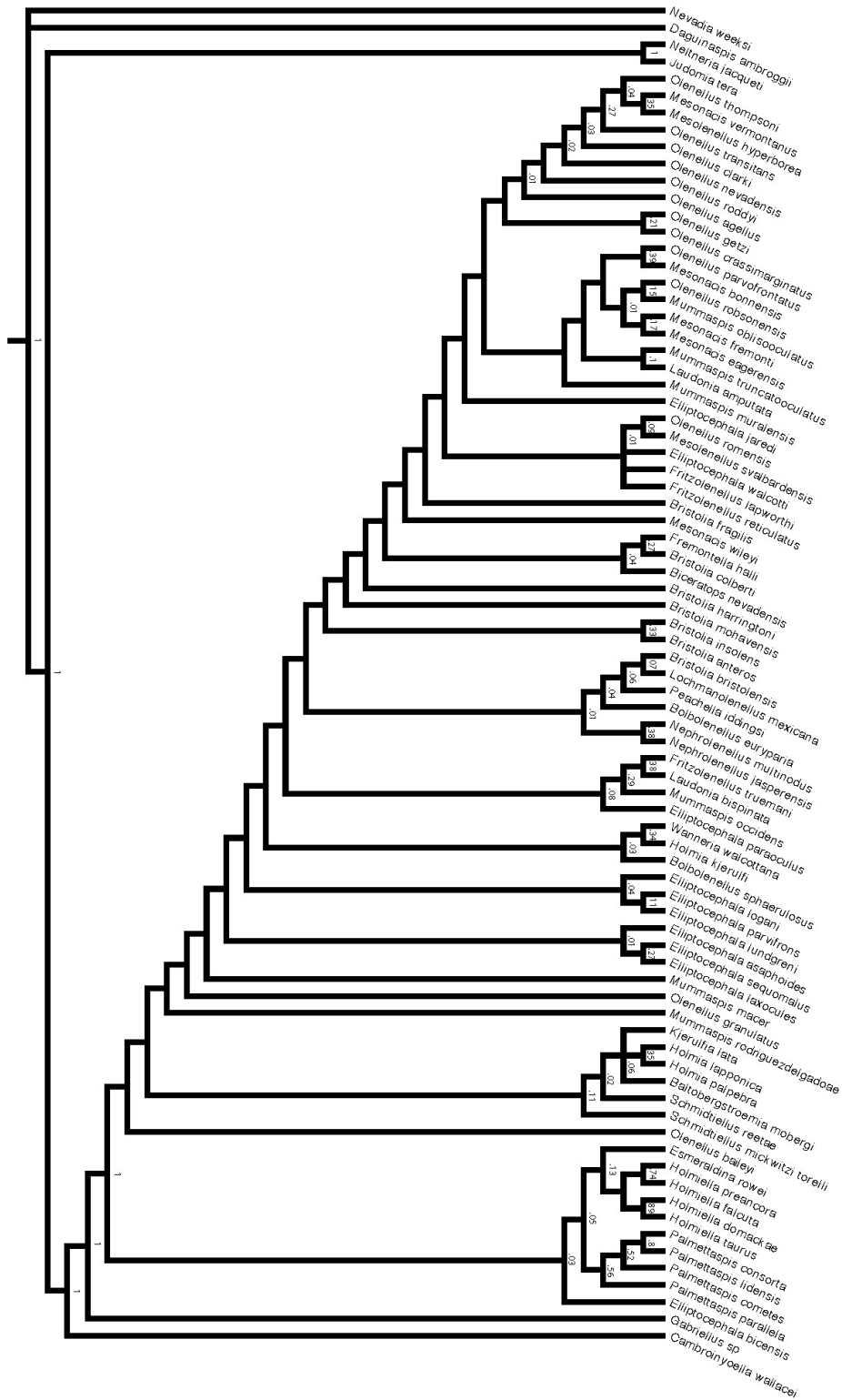


Figure 1.

