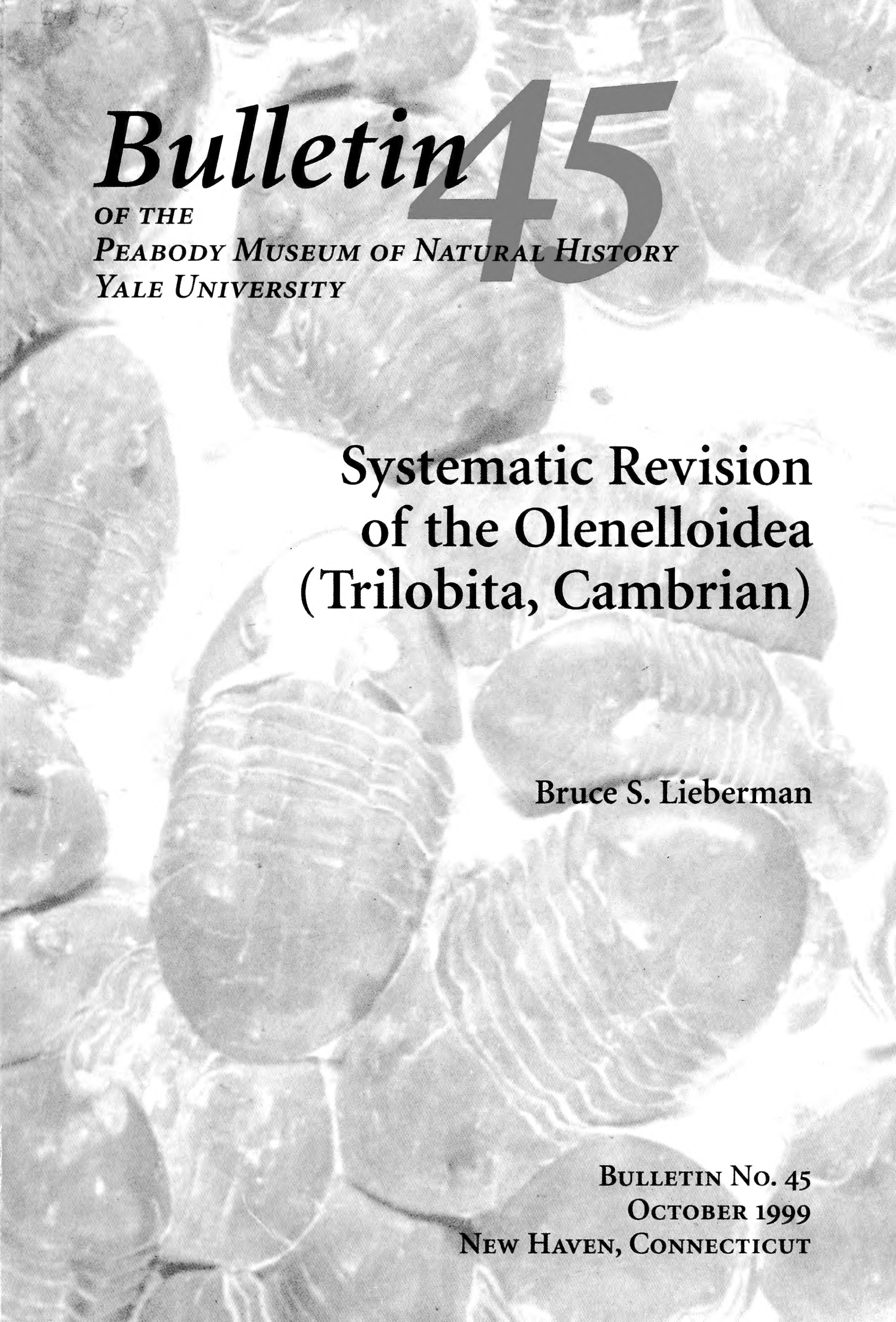

Bulletin 45

OF THE
PEABODY MUSEUM OF NATURAL HISTORY
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Systematic Revision of the Olenelloidea (Trilobita, Cambrian)

Bruce S. Lieberman

BULLETIN NO. 45
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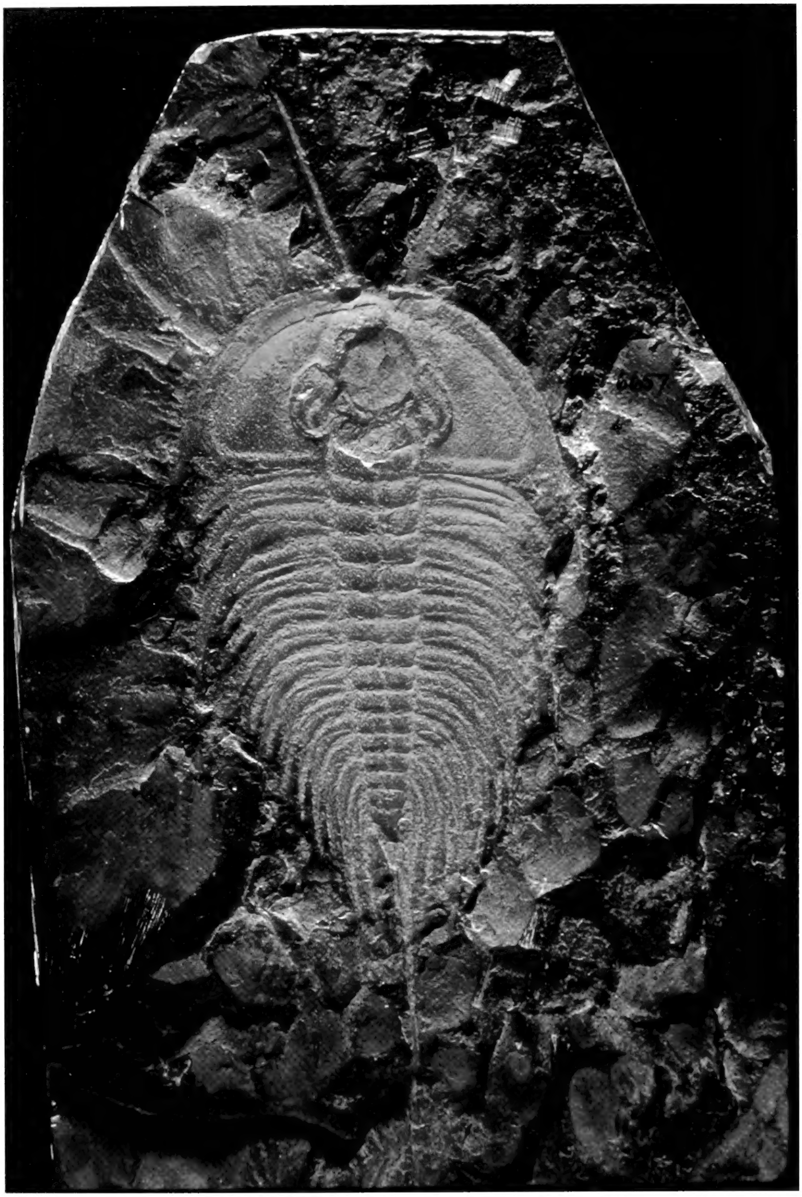

Olenellus getzi Dunbar [YPM 6657], holotype.
Early Cambrian, Pennsylvania, U.S.A.

Photograph by William K. Sacco.

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Systematic Revision of the Olenelloidea (Trilobita, Cambrian)

Bruce S. Lieberman, Ph.D.
Department of Geology
University of Kansas

Curatorial Affiliate
Division of Invertebrate Paleontology
Peabody Museum of Natural History
Yale University

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On the cover: *Homotelus bromidensis* [YPM 10186]. Early Ordovician, Oklahoma, U.S.A.

Photograph by B.S. Lieberman.

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ABSTRACT

Phylogenetic analyses for all the available species comprising eight clades of trilobites within the monophyletic superfamily Olenelloidea (Trilobita, Cambrian) are presented. These trilobites are among the dominant elements of Early Cambrian faunas in Laurentia, and are the direct by-products of the Cambrian radiation. These phylogenetic analyses, along with a higher level phylogenetic analysis of the Olenelloidea, are used to obtain a perspective on patterns of speciation in this exclusively Early Cambrian trilobite group. A total of 78 species were considered.

Based on phylogenetic patterns and the distribution of olenelloid species in the stratigraphic record, there appears to be an evolutionary gap of indeterminate duration in the early history of the Olenelloidea. This gap is in some way associated with the Cambrian radiation, and implies that part of the record of that radiation is effaced. Phylogenetic analysis also indicates substantial revision may be needed for Early Cambrian biostratigraphy. In particular, one of the important biostratigraphic zones in the Early Cambrian is the *Olenellus* zone. However, species that have been assigned to the genus *Olenellus* in past studies are in fact distantly related, and include representatives from several distinct clades within the Olenelloidea. Therefore, the genus *Olenellus,* as defined in past studies, is polyphyletic. The polyphyletic nature of this assemblage implies that past correlations that recognized an *Olenellus* zone may have little biostratigraphic meaning.

In addition to phylogenetic analyses, three new species, *Elliptocephala walcotti, Bristolia harringtoni* and *Nephrolenellus jasperensis,* are described, and one new genus, *Baltobergstroemia,* is diagnosed.

KEYWORDS

Cladistics, Laurentia, stratigraphy, invertebrate paleontology.

ACKNOWLEDGMENTS

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Systematic Revision of the Olenelloidea (Trilobita, Cambrian)

Introduction

Trilobites dominate Early Cambrian metazoan diversity, and the suborder Olenellina Walcott 1890 is the primary element in the Early Cambrian trilobite biota (Palmer and Repina 1993). Recently, the Olenellina were subjected to character analysis by Lieberman (1998), who concluded that the Olenellina as traditionally defined (e.g., Palmer and Repina 1993) actually represented a paraphyletic assemblage containing some superfamilies more closely related to the Redlichiina Richter 1933 than to other superfamilies within the "Olenellina." However, within the Olenellina there is at least one monophyletic superfamily, the Olenelloidea Walcott 1890. Lieberman (1998) also presented a cladogram displaying the evolutionary relationships of almost all the major generic clades within the Olenelloidea. That analysis considered a large number of genera, but only a small number of exponents (species) from each of the generic clades; however, this made it possible to recognize characters diagnostic for each of the clades. Moreover, it facilitated recognition of appropriate outgroup taxa that could be used in subsequent studies to elucidate patterns of specific differentiation within each of those clades.

The present paper builds on Lieberman (1998) and pursues in greater detail phylogenetic studies within the Olenelloidea. Here I present the results of eight phylogenetic analyses of all available species within almost all of these generic clades. These analyses include the genera: *Olenellus* Hall 1862; *Mesolenellus* Palmer and Repina 1993; *Mesonacis* Walcott 1885; *Elliptocephala* Emmons 1844; *Holmia* Matthew 1890; *Kjerulfia* Kiaer 1917; *Schmidtiellus* Moberg in Moberg and Segerberg 1906; *Esmeraldina* Resser and Howell 1938; *Palmettaspis* Fritz 1995; *Holmiella* Fritz 1972; *Fritzolenellus* Lieberman 1998; *Mummaspis* Fritz 1992; *Laudonia* Harrington 1956; *Lochmanolenellus* Lieberman 1998; *Fremontella* Harrington 1956; *Bristolia* Harrington 1956; *Nephrolenellus* Palmer and Repina 1993; *Bolbolenellus* Palmer and Repina 1993; and one new genus, *Baltobergstroemia.* Three new species are described: *Elliptocephala walcotti, Bristolia harringtoni* and *Nephrolenellus jasperensis.* A morphometric analysis of relationships among some species of the genus *Bristolia* is also included. Along with each of these phylogenetic analyses, emended generic diagnoses are provided for all of the aforementioned genera in order to aid in future generic assignments. In addition, a revised subfamilial and familial classification and diagnosis are presented for the Olenelloidea. Type specimens were designated for the following species: neotypes for *Olenellus thompsoni* (Hall) and *Mesonacis vermontana* (Hall); and lectotypes for *Olenellus clarki* (Resser), *O. nevadensis* (Walcott), *Elliptocephala logani* (Walcott), *Mummaspis truncatooculatus* (Fritz), *M. oblisooculatus* Fritz, *M. muralensis* (Fritz), *Laudonia amputata* Fritz and *Bristolia insolens* (Resser).

Although it would be redundant to consider the results of Lieberman (1998) in great detail, a brief summation of the conclusions of that paper is worthwhile. Several taxa traditionally assigned to the Olenelloidea, such as *Callavia* Matthew 1897, *Andalusiana* Sdzuy 1961, *Gabriellus* Fritz 1992 and *Cambropallas* Geyer 1993, were excluded from that superfamily by Lieberman (1998) because they lacked some of its diagnostic characters. Within the Olenelloidea, Lieberman (1998) recognized two major clades. One of these, the family Olenellidae, contains the genera *Olenellus, Mesonacis* and *Mesolenellus.* This clade is sister to a clade containing the rest of the taxa referable to the Olenelloidea. Within this second clade Lieberman (1998) recognized additional phylogenetic structure. For example, the genera *Wanneria* and *Elliptocephala* are successively distant outgroups to a large clade that includes the Holmiidae (treated as containing minimally the genera *Holmiella, Esmeraldina, Kjerulfia* and *Holmia*) and the remaining olenelloid genera. The remaining clade of olenelloids can be further subdivided into a set of three genera, *Laudonia, Mummaspis* and *Fritzolenellus,* that form successively distant outgroups to another clade that Lieberman (1998) referred to the family Biceratopsidae. The three genera *Laudonia, Mummaspis* and *Fritzolenellus* were assigned to the paraphyletic family "Laudoniidae." Within the Biceratopsidae Lieberman (1998) identified two subfamilies, the Bristoliinae, which contained the genera *Bristolia, Fremontella* and *Lochmanolenellus,* and the Biceratopsinae, which contained the genera *Nephrolenellus, Bolbolenellus, Olenelloides, Biceratops* and *Peachella* Walcott.

The present study was motivated by the need to revise relationships within the Olenelloidea, and place them within a rigorous framework. Past studies of the olenellids, such as Palmer and Repina (1993), have relied on circular and/or subjective criteria, placing them on quite dubious phylogenetic grounds. This has also had a negative impact on stratigraphic studies. For example, in some papers stratigraphic units were defined by the inferred phylogenetic position of the contained olenellid taxa, and this stratigraphic information was further used to determine evolutionary relationships. Moreover, what had originally been treated as the genus *Olenellus* (e.g., see Fritz 1992; Palmer and Repina 1993) actually represents a polyphyletic assemblage of taxa. Therefore, the eponymous *Olenellus* stratigraphic zone, an important division within the Early Cambrian, may be correlated on the basis of spurious criteria.

From an evolutionary perspective, the Olenelloidea persisted during an important episode in the history of life, the Cambrian Radiation. Recently our understanding of the timing of this radiation, and the environmental changes that may have been associated with it, have greatly improved thanks to the studies of Knoll (1991, 1992), Bowring et al. (1993), Grotzinger et al. (1995) and Knoll et al. (1995), all detailed in Knoll (1996). It is now possible to place evolutionary patterns during the Cambrian radiation into a detailed geologic context. This in turn makes it possible to make inferences about evolutionary processes. With this in mind, information about evolutionary patterns from the phylogenetic analyses presented herein are combined with stratigraphic information and the results from Lieberman (1998) to give an overall picture of patterns of evolution within the Olenelloidea. These patterns can then be used to adduce biogeographic patterns and also levels of speciation during the Early Cambrian. One pattern evident in this study, based on information from phylogeny and stratigraphy, is that much of the actual history of the diversification of the Cambrian Radiation may be missing, as Fortey and Owens (1990) suggested. The size of this gap is indeterminate. Although it is probably not too appreciable, it may be equivalent to the length of the Atdabanian stage. This pattern of limited gaps in the record is analogous to what has been found during other events of explosive radiation. For instance, Lieberman et al. (1991) and Lieberman (1993) recognized that much of the explosive adaptive radiation of the trilobite family Calmoniidae Delo 1935 was probably missing from the fossil record, with only the subsequent products of that radiation preserved.

This paper is organized into several parts, each with a systematic paleontology section, and presenting the results of a phylogenetic analysis. Each phylogenetic analysis uses either the heuristic search option or, when possible, the exhaustive search option of PAUP v. 3.1.1 (Swofford 1993) to uncover the most parsimonious tree(s), presented as a hypothesis of relationship, based on the character data analyzed. For each phylogenetic analysis several tests were undertaken to determine the resiliency of the hypothesis of phylogenetic relationship presented. When possible, the protocol of Hillis (1991) was used to assess the amount of phylogenetic signal in the data. The distribution of all tree lengths was determined using PAUP (Swofford 1993). Bootstrap analyses were also conducted to assess the relative support for each of the nodes in the most parsimonious tree(s). Whether or not all requirements for rigorous statistical application of bootstrap analysis are met, it can serve as a qualitative demonstration of the relative degree of support for specific cladogram topologies. Unless otherwise indicated, 100 bootstrap replications were employed in a heuristic, stepwise search that used five random replications per bootstrap replication, and groups were retained that were compatible with the 50% majority rule consensus tree. The confidence values for the nodes of the tree duplicated in the bootstrap analysis are presented. Finally, to further assess the support for various nodes of cladograms, the analysis described in Bremer (1994) was conducted. This method calculates consensus trees using all cladograms first one, then two, then three, etc., steps longer than the most parsimonious tree. The amount of branch support a node has is equal to the difference between the largest tree that node is still maintained in, minus the length of the most parsimonious tree. The total support index of Bremer (1994) was also calculated. All morphological terminology follows Palmer and Repina (1993) and Lieberman (1998).

• ONE •

Phylogenetic Analysis of the Olenellinae

The Olenellinae is a diverse clade distributed throughout Laurentia that includes species traditionally assigned to *Olenellus* (*Olenellus*) Hall 1862 and *O.* (*Paedeumias*) Walcott. This family represents the paradigm exponents of olenelloid morphology. Here a core group of 11 species is subjected to phylogenetic analysis, with special emphasis on species from the Parker Slate and Kinzers Shale of eastern Laurentia (four species from western Laurentia are also considered). Other species that clearly belong within the Olenellinae are listed below under the discussion for the genus *Olenellus.* These taxa are too poorly preserved and/or unavailable and therefore could not be incorporated into the phylogenetic analysis. However, they clearly belong in *Olenellus* based on the diagnosis of that genus given below.

A total of 12 taxa was subjected to phylogenetic analysis. These include all available and adequately preserved species of the genus *Olenellus,* and one outgroup taxon, *Mesonacis fremonti* (Walcott 1910). This is an appropriate outgroup to the genus *Olenellus* based on the higher level phylogenetic analysis presented in Lieberman (1998), as well as the species' near basal phylogenetic position within the Mesonacinae. Species of the genus *Mesolenellus* Palmer and Repina 1993 occupy a more basal position within the Mesonacinae but are less well known, and therefore less appropriate, outgroups. Phylogenetic patterns were determined by parsimony analysis of 13 holaspid exoskeletal characters (Table 1). The codings for the taxa analyzed are given in Table 2. All characters were treated as unordered (nonadditive). These data were subjected to an exhaustive search on PAUP v. 3.1.1 (Swofford 1993). Forty most parsimonious trees were recovered, of length 36 steps, consistency index = 0.72 and retention index = 0.71. A strict consensus of these trees is shown in Figure 1.

The distribution of all tree lengths (Hillis 1991) was determined using PAUP (Swofford 1993). This distribution was significantly left-skewed relative to the distribution of tree lengths produced by random data. The g_1 statistic, used to measure tree length skewness distributions, was –0.32. This value differs significantly ($p<0.05$) from those of distributions using random character data, and this indicates a strong phylogenetic signal in the data. The confidence values for the nodes of the consensus tree duplicated in the bootstrap analysis are given in Figure 1. Using the analysis presented in Bremer (1994), 1,968 trees of length less than or equal to 37 steps were recovered before the analysis was terminated because the consensus cladogram was a complete polytomy. Thus, the total support index (Bremer 1994) for the tree is very low.

All species considered in this analysis are known from the *Olenellus* zone, so there appears to be good correspondence between phylogenetic position and stratigraphic first occurrence. However, as mentioned above, circular criteria have been used to recognize the *Olenellus* zone in prior studies of olenellid trilobites (e.g., Palmer and Halley 1979; Palmer and Repina 1993), so the exact stratigraphic position of these samples must await the application of more rigorous methods of correlation.

Systematic Paleontology

SUPERFAMILY Olenelloidea Walcott 1890
FAMILY Olenellidae Walcott 1890
SUBFAMILY Olenellinae Walcott 1890

Phylogenetic analysis of the Olenelloidea in Lieberman (1998) revealed the relationships of generic clades within the superfamily, and indicated that there was an easily distinguished and strongly supported clade within that superfamily composed of the genera *Olenellus* (*Olenellus*), *Olenellus* (*Paedeumias*), *Mesolenellus* and *Mesonacis*. Lieberman (1998) assigned these taxa to the family Olenellidae, partly reiterating the classification of Palmer and Repina (1993); however, Palmer and Repina (1993) also assigned all olenelloid genera to the Olenellidae, except those they assigned to Holmiidae Hupé 1953. Based on phylogenetic topology within the Olenelloidea determined in Lieberman (1998), the Holmiidae are more closely related to some of the subfamilies Palmer and Repina (1993) assigned to the Olenellidae than some of the other subfamilies are to one another, thereby making the Olenellidae polyphyletic. According to the tenets of cladistic analysis, polyphyletic taxa are not valid, and therefore Palmer and Repina's (1993) classification of the Olenelloidea cannot be accepted. In addition, most of Palmer and Repina's (1993) subfamilies were established on the basis of inadequate character evidence. Here, to rectify this, the Olenellidae is constrained to be a monophyletic family. The other families and subfamilies within the Olenelloidea are discussed in greater detail below.

Lieberman (1998) divided the Olenellina into two superfamilies, a monophyletic Olenelloidea and a paraphyletic Fallotaspididoidea (the latter is the subject of a future study). Therefore, the classification of the Olenelloidea promulgated in Lieberman (1998) and herein is not exactly comparable to the classifications of the olenellids presented in Bergström (1973) and Ahlberg et al. (1986). However, there are some key differences that emerge between their classification of the Olenellidae and the one presented here (their classifications are fairly similar in terms of the taxa they allocate to the Olenellidae and will be treated together). They each assigned a large number of genera to the Olenellidae, including *Olenellus, Biceratops* Pack and Gayle 1971, *Bristolia*, *Fremontella*, *Laudonia* and *Peachella*. Based on phylogenetic topology within the Olenelloidea from Lieberman (1998), some of these genera are distantly related, and the family Holmiidae is nested within them. Therefore, their respective classifications cannot be accepted without either erecting para- or polyphyletic families and/or subfamilies, or placing all olenelloid genera within the Olenellidae.

To establish a monophyletic Olenellidae, it is necessary to establish a series of shared derived characters that define the Olenellidae, and allow the Olenellidae to be discriminated from all other families. Here, the Olenellidae are defined by their shared possession of the following combination of characters, some derived and some primitive for the Olenelloidea: 1. and 2. anterior cephalic border developed as flattened ledge, prominently separated from extraocular area by furrow; 3. anterior cephalic border between lateral margins of frontal lobe and genal spine angle short, length exsagittally (exsag.) less than or equal to one-half length sagittally (sag.) of L0; 4. anterior part of glabella not prominently separated from extraocular area or preglabellar area by furrow (except in *Mesolenellus hyperborea* [Poulsen 1974]); 5. prominent parafrontal band not visible in dorsal view; 6. anterolateral margins of frontal lobe of glabella at each side of midline deflected posteriorly at roughly 40 degree angle relative to transverse line; 7. length (sag.) of L4 equal to 1.5

times length (sag.) of L0 and L1; 8. L4 does not expand prominently dorsally; 9. ocular lobes contact posterolateral margins of frontal lobe; 10. pre-ocular furrow on L4 transverse or not visible; 11. abrupt dorsal notch-like truncation of ocular lobes at margin of L4 absent; 12. ocular lobes of constant dorso-ventral elevation between axial furrows and midpoint of ocular lobes; 13. ocular lobe smoothly merges into extraocular area; 14. posterolateral margins of L4 divergent anteriorly or subparallel; 15. anterior part of ocular lobe between visual surfaces and L4 narrow transversely (tr.); 16. line from posterior tip of ocular lobe to junction of posterior margin of lobe with glabella forms 0 to 20 degree angle with sagittal line; 17. interocular area developed as flattened shelf; 18. width (tr.) of interocular area approximately equal to width of ocular lobe; 19. anterodistal margins of L3 formed by ocular lobes; 20. distal margins of L3 convex outward (may be straight in *Mesolenellus svalbardensis* [Kielan 1960]); 21. S3 jaggedly convex or carat shaped; 22. L1 to L3 gently convex (tr.); 23. L2 and L3 merge distally (except in *M. hyperborea*); 24. S2 straight; 25. lines parallel to distal margins of L2 diverge anteriorly (except in *Mesolenellus*); 26. and 27. distal sector of S0 straight, with medial end posterior of lateral end; 28. intergenal ridge visible as trace; 29. intergenal angle with distinct dorsal swelling, node or small pointed spine; 30. thorax broken up into pro- and opisthothorax; 31. third thoracic segment macropleural; 32. prothoracic axial rings without lateral furrows, forming uniform rectangular or trapezoidal blocks; 33. single nodes on median part of thoracic axial rings; 34. thoracic pleural furrows extend onto spines; 35. boundary between thoracic pleural furrows and anterior pleural band sharp; 36. tips of thoracic pleural segments distally in roughly same dorso-ventral plane as medially; 37. prominent spine present on 15th thoracic axial ring (or at pro- opisthothoracic boundary). None of these characters are uniquely diagnostic of the Olenellidae; however, character 23 is confined to the Olenellidae, except for a few occurrences in members of the Biceratopsinae.

Within the Olenellidae, Lieberman (1998) recognized additional phylogenetic structure. In particular, the type species of what had been formerly treated as *O.* (*Olenellus*) and *O.* (*Paedeumias*) formed a clade, as did the type species of *Mesolenellus* and *Mesonacis*. Each of these clades contains a large number of species, and the node containing *Mesolenellus* and *Mesonacis* also is strongly supported in the phylogeny of Lieberman (1998). In Lieberman (1998) *Mesolenellus* and *Mesonacis* were treated as distinct genera, rather then as subgenera of the genus *Olenellus* as Palmer and Repina (1993) had suggested, because there appeared to be a clear distinction between these taxa and species of *O.* (*Olenellus*) and *O.* (*Paedeumias*). The genera *Mesolenellus* and *Mesonacis* are discussed in the next section of this paper, where they are subjected to phylogenetic analysis. Because the phylogenetic structure within the Olenellidae is broken up into two clades, each of which contains a large number of species, it is appropriate to further divide the family into subfamilies to increase the information content of the classification. This paper presents the results of phylogenetic studies of several genera within the Olenelloidea, and this part of the paper deals explicitly with the relationships of species formerly assigned to *O.* (*Olenellus*) and *O.* (*Paedeumias*).

Palmer and Repina (1993), in their classification of the Olenelloidea, suggested that the Olenellinae included *Olenellus* as well as *Fremontella* and *Mummaspis*. These genera have to be excluded from the Olenellinae because they are distantly related to *Olenellus* as well as to other members of the Olenellidae, such as *Mesolenellus* and *Mesonacis*. Placing *Fremontella* and/or *Mummaspis* within the Olenellinae would necessitate either placing every genus of the Olenelloidea into the Olenellinae, or constructing a para- or polyphyletic subfamily as Palmer and Repina (1993) did. Neither of these approaches are advocated by

Table 1.

Description of characters and character states used in phylogenetic analysis of *Olenellus*; (0) represents the primitive state and (1) and (2) are derived states.

	Primitive state	Derived states
1. Anterior cephalic border	(0) elevates anteriorly from anterior border furrow at approximately 45° angle relative to a dorsal, flat plane, then dorsally flattens, such that border is broadly convex	(1) elevates anteriorly from anterior border furrow at approximately 70° to 90° angle relative to dorsal plane, then flattens, such that border is developed as a raised ridge
2. Plectrum	(0) absent	(1) present
3. Length (sag.) of preglabellar field	(0) preglabellar field absent	(1) approximately 15% to 25% length (sag.) L4 (2) approximately 35% to 50% length (sag.) L4[a]
4. Lateral margins of L4	(0) abaxial to lateral margins of L0	(1) directly anterior of lateral margins of L0 (2) adaxial to lateral margins of L0
5. S2	(0) conjoined medially	(1) not conjoined medially[b]
6. Lateral margins of L2	(0) diverging anteriorly, such that they bulge laterally relative to L1	(1) subparallel, such that they do not bulge laterally relative to L1[c]
7. S1	(0) conjoined medially	(1) not conjoined medially[d]
8. Ocular lobe	(0) with prominent furrow across entire margin	(1) with furrow only present at anterior margin of ocular lobe

Continued

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[a] The polarity of this character was determined using the outgroup criterion. However, polarity might be reversed if ontogenetic criteria are used (Westrop, pers. comm. 1998). Specifically, some olenelloids during the course of their ontogeny show the progressive shortening and loss of the preglabellar field.

[b] There is no evidence that this character is taphonomic because its states are independent of preservational regime.

[c] As with character 3, the polarity of this character was determined using outgroup comparison. Ontogenetic criteria might potentially reverse the polarity.

[d] There is no evidence that this character is taphonomic because its states are independent of preservational regime.

Table 1 continued.

	Primitive state	Derived states
9. Posterior margin of ocular lobe extends back to	(0) medial part of distal margin of L1	(1) medial part of distal margin of L0 (2) distal tips of S0
10. Extraocular area	(0) gently convex	(1) prominently flattened
11. Anterior margins of T3, excluding spine	(0) deflected anteriorly relative to transverse line at 5° to 10° angle	(1) deflected anteriorly relative to transverse line at 0° to 5° angle
12. T3 extends back	(0) length of entire prothorax	(1) 6 to 8 thoracic segments
13. 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

the present analysis, which seeks to construct an informative (sensu Eldredge and Cracraft 1980) classification and takes a cladistic approach to supra-generic classification, where possible, with the caveat that to preserve taxonomic stability establishing a large number of monotypic families or subfamilies should be avoided. Herein, the Olenellinae is restricted to the genus *Olenellus.* The clade containing *Mesonacis* and *Mesolenellus* therefore must also be elevated to subfamilial status and is discussed in greater detail in the next section, which deals explicitly with those genera.

The Olenellinae is characterized by the following shared characters when present in combination: 1. posterolateral margins of L4 divergent anteriorly; 2. transverse profile of ocular lobes flattened dorsally; 3. posterior tips of ocular lobes developed opposite medial part of distal margin of L0 or distal tip of S0; 4. S3 not conjoined medially; 5. line between ends of S2 directed inward and posteriorly at 45 degree angle relative to transverse line; 6. S0 not conjoined medially; 7. lateral lobes on L0 absent; 8. glabellar furrows moderately to strongly incised; 9. genal ridge prominently developed; 10. extraocular region opposite L1 broad, width (tr.) greater than or equal to 75% of width of glabella at L1; 11. genal spine near where it hits cephalic border directed posterolaterally at roughly 10 to 20 degree angle relative to sagittal line; 12. length (exsag.) of genal spine roughly equal to length (sag.) of first four to six thoracic segments; 13. genal spine angle developed opposite medial part of distal margin of L0; 14. intergenal angle developed adjacent to or directly behind genal spine angle; 15. intergenal angle with small, pointed spine; 16. intergenal angle deflected at roughly 10 degree angle relative to transverse line; 17. medial part of cephalic posterior border between intergenal angle and L0 weakly flexed anteriorly; 18. anterior margin of

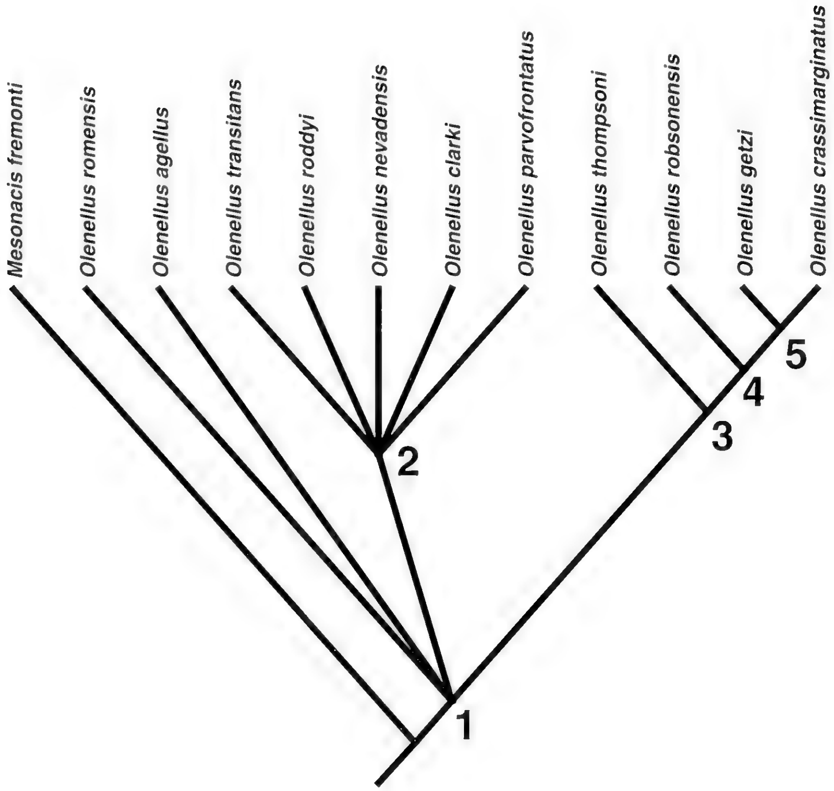

Figure 1.
A strict consensus of 40 most parsimonious trees of length 36 steps produced from analysis of character data in Table 2 with PAUP v. 3.1.1 (Swofford 1993). The cladogram is constructed using an exhaustive search. The retention index is 0.71, and the consistency index is 0.72. The value of the g_1 statistic is –0.32. The following nodes in the text were supported by the following bootstrap confidence values (see text for bootstrapping procedure used): Node *2* = 0.72; Node *3* = 0.53; Node *4* = 0.44; Node *5* = 0.63. Character states are placed at nodes, using MacClade v. 3.04 (Maddison and Maddison 1992), with the characters given in Table 1. The apomorphic state is given in parentheses. Square parentheses indicate equivocal character states that are ambiguous because of missing data, polymorphisms or multiple equally parsimonious resolutions. Equivocal characters are placed only at their basal phylogenetic position, and only unambiguous reversals are shown. Node *1*, 5[0, 1], 7[0, 1], 9[0, 1, 2]; Node *2*, 1(1), 2(1), 3(1), 4[1, 2], 5(1), 11[0, 1], 13(1); Node *3*, 5(1), 7(1), 9(1), 11(1), 12(1); Node *4*, 4(1); Node *5*, 6(1), 11[0, 1].

third thoracic pleural segment, before flexing strongly posteriorly, parallel to transverse line or weakly deflected posteriorly; 19. posterior margin of thoracic pleural furrow on third thoracic segment directed evenly posterolaterally; 20. thoracic pleural spines on segments T5 to T8 developed as broad sweeping projections extending roughly four segments back; 21. length (exsag.) of thoracic pleural furrows (excluding those of T3) at medial part of segment equal to roughly 1.3 times length (exsag.) of posterior band of pleural segment; 22. width of thoracic pleural spines T5 to T8 at spine midlength more than two-thirds length (exsag.) of medial part of inner pleural region; 23. length (sag.) of spine on 15th thoracic segment roughly equal to length of whole prothorax; 24. base of spine on 15th thoracic segment nearly as wide (tr.) as axis of segment; 25. segments of opisthothorax with reduced pleurae; 26. pygidium length (sag.) 1.5 times width (tr.); 27. posterior margin of pygidium weakly convex. Of these characters, only character 25 is unique to the Olenellidae.

Since the subfamily Olenellinae contains only a single genus, *Olenellus,* the generic and subfamilial diagnoses are identical. A synonymy and discussion for the outgroup used in phylogenetic analysis of the Olenellinae, *Mesonacis fremonti,* is given below under the heading of the genus *Mesonacis.*

Included Taxa

GENUS *OLENELLUS* HALL 1862

Type species: *Olenus thompsoni* Hall 1859.
Assigned taxa: *Olenellus agellus* Resser and Howell 1938; *O. getzi* Dunbar 1925; *O. parvofrontatus* Fritz 1991; *O. roddyi* Resser and Howell 1938; *O. romensis* Resser and Howell 1938; *O. thompsoni crassimarginatus* Walcott 1910; *O. gilberti* Meek 1874; *O.* sp. 5 Fritz 1972; *Paedeumias transitans* Walcott 1910; *P. clarki* Resser 1928; *P. granulatus* Palmer 1964; *P. puertoblancoensis* Lochman in Cooper et al. 1952; *P. robsonensis* Burling 1916; *P. groenlandicus* Poulsen 1958; *P. turmalis* Cowie 1968; *P.* sp. undet. Rasetti 1948; *Callavia*? *nevadensis* Walcott 1910.
Diagnosis: Given above for Olenellinae.
Discussion: Some of the taxa assigned to the genus and listed above were poorly preserved and therefore were not subjected to phylogenetic analysis. However, based on their possession of the diagnostic characters of the Olenellinae and *Olenellus,* these taxa were tentatively assigned to the genus *Olenellus,* although not all of the diagnostic characters of the genus were always preserved. In the case of *O. puertoblancoensis,* this species is based on somewhat problematic material so its precise status as one or more species could not be considered by this analysis.

Several other species traditionally assigned to the genus *Olenellus* belong instead to other genera within the Olenelloidea. These are discussed at length under the several generic clades listed below, including *Fremontella, Bristolia, Mummaspis, Mesonacis, Bolbolenellus* and *Elliptocephala,* along with reasons why these taxa must be excluded from *Olenellus.*

Phylogenetic topology within the Olenellinae (Figure 1) suggests that the distinction between *Olenellus* (*Olenellus*) and *O.* (*Paedeumias*) may not be meaningful. Although phylogenetic analysis predicts that there is a clade of species, some of which have traditionally been assigned to the genus *Paedeumias* (e.g., *O. transitans, O. clarki, O. nevadensis, O. roddyi* and *O. parvofrontatus*), this clade is nested within a group of other species traditionally assigned to the genus *Olenellus.* Retaining the genus or subgenus name *Paedeumias* would necessitate either making *Olenellus* paraphyletic, establishing a new paraphyletic genus, or creating two new monotypic genera. Instead, it makes more sense to drop *Paedeumias,* a name devoid of significance as a phylogenetic unit, and assign all taxa within the Olenellinae to the genus *Olenellus.*

Rasetti (1966, 1967) assigned several specimens from the Lower Cambrian of New York State to the genera *Olenellus* and *Paedeumias.* Because of the small size of these specimens and their fragmentary state of preservation, their precise affinities could not be determined. However, they more closely resemble specimens of *Elliptocephala,* especially in the condition of the glabellar furrows, and it appears likely they should be referred to that genus instead of *Olenellus.*

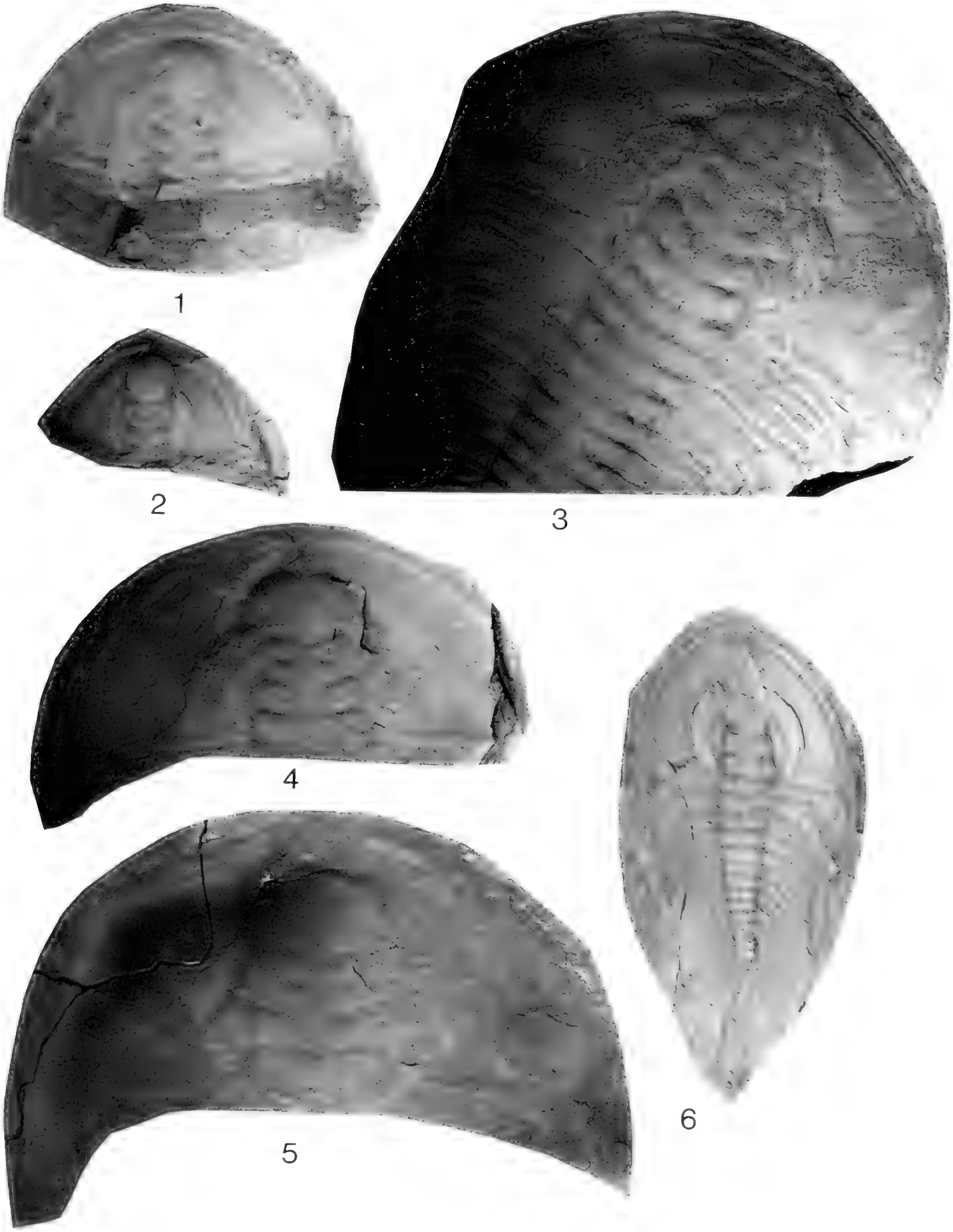

Figure 2.
Olenellus spp. **1, 2.** *Olenellus romensis* Resser and Howell, Rome Fm., Mason Creek, Salem, Virginia. **1.** MCZ 2516, ×1.5. **2.** MCZ 2518, ×1.1. **3–5.** *Olenellus agellus* Resser and Howell, Parker Slate, Parker Quarry, Georgia, Vermont. **3.** MCZ 1793, ×0.8. **4.** AMNH 243, ×1.1. **5.** YPM 72905, ×1.1. **6.** *Olenellus roddyi* Resser and Howell, Kinzers Shale, York, Pennsylvania, YPM 72904, ×1.8.

OLENELLUS THOMPSONI (HALL 1859)

Olenellus thompsoni (Hall); Resser and Howell 1938:219, pl. 3, figs. 17–19 (see for more complete synonymy); Shaw 1955:792; Harrington 1956:59, text fig. 1a; Harrington et al. 1959:O192, fig. 132; Whittington 1989:114, figs. 3–5, 7 (only).
Olenellus (*Olenellus*) *thompsoni* (Hall); Palmer and Repina 1993:22, fig. 3.1; Palmer and Repina 1997:404, fig. 255.1; Lieberman 1998:68, fig. 3.1.
Olenellus agellus; Resser and Howell 1938:223, pl. 9, figs. 12 and 13 (only).

Types: This species is in need of a neotype to stabilize its taxonomy. I designate YPM 8189, Lieberman (1998, fig. 3.1), a counterpart of an external mold of a nearly complete individual, the **neotype** of the species because of its good state of preservation and because records indicate it hails from the original type locality, Georgia Township, Vermont, probably Parker's Quarry.
Discussion: This species is treated in detail in Lieberman (1998).
Material examined: AMNH 225, 231; MCZ 2451, 2460, 2467, 2469 and possibly 2482; YPM 8189. Because of its state of preservation, it could not be determined whether MCZ 2482 is a specimen of *O. thompsoni* or *O. agellus.*
Occurrence: Vermont: the Parker Slate, Georgia, treated as in the middle upper *Olenellus* zone, following Palmer and Repina (1993).

OLENELLUS TRANSITANS (WALCOTT 1910)

Paedeumias transitans; Walcott 1910:305, pl. 34, fig. 1; Resser and Howell 1938:226, pl. 8, fig. 13; Harrington et al. 1959:O192, fig. 135.5;
Olenellus (*Paedeumias*) *transitans*; Walcott. Palmer and Repina 1993:22, fig. 3.3; Palmer and Repina 1997:404, fig. 255.3; Lieberman 1998:70, figs. 3.2, 3.3.
Paedeumias perkinsi; Resser and Howell 1938:226, pl. 8, fig. 1.
Olenellus agellus; Resser and Howell 1938:223, pl. 9, fig. 11, y 12, 13.
Olenellus brachycephalus (Emmons); Shaw 1955:791, pl. 75, figs. 1–3.
Olenellus thompsoni (Hall); Whitfield 1884:151, pl. 15, figs. 1–4.

Types: Lectotype, USNM 56808b, see Resser and Howell (1938).
Discussion: This species is treated in detail in Lieberman (1998).
Material examined: AMNH 223, 227, 243; MCZ 2427–2429, 2431, 2433, 2435, 2437, 2438, 2444, 2447, 2449–2451, 2453, 2455, 2461, 2465, 2467, 2470, 2474, 2476, 2478, 2480, 2522, 7368, 108661; and possibly YPM 72900. Because of its state of preservation, it could not be determined whether YPM 72900 is a specimen of *O. transitans* or *O. agellus.*
Occurrence: Vermont: the Parker Slate, Georgia, treated as in the middle upper *Olenellus* zone, following Palmer and Repina (1993).

OLENELLUS ROMENSIS RESSER AND HOWELL 1938

See Figure 2.1, 2.2.

Olenellus romensis; Resser and Howell 1938:221, pl. 7, figs. 4–6, pl. 12, figs. 2, 3; Resser 1938:52, pl. 5, fig. 12.
Olenellus buttsi; Resser 1938:52, pl. 5, figs. 9, 19.

Types: Resser and Howell (1938) treated USNM 92718–92721 as the cotypes of this species,

Table 2.
Character state distributions for *Olenellus* and outgroup used in phylogenetic parsimony analysis. Characters and alternative states are as listed in Table 1. Missing data are indicated by ?. Character states listed as X and Y are polymorphic, where X=(0&1) and Y=(1&2).

										1	1	1	1
	1	2	3	4	5	6	7	8	9	0	1	2	3
Mesonacis fremonti	0	0	0	0	0	0	0	0	0	0	0	0	0
Olenellus romensis	1	0	0	0	X	0	X	0	2	0	0	0	1
Olenellus agellus	0	1	1	0	1	0	X	0	1	0	1	0	0
Olenellus transitans	1	1	Y	2	1	0	0	1	1	1	0	0	1
Olenellus roddyi	1	1	1	Y	1	0	0	0	1	0	0	0	1
Olenellus clarki	1	1	1	Y	X	0	X	0	2	1	1	0	1
Olenellus nevadensis	1	1	Y	2	X	0	0	0	Y	1	?	?	?
Olenellus parvofrontatus	1	1	1	2	1	0	1	1	1	0	1	?	1
Olenellus thompsoni	0	0	0	0	1	0	1	0	1	0	1	1	0
Olenellus robsonensis	0	?	?	1	1	0	1	?	1	0	1	?	0
Olenellus getzi	0	0	0	1	1	1	1	0	2	0	0	1	0
Olenellus crassimarginatus	0	0	0	2	1	1	1	0	1	0	?	?	?

but they identify the specimen in their pl. 12, fig. 2 as the holotype of the species. This holotype designation is valid.

Discussion: Fritz (1991, pl. 17, figs. 11–14) figured a set of partial cephala from the Illtyd Formation, Yukon, Canada that he assigned questionably to *O. romensis*. These specimens clearly bear the characters diagnostic of *Olenellus*, and do match *O. romensis* in the condition of several characters. In particular, they have a similar anterior cephalic border, they both lack a plectrum, and they have the lateral margins of L4 distal of the lateral margins of L4. However, these cephala appear to differ from *O. romensis* in the condition of at least one character: the posterior margins of the ocular lobes extend back to the distal tips of S0 in *O. romensis* whereas in Fritz's (1991) material they extend back to the medial part of the distal margin of L0. On the basis of this character difference they are tentatively treated as distinct from, though closely related to, *O. romensis* and are retained within the genus *Olenellus*.

Material examined: MCZ 2516 (lot with 5 specimens), 2517, 2518 (lot with 11 specimens), 2520.

Occurrence: In what Resser and Howell (1938) and Resser (1938) referred to as the Rome Formation, treated as late Early Cambrian, middle upper *Olenellus* zone, based on Rankin et al. (1989) and Barnaby and Read (1990) from the following localities: Virginia: Mason Creek, Salem; near Webster, NE of Roanoke; 2 mi SW of Blue Ridge Springs, 2 mi S of Max Meadows; Mason Creek, 1 mi E of Salem; 0.5 mi SE of Indian Rock; 1 mi E of Cleveland. Alabama: 1.5 mi N of Montevallo; 1.5 mi W of Montevallo.

OLENELLUS AGELLUS RESSER AND HOWELL 1938
Figure 2.3 to 2.5

Olenellus agellus; Resser and Howell 1938:223, pl. 9, figs. 11–13.

Types: Holotype, USNM 90806, see Resser and Howell (1938). Oddly, Resser and Howell (1938) state that AMNH 244 is the paratype of this species. This specimen is known to be the original type of *O. thompsoni,* which is missing, so there must be some typographical error in Resser and Howell (1938), particularly as they state on the previous page in the same publication that AMNH 244 is the missing holotype of *O. thompsoni.* Perhaps they meant AMNH 243, figured herein, or possibly AMNH 244 referred to several specimens, all of which are now lost.
Discussion: Resser and Howell (1938) placed several specimens in synonymy with this species, but these could not be verified. This species is similar to *O. thompsoni,* differing chiefly in the condition of a preglabellar area between L4 and the anterior cephalic border furrow. The preglabellar area is present in *O. agellus* and absent in *O. thompsoni.* At this time these taxa are treated as distinct species, as several specimens for each species had distinct and non-overlapping character states. Resser and Howell (1938) also asserted that these two taxa may have hailed from rocks with different lithologies.
Material examined: AMNH 243; MCZ 1793, 2441, 2433, 2443, 2471, 3684, 7369, and possibly 2482; YPM 72905 and possibly 72900. Because of their state of preservation, it could not be determined whether YPM 72900 is a specimen of *O. transitans* or *O. agellus,* or whether MCZ 2482 is a specimen of *O. thompsoni* or *O. agellus.*
Occurrence: Vermont: Parker Quarry, Parker Slate, Georgia, middle upper *Olenellus* zone, based on Palmer and Repina (1993).

OLENELLUS PARVOFRONTATUS FRITZ 1991

Olenellus parvofrontatus; Fritz 1991:13, pl. 11, figs. 1–11, pl. 12, figs. 1, 2.

Types: Holotype, GSC 91842, see Fritz (1991).
Occurrence: Canada: Yukon territory, Unit 6, upper Illtyd Formation, upper Lower Cambrian, *Olenellus* zone, Wernecke Mountains (see Fritz 1991).

OLENELLUS RODDYI RESSER AND HOWELL 1938
Figures 2.6, 3.1

Olenellus roddyi; Resser and Howell 1938:221, pl. 6, figs. 6, 7.
Olenellus similaris; Resser and Howell 1938:221, pl. 4, figs. 11–14.
Olenellus jonasae; Resser and Howell 1938:222, pl. 8, figs. 4–6.
Olenellus nodosus; Resser and Howell 1938:224, pl. 6, figs. 1–3.
Olenellus nitidus; Resser and Howell 1938:222, pl. 8, figs. 7–9.
Paedeumias glabrum; Resser and Howell 1938:226, pl. 8, figs. 2, 3.
Paedeumias yorkense; Resser and Howell 1938:227, pl. 10, figs. 1, 2.
Paedeumias eboracense; Resser and Howell 1938:227, pl. 8, figs. 14, 15.
Paedeumias transitans; Walcott 1910:305, pl. 32, figs. 10, 12, 13, pl. 34, figs. 2–7.
Olenellus thompsoni (Hall); Whittington 1989:114, figs. 1, 2, 6, 8–10, 12, 13, 15, 17, 19, 27, 29, 31, 34.

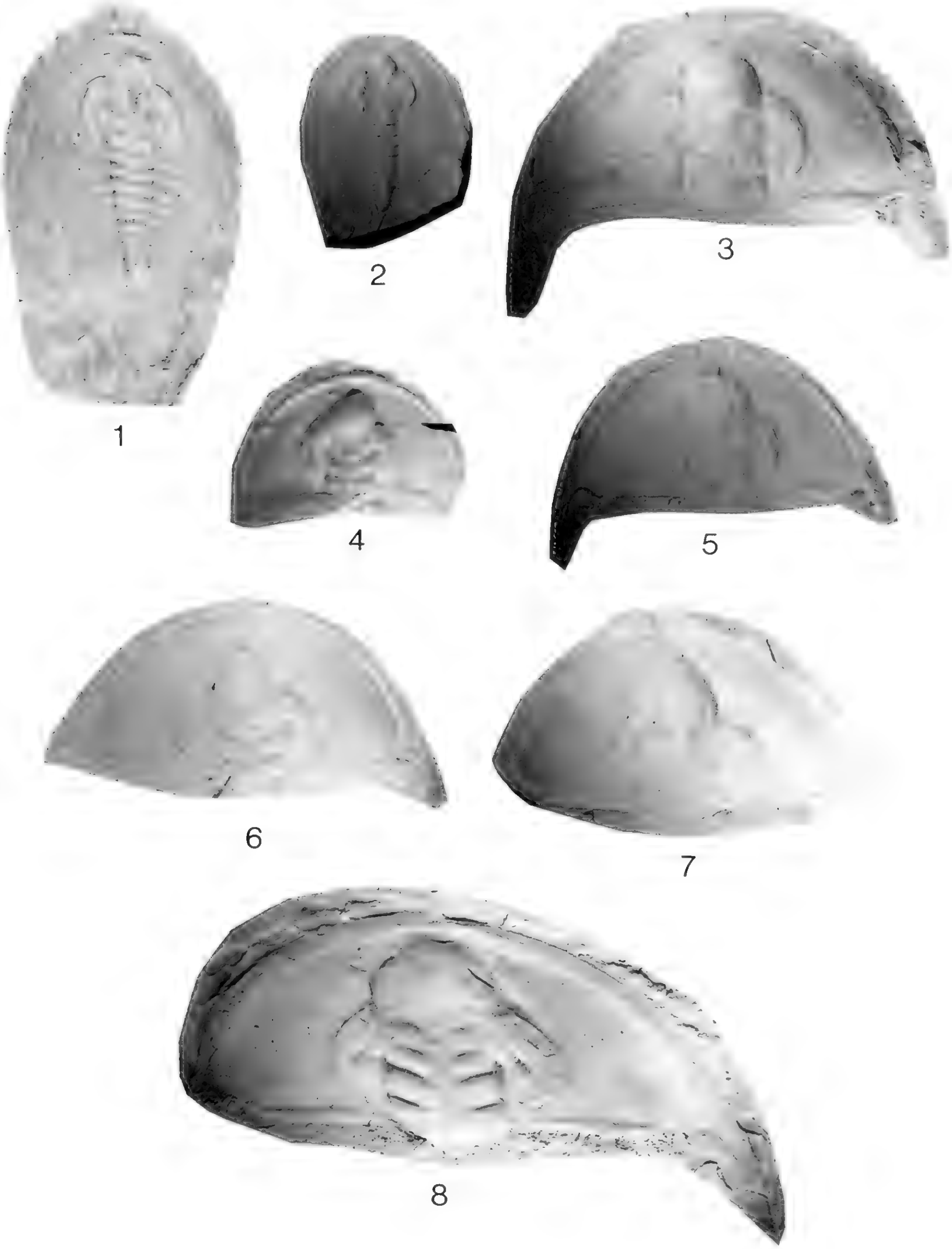

Figure 3.
Olenellus spp. **1.** *Olenellus roddyi* Resser and Howell, Kinzers Shale, York, Pennsylvania, YPM 72902, ×1.4. **2–5.** *Olenellus clarki* (Resser), Latham Shale, San Bernardino Co., California. **2.** at upper end of Summit Wash on opposite side of ridge, at elevation of 1551 m, 930 m SW of summit spring, 120 m W and 150 m N of SE corner sec 17, W side from old Providence Mine, Providence Mtns., SE 1/4 sec 17, T 11 N, R 14 E, UCR 7002/4, ×1.0. **3.** E slope of hill 1440 in S end of Marble Mtns., 834 ft E and 1999 ft N of the SW corner sec 12, T 5 N, R 14 E, UCR 7271/2, ×0.9. **4, 5.** At the end of the dirt road on the opposite side of the hill from the quarry about 1.25 mi N 28 E of Cadiz station. Locality is in the same horizon as Hazzard and Crickmay's (1933) M-5. Just above a prominently crossbedded quartzite and at the end of the dirt road, S end of Marble Mtns. **4.** UCR 10/1135, ×1.1. **5.** UCR 10/1144, ×1.1. **6, 7.** *Olenellus nevadensis* (Walcott). **6.** UCR 7271, locality is the same as 3, ×0.9. **7.** UCR 10/2005, locality is the same as 4, 5, ×1.0. **8.** *Olenellus getzi* Resser and Howell, Kinzers Fm., road metal quarry and walls of demolished tenement house on Noah L. Getz Farm, on Harrisburg Pike, about 1 mi N of Rohrerstown, and 2.5 mi W of Lancaster, Lancaster Co., Pennsylvania, YPM 94088, ×1.1.

?*Paedeumias yorkense* Resser and Howell 1938:227, pl. 6, figs. 4, 5, pl. 9, figs. 5–7.
?*Paedeumias transitans* Walcott 1910:305, pl. 32, figs. 1–9, 11, pl. 33, figs. 2–5.

Types: Holotype, USNM 90803, see Resser and Howell (1938).
Diagnosis: Plectrum present; length (sag.) of preglabellar field approximately 15% to 25% length (sag.) of L4; lateral margins of L4 directly anterior of L0 or medial of L0; S2 not conjoined medially; lateral margins of L2 bulging laterally relative to L1; S1 conjoined medially; ocular lobe with prominent furrow across entire margin; posterior margin of ocular lobe extends back to medial part of distal margin of L0; extraocular area gently convex; anterior margins of T3 deflected anteriorly relative to transverse line at 5 to 10 degree angle; T3 extends back length of entire thorax; ratio of width (tr.) T7, at articulating tips, relative to width of T3 at same position, 0.70 to 0.75.
Discussion: A new diagnosis is provided because historically there has been some confusion surrounding this species and other olenelloids from the Kinzers Shale. On the basis of this analysis, there are definitive records for three species of olenelloids in the Kinzers Shale: *Wanneria walcottana* (Wanner 1901), *Olenellus getzi* and *O. roddyi*. All other previously defined species are either synonyms or too poorly preserved to ascertain their taxonomic status. A large number of the olenelloid species that Resser and Howell (1938) described, including *O. roddyi, O. similaris, O. nodosus, O. nitidus, O. jonasae, Paedeumias glabrum, P. yorkense* and *P. eboracense,* appear to be identical, differing in no morphological characters, except perhaps those relating to structural deformation of the rocks where they occur, and are treated herein as comprising a single species. As all were established in the same publication, and *O. roddyi* was arguably originally defined based on the most complete material, its species name is preserved. Some specimens assigned to *P. yorkense* by Resser and Howell (1938) and *P. transitans* by Walcott (1910) bear strong similarity to material typical of *O. roddyi* and *O. getzi,* but are known only from larval stages or thoracic material. This material could be conspecific with either *O. getzi* or *O. roddyi,* as these taxa do not differ meaningfully in the condition of their thoraxes, and the extent of ontogenetic variation at this time is not known. Therefore, these specimens are only questionably assigned to *O. roddyi.*

Whittington (1989) assigned several beautifully preserved, complete individuals from the Kinzers Shale to *O. thompsoni.* However, this material differs from that typical of *O. thompsoni* in the condition of several characters, including: the anterior cephalic border rises from the extraocular area at a roughly 70 to 90 degree angle relative to a dorso-ventral plane and is then flattened such that it is developed as a raised ridge, rather than rising at a roughly 45 degree angle and then being broadly convex; a plectrum and relatively long (sag.) preglabellar field are present; the lateral margins of L4 are directly anterior of L0 or medial of L0, rather than being distal of L0; S2 is not conjoined medially; S1 is conjoined medially; the anterior margins of T3 are deflected anteriorly at a roughly 5 to 10 degree angle relative to a transverse line, rather than roughly paralleling a transverse line; T3 extends back the length of the entire thorax, rather than 6 to 8 thoracic segments; and the ratio of the width (tr.) of T7 (excluding the articulating tips) to T3 is 0.70 to 0.75 rather than 0.50 to 0.64. In the condition of these and other characters it is identical to *O. roddyi,* and therefore his material is henceforth assigned to that species.

Olenellus roddyi from the Kinzers Shale of Pennsylvania is similar to *O. transitans* from the Parker Slate of Vermont. However, they differ in the condition of a few qualitative characters. In particular, in *O. roddyi* the lateral margins of L4 are either directly anterior of L0 or medial of L0, whereas in *O. transitans* they are only medial of L0; in *O. roddyi* the ocular lobe has a prominent furrow circumscribing its entire margin, whereas in *O. transitans* the

1

Figure 4.
1. *Olenellus robsonensis* (Burling), ?Upper Mahto Fm., drift block on the slope of the Mural glacier below Mumm Peak, near Mount Robson, British Columbia, Canada, GSC 5272, holotype, ×1.1.

furrow is not visible at the anterior margin of the ocular lobe; and in *O. roddyi* the extraocular area is gently convex, whereas in *O. transitans* it is prominently flattened.

In addition to these qualitative characters, there exist quantitative character differences between these taxa that allow them to be discriminated at a high level of statistical significance. One such quantitative character difference is the ratio of the length (sag.) of the preglabellar area relative to the length (sag.) of L4. The following ratios for these variables were calculated for all adequately preserved and available specimens of *O. transitans* (0.225, 0.375, 0.303, 0.304, 0.543, 0.391) and *O. roddyi* (0.144, 0.278, 0.179, 0.180, 0.207, 0.184, 0.141, 0.245, 0.209, 0.095, 0.082, 0.098, 0.176, 0.200, 0.205). The mean value of this ratio in *O. transitans* is 0.357±0.109, whereas the mean value of this ratio in *O. roddyi* is 0.18±0.06, and these values differ significantly ($p<0.01$ by the two sample t-test, Minitab 1995 v. 10Xtra [1995]). The median values of this ratio in *O. transitans* (0.34) and *O. roddyi* (0.18) differ ($p<0.001$ by Mann Whitney u-test, Minitab 1995 v. 10Xtra [1995]). Thus, on the basis of these character differences, these two species are treated as distinct, although they are assumed to be very closely related.

Material examined: AMNH 24214 (3 specimens), 24215 (2 specimens), 24256, 24263 (4

specimens), 24297 (3 specimens), 24300, 24871, 24872, 41556 (4 specimens); MCZ 2491, 2496, 2497, 2502, 2503, 2506, 2508, 2513, 2545, 5574 (3 specimens); YPM 8199, 9663, 35859, 35860, 35868, 35893, 35896, 72902–72904, 94037, 94167.
Occurrence: Pennsylvania: the Kinzers Shale, middle upper *Olenellus* zone following Palmer and Repina (1993), 2 mi N of York, Fruitville, 3 mi N of Lancaster, Getz Quarry, 1 mi N of Rohrerstown, and 0.5 mi S of East Petersburg.

OLENELLUS CLARKI (RESSER 1928)
Figures 3.2 to 3.5

Paedeumias clarki; Resser 1928:9, pl. 3, figs. 1, 2; Riccio 1952:33, pl. 9, figs. 1–4.
Olenellus clarki (Resser); Mount 1976:175, fig. 6; Palmer in Palmer and Halley 1979:68, pl. 3, figs. 1–5; Mount 1980:27, fig. 6.

Types: Resser (1928) designated USNM 78393, a complete individual, and USNM 78394, a cephalon, as cotypes. In addition, Resser (1928) noted that two unnumbered cephala appear on the same slab as USNM 78393. Because of its excellent state of preservation, USNM 78393 is designated herein the **lectotype,** and the two unnumbered cephala and 78394 become paralectotypes. The type locality is the soft shale (probably the Latham Shale) at Bristol Mountain, near Cadiz, on the Santa Fe Railroad, about 100 mi E of Barstow, in the Mohave Desert, California.
Discussion: This species is closely related to *O. gilberti,* which unfortunately could not be considered in this phylogenetic analysis because adequate material was not available. However, Palmer (Palmer and Halley 1979) provided characters that discriminate between these two taxa. *Olenellus clarki* and *O. nevadensis* cannot be consistently discriminated by the qualitative characters given in Table 1. However, these taxa are polymorphic for some of these characters, and not all of their polymorphic character states overlap. In particular, in *O. clarki* the length (sag.) of the preglabellar field is 15% to 25% of the length (sag.) of L4, whereas in *O. nevadensis* it is from 15% to 50% of the length (sag.) of L4; in *O. clarki* the lateral margins of L4 are either medial of the lateral margins of L0 or directly anterior of them, whereas in *O. nevadensis* they are medial of L0; in *O. clarki* S2 is variably conjoined or not conjoined medially, whereas in *O. nevadensis* it is conjoined medially; and in *O. clarki* the posterior margins of the ocular lobes extend back to the distal tips of S0, whereas in *O. nevadensis* they extend back to S0 or to the medial part of the distal margin of L0. Because these taxa have identical character states for many of the characters in Table 1 and overlap in the condition of some of the other characters, it is important to demonstrate that these taxa are indeed distinct and do not represent just a single, highly variable taxon. Bivariate character data show that *O. clarki* can be consistently discriminated from *O. nevadensis,* and therefore these are two distinct species. One quantitative difference between these taxa is in the ratio of the maximum width of L4 relative to the maximum width of L0: for *O. clarki* (0.90, 1.0, 0.80, 0.86, 0.94, 0.90, 0.96, 0.96, 0.93, 0.88, 1.0, 0.89, 0.97, 1.0, 0.83, 0.88, 1.0, 0.83, 0.95, 1.01, 0.88, 0.97, 0.98, 0.94, 0.95, 1.0, 0.97, 1.01); for *O. nevadensis* (0.63, 0.72, 0.74, 0.77, 0.71, 0.65, 0.78). These ratios, 0.94±0.06 for *O. clarki,* 0.72±0.06 for *O. nevadensis,* are significantly different ($p<0.00001$ by the two sample t-test, Minitab 1995 v. 10Xtra [1995]). The median value of the ratio for *O. clarki* (0.95) differs from that of *O. roddyi* (0.72) ($p<0.0001$ by Mann-Whitney u-test, Minitab 1995 v. 10Xtra [1995]). Thus, on the basis of these character differences, these two species are treated as distinct although assumed to be very closely related.

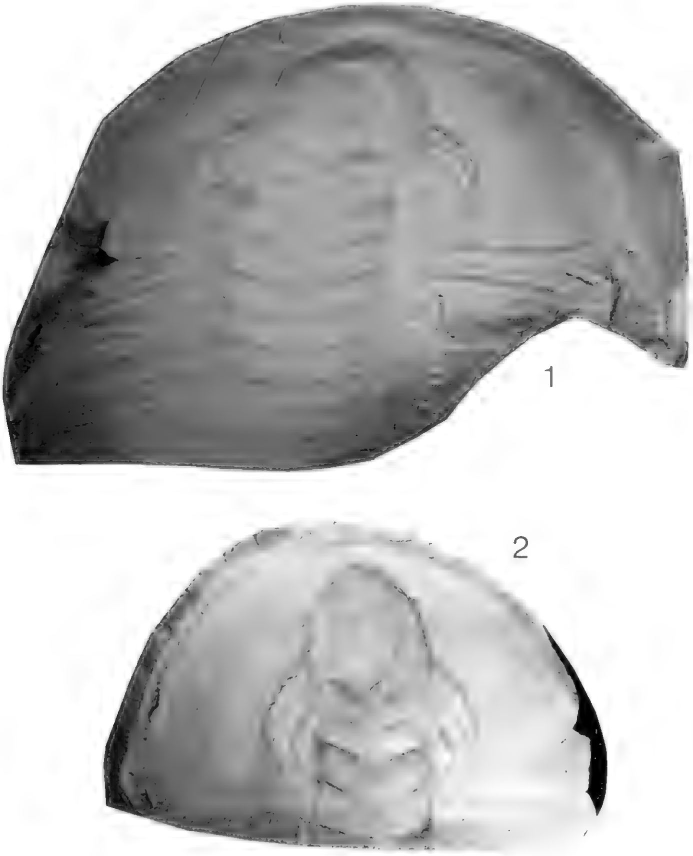

Figure 5.
Olenellus getzi Dunbar, locality is the same as Figure 3.8. **1.** YPM 94073, ×0.9. **2.** YPM 35873, ×0.9.

Material examined: LACMIP 200-A (2 specimens), 200-B, 3376, 4908–21, 5872 (3 specimens), 9690; MCZ 7372; SDSNH 17001, 20707 (4 specimens), 20708 (10 specimens), 20802 (2 specimens); UCR 10 (5 specimens), 10/197, 10/586, 10/985, 10/1135, 10/1144, 10/1160, 10/1421, 10/2009, 10/2022, 7002/4, 7271/2, 7899.

Occurrence: Carrara Formation, upper *Olenellus* zone, Funeral Mountains, Resting Springs Range, Eagle Mountain, Grapevine Mountains, Salt Spring Hills, all in California; Nevada Test Site and Desert Range, Nevada; and from the Latham Shale, treated as in the Bristolia zonule, upper *Olenellus* zone, at the southern end of the Marble Mountains, near Chambless in the Mojave Desert portion of San Bernardino County, California, at the end of the dirt road on the opposite side of the hill from the limestone quarry (Chambless Limestone), about 1.25 mi N, 28 degrees E of Cadiz railroad station, Hazzard and Crickmay's (1933) locality M-5. Locality lies just above the crossbedded Zabriskie Quartzite at the end of the dirt road. Fossils in gray-brown shale, equal to the upper Latham Shale, 6 to 10 m thick. It is 416 ft W, 216 ft S of NE corner sec 11, T 5 N, R 14 E, San Bernardino Baseline and Meridian, on the USGS 15 ft Danby Quadrangle. Also from Latham Shale, near Summit Springs, W side of Providence Mountains, San Bernardino County, California. Riccio (1952) also reports the species from the Latham Shale, Marble Mountains, 190 m W of the limestone quarry, 0.5 mi E of Cadiz, in the Mojave Desert portion of San Bernardino County, California, possibly equivalent to Hazzard and Crickmay's (1933) locality M-5.

OLENELLUS NEVADENSIS (WALCOTT 1910)

Figures 3.6, 3.7

Callavia? *nevadensis;* Walcott 1910:285, pl. 38, fig. 12.
Paedeumias nevadensis (Walcott); Resser 1928:9, pl. 3, figs. 3–7; Riccio 1952:33, pl. 9, figs. 5, 6.
Olenellus nevadensis (Walcott); Mount 1976:175, fig. 10; Palmer in Palmer and Halley 1979:73, pl. 4, figs. 10, 13, 17; Mount 1980:27, fig. 10; Fritz 1991:13, non pl. 12, figs. 3–5.

Types: The type locality of this species, according to Walcott (1910), is from the Pioche Formation, at the summit of Prospect Mountain, the Eureka District, Nevada. Walcott (1910) figured three specimens that he assigned to this species; however, they represent three separate taxa. One of these (Walcott 1910, pl. 38, fig. 13) appears to be a specimen of *Bristolia* anteros Palmer (Palmer and Halley 1979) or belongs to a species closely related to that taxon. The other (Walcott 1910, pl. 38, fig. 14) is another olenelloid species of indeterminate taxonomy, though it clearly is not a specimen of *O. nevadensis.* Resser (1928) restricted *nevadensis* to Walcott's specimen (1910, pl. 38, fig. 12), and this decision is supported here. Resser (1928) illustrated several specimens that he referred to as plesiotypes, but these are not from the type locality and therefore cannot be considered valid types. These are conspecific with *O. nevadensis,* but hail from Resser's (1928) Bristol Mountain section in California. The only possible valid type of this species would be Walcott's specimen (1910, pl. 38, fig. 12), USNM 56799a, and is designated as a **lectotype** here.

Discussion: Fritz (1991) illustrated two specimens from the Lower Cambrian Illtyd Formation of the Yukon that he questionably assigned to *O. nevadensis.* These specimens are fragmentary, but similar to *O. nevadensis* in that they bear a long (sag.) preglabellar area, a plectrum and a narrow (tr.) L4. However, they do differ from typical *O. nevadensis* in the condition of a few characters, including: the ocular lobes extend further posteriorly than those typical of *O. nevadensis*; and the distal tips of S2 extend further laterally than those typical of *O. nevadensis.* Based on these character differences, the Yukon material is provisionally excluded from *O. nevadensis,* though it is held to be closely related to that species. Because Fritz's (1991) material is so fragmentary, it is not treated in any greater detail herein. Quantitative means for distinguishing this species from *O. clarki* are presented above.

Material examined: LACMIP 200A, 3376; SDSNH 16783–16785, 16812, 20710 (10 specimens), 20804 (2 specimens); UCR 10, 10/175, 10/2005, 4079, 7271.

Occurrence: California: Carrara Formation, *Bristolia* zonule, upper *Olenellus* zone, Funeral Mountains and Grapevine Mountains; Latham Shale, treated as in the *Bristolia* zonule, upper *Olenellus* zone, at the southern end of the Marble Mountains, near Chambless in the Mojave Desert portion of San Bernardino County, at the end of the dirt road on the opposite side of the hill from the limestone quarry (Chambless Limestone), about 1.25 mi N, 28 degrees E of Cadiz railroad station, Hazzard and Crickmay's (1933) locality M-5. Locality lies just above the crossbedded Zabriskie Quartzite at the end of the dirt road. Fossils in gray-brown shale, equal to the upper Latham Shale, which is 6 to 10 m thick. It is 416 ft W, 216 ft S of NE corner sec 11, T 5 N, R 14 E, San Bernardino Baseline and Meridian, on the USGS 15 ft Danby Quadrangle. Riccio (1952) also reports the species from the Latham Shale, Marble Mountains, 190 m W of the limestone quarry, 0.5 mi E of Cadiz, in the Mojave Desert portion of

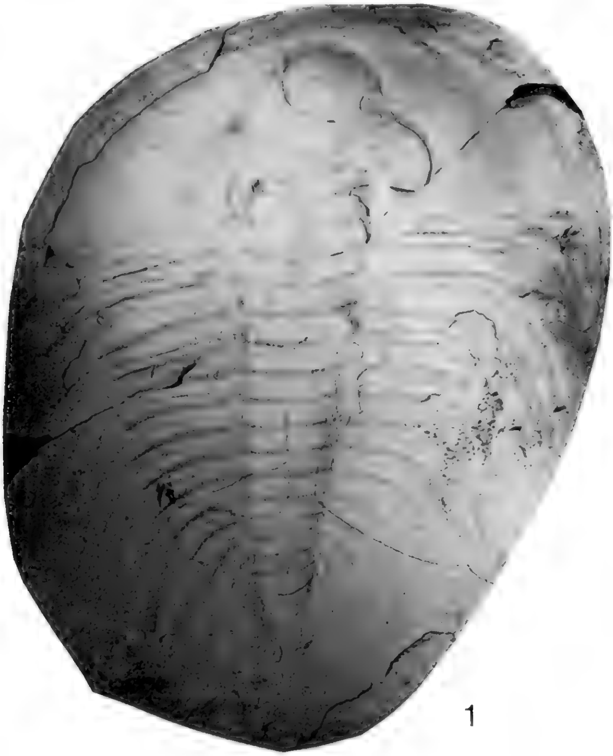

Figure 6.
Olenellus getzi Dunbar, locality is the same as Figure 3.8. **1.** YPM 94061, ×0.8.

San Bernardino County, possibly equivalent to Hazzard and Crickmay's (1933) locality M-5. Nevada: Carrara Formation, *Bristolia* zonule, upper *Olenellus* zone, Desert Range, Nevada.

OLENELLUS ROBSONENSIS (BURLING 1916)

Figure 4.1

Paedeumias robsonensis; Burling 1916:53.
Olenellus robsonensis (Burling); Fritz 1972:15; Whittington 1989:121, figs. 20, 25; Fritz 1992:9.

Types: Holotype, GSC 5272, see Fritz (1972).
Discussion: This species is based on a single spectacular specimen that possesses more than 42 thoracic segments, including the usual complement of 13 prothoracic segments. Such a large number of opisthothoracic segments is unknown for any other olenelloid (as defined in Lieberman 1998), and therefore represents a distinct autapomorphy of the species; however, *Kleptothule rasmusseni* Budd 1995, a trilobed arthropod from the Lower Cambrian of Greenland, although presumably distantly related to *O. robsonensis,* also bears a many segmented thorax. In all other features of its morphology, *O. robsonensis* matches those characters typical of the genus *Olenellus.*

Material examined: GSC 5272, the holotype.
Occurrence: Canada, British Columbia: ?Upper Mahto Formation, ?middle *Olenellus* zone (according to Fritz 1992), drift block on the slope of the Mural Glacier below Mumm Peak, near Mount Robson.

Olenellus getzi Dunbar 1925

Figures 3.8, 5.1, 5.2, 6.1

Olenellus getzi; Dunbar 1925:307, figs. 1, 2; Resser and Howell 1938:221, pl. 5, figs. 1–5; Fritz 1972:11; Whittington 1989:120.
Olenellus alius; Resser and Howell 1938:224, pl. 7, figs. 7, 8.
?*Olenellus peculiaris*; Resser and Howell 1938:223, pl. 6, fig. 10.
?*Paedeumias yorkense*; Resser and Howell 1938:227, pl. 6, figs. 4, 5, pl. 9, figs. 5–7.

Types: Holotype, YPM 14365, see Dunbar (1925).
Discussion: As mentioned above, some of the specimens assigned to *P. yorkense* by Resser and Howell (1938) and *P. transitans* by Walcott (1910) bear a strong similarity to material typical of *O. roddyi* and *O. getzi* but are known only from larval stages or thoracic material. This material could be conspecific with either *O. getzi* or *O. roddyi*, as these taxa do not meaningfully differ in the condition of their thoraxes and the extent of ontogenetic variation is not known. Therefore, these specimens are only questionably assigned to *O. getzi*. Consistent differences between *O. getzi* and *O. roddyi* include a more convex anterior cephalic border in the former; a plectrum missing in *O. getzi* but present in *O. roddyi*; the lateral margins of L2 in *O. getzi* not deflected laterally relative to L1, as in *O. roddyi*; the posterior margins of the ocular lobes extend back to S0 in *O. getzi*, but back to the medial part of the distal margin of L0 in *O. roddyi*; and T3 extends further posteriorly in *O. roddyi* than in *O. getzi*.

Fritz (1972) and Whittington (1989) suggested that *O. getzi* was conspecific with *O. thompsoni*. Although these taxa are closely related, there are consistent differences between them and therefore cannot be considered conspecific (they also are known from disjunct localities). Such character differences include: in *O. thompsoni* the lateral margins of L4 are distal of the lateral margins of L0, while in *O. getzi* they are directly anterior of L0; in *O. getzi* the lateral margins of L2 are not deflected laterally relative to L1, as in *O. thompsoni*; the posterior margins of the ocular lobes extend back to S0 in *O. getzi*, but back to the medial part of the distal margin of L0 in *O. thompsoni*; and in *O. getzi* the anterior margins of T3 are deflected anteriorly relative to a transverse line at a 5 to 10 degree angle, while in *O. thompsoni* they roughly parallel a transverse line.
Material examined: MCZ 2488; YPM 9294, 9297, 9298, 14365, the holotype, 31962, 35867, 35869–35871, 35873, 35874, 35887–35891, 35894, 63304, 94060–94062, 94073, 94088, 94090, 94160, 94168, 94306–94308, 94310, 94312.
Occurrence: Pennsylvania: Kinzers Shale, middle upper *Olenellus* zone, 2 mi N of York, and Noah Getz Farm, 1 mi N of Rohrerstown.

Olenellus crassimarginatus Walcott 1910

Olenellus thompsoni crassimarginatus; Walcott 1910:340, pl. 35, figs. 8, 10.
Olenellus crassimarginatus Walcott; Resser and Howell 1938:224, pl. 7, fig. 2.
Olenellus wanneri; Resser and Howell 1938:224, pl. 7, fig. 2.

Olenellus latilimbatus; Resser and Howell 1938:222, pl. 6, fig. 9.
Olenellus thompsoni Hall; Walcott 1886:167, pl. 17, fig. 1.
Olenellus thompsoni Hall; Walcott 1891, pl. 83, fig. 1b.

Types: Walcott (1910) figured three specimens that he assigned to his new variety, *O. thompsoni crassimarginatus*. One of these specimens (Walcott 1910, pl. 35, fig. 9) shows a poorly preserved indeterminate species of olenelloid. It clearly is not *O. crassimarginatus* because it lacks the prominent intergenal spines, has a relatively broad L4 and has the glabellar furrows conjoined. Walcott (1910, pl. 35, fig. 8) shows the only specimen that hails from the type locality, Parker's Quarry, Georgia, Vermont, and appears to be Walcott's (1910) intended type of the species. This specimen is therefore the holotype, USNM 56836a. Resser and Howell (1938) inexplicably designated USNM 90810 the holotype of the species.
Discussion: One of the specimens Walcott (1910, pl. 35, fig. 9) figured and assigned to what is here treated as *O. crassimarginatus* is poorly preserved. However, based on the illustrated material, it appears that this specimen belongs to some other indeterminate olenellid species (see above). *Olenellus wanneri* and *O. latilimbatus* are identical to *O. crassimarginatus* in the characters considered in this analysis, and therefore they are treated as conspecific, with *O. wanneri* and *O. latilimbatus* representing junior subjective synonyms. *Olenellus crassimarginatus* is the only species of olenellid known from both the Kinzers Shale and the Parker's Slate.
Occurrence: Vermont: Parker Slate, middle upper *Olenellus* zone, Parker's Quarry, Georgia. Pennsylvania: Kinzers Shale, middle upper *Olenellus* zone, 0.5 mi S of East Petersburg, 2 mi N of York, and Fruitville, 3 mi N of Lancaster.

· TWO ·

Phylogenetic Analysis of the Mesonacinae

The Mesonacinae clade includes the genera *Mesolenellus* and *Mesonacis*, which are in turn sisters to the species of *Olenellus*. Evidence for this sister group relationship is discussed in greater detail below, and justification for reviving the subfamilial term Mesonacinae is also presented.

A total of 10 taxa was subjected to phylogenetic analysis, including all available and adequately preserved species of the genera *Mesonacis* and *Mesolenellus*, and two outgroup taxa: *Olenellus thompsoni* and *O. transitans*. These taxa are appropriate outgroups to the genus *Mesonacis* based on the higher level phylogenetic analysis presented in Lieberman (1998). Phylogenetic patterns were determined by parsimony analysis of 25 holaspid exoskeletal characters (Table 3). The codings for the taxa analyzed are given in Table 4. All characters were treated as unordered (nonadditive). These data were subjected to an exhaustive search on PAUP v. 3.1.1 (Swofford 1993). One most parsimonious tree (Figure 7) was recovered of length 60 steps, consistency index = 0.57, and retention index = 0.57.

The distribution of all tree lengths (Hillis 1991) was significantly left-skewed relative to the distribution of tree lengths produced by random data. The g_1 statistic was –0.59, which is statistically significant ($p<0.01$), indicating these data have a strong phylogenetic signal. The confidence values for nodes of the consensus tree duplicated in bootstrap analysis are given in Figure 7. Using the method of Bremer (1994), five trees of length less than or equal to 61 steps, 44 trees of length less than or equal to 62 steps, 138 trees of length less than or equal to 63 steps, and 451 trees of length less than or equal to 64 steps were recovered before the analysis was terminated because the consensus cladogram was a complete polytomy. The amount of branch support for the various nodes is given in Figure 7. The total support index (Bremer 1994) for the tree is 0.10, a moderately low value according to the examples given in Bremer (1994).

Any potential incongruence between stratigraphy and phylogeny, or any potential gap in the history of the Mesonacinae, centers around the first occurrences of species within the two major clades within that subfamily. These two clades, *Mesolenellus* and *Mesonacis*, are sisters to one another, but there is some controversy about the stratigraphic first occurrence of species within the genus *Mesolenellus*. Species of that genus first appear either in the "*Nevadella*" zone or in the *Olenellus* zone, whereas species of *Mesonacis* are distributed throughout the *Olenellus* zone. If the former stratigraphic assignment is accepted, this would imply a potentially large stratigraphic gap in the history of this group. The stratigraphic first appearance of *Mesolenellus hyperborea*, the type of the genus *Mesolenellus*, was treated as in the "*Nevadella*" zone by Palmer and Peel (1979), but this first appearance was later adjusted upward into the *Olenellus* zone by Palmer and Repina (1993). It is not clear, based on the biostratigraphic evidence, why the stratigraphic first appearance of this species was subsequently changed. There appears to be more congruence between stratigraphic first appearance and phylogenetic position within the genus *Mesonacis*. The basal member of that clade, according to the phylogeny shown in Figure 7, *M. fremonti*

(Walcott 1910), appears early in the *Olenellus* zone according to Nelson (1976) and Palmer and Halley (1979), and subsequent species appear later in the *Olenellus* zone, for example, *M. vermontanus* (Hall 1859).

Systematic Paleontology

Superfamily Olenelloidea Walcott 1890
Family Olenellidae Walcott 1890
Subfamily Mesonacinae Walcott 1890

As defined in Palmer and Repina (1993), the Olenellinae is identical to the Olenellidae, and contains the same genera. Here the Olenellinae is restricted to the genus *Olenellus,* and discussed above. The clade containing *Mesonacis