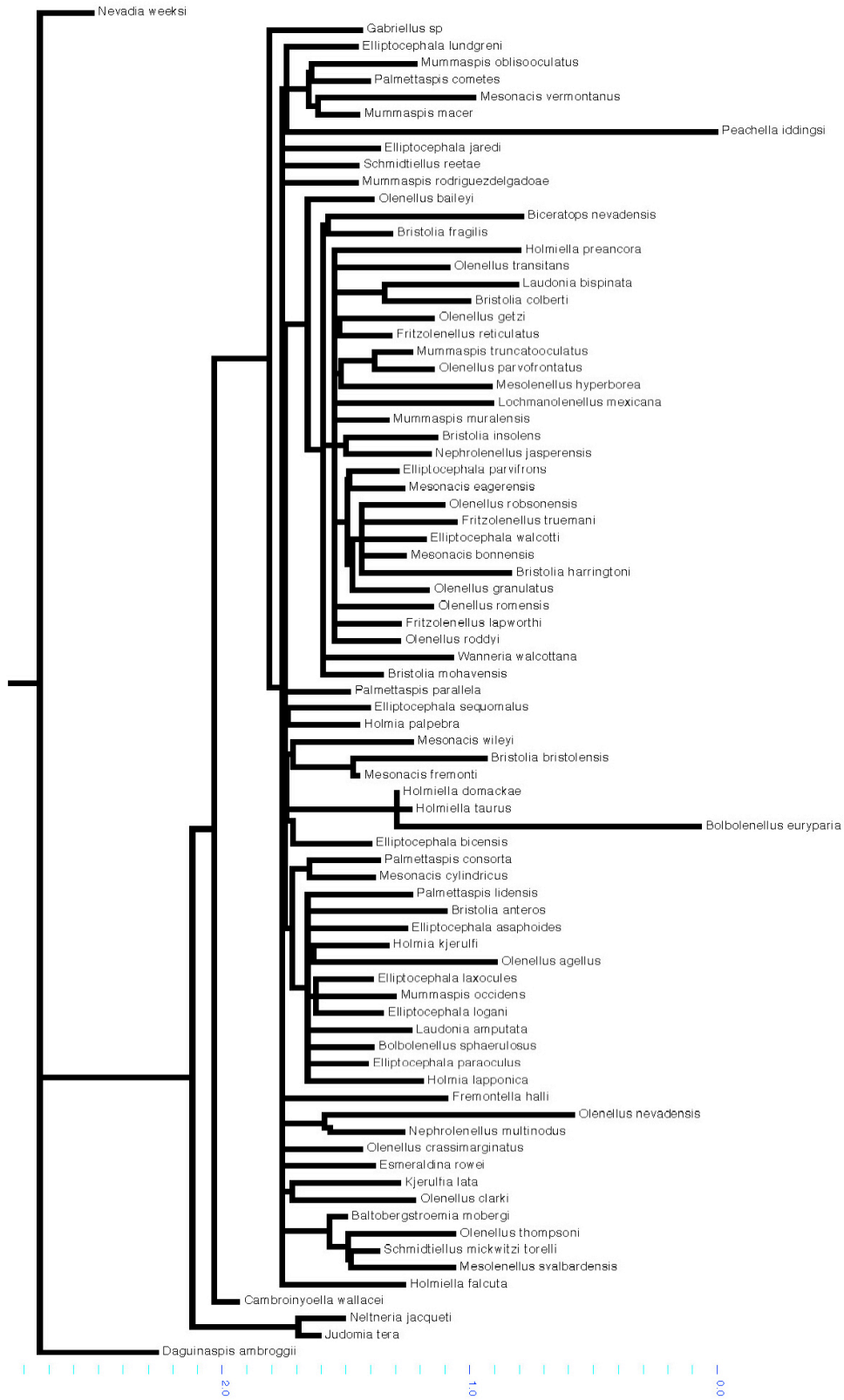


Figure 2.

Figure Captions

Figure 1 – A strict consensus of the six most parsimonious trees of length 1,141 steps recovered from parsimony analysis. Bootstrap values are presented here on the nodes.

Figure 2 – The most likely tree with a score of -4693.3309 and tree length of 36.501 recovered using the Mkv ML model.

Conclusions

This dissertation focused on the systematics and phylogenetic relationships for several groups of trilobites that occurred during two important evolutionary radiations during the history of life. Results of this research have furthered our knowledge of trilobite history, with specific attention to the Cambrian and Ordovician radiations.

Phylogenetic analysis of the Eccoptochilinae has altered many traditional assignments for this Ordovician clade. Importantly, results of this study revealed that Lane's original treatment of the group is not monophyletic. Our tree suggests that more derived genera, such as *Pseudosphaerexochus*, belong to the closely related Sphaerexochinae, while less derived taxa such as *Areia*, *Placoparina*, and some species of *Eccoptochile*, belong to a paraphyletic grade, basal to the sphaerexochines.

New trilobite material from the Sekwi Formation of the Northwest Territories has increased known species of Cambrian olenelloid trilobites. Specifically seven new species were described, adding more taxa to an already specious clade. Further, a number of specimens were identified with affinities to previously described taxa.

Newly described taxa were incorporated into a phylogeny for the Olenelloidea. This study presented the opportunity to explore new phylogenetic techniques. We are developing new methodologies with maximum likelihood approaches to assess tree topologies for large clades using morphological data. While in its infancy, these methods have the potential to allow for phylogenetic studies of large fossil clades. Ultimately we hope that this will allow us to incorporate information of the extinct with the extant and to study rates of evolution.

While some may say that all there is to know about trilobites has already been uncovered, I argue that there is much more to do. This dissertation illustrates just some of the work being done regarding the systematics and phylogenetics of trilobites. There are many groups of trilobites throughout the Paleozoic that still require similar treatment. The small-scale and detailed work that is currently being done to assess the relationships among trilobite species is laying the solid foundation needed for future work to evaluate rates of speciation and extinction, modes of speciation, and paleobiogeographic patterns. It is not until this work has been done that we can seriously tackle many of the larger questions regarding macroevolution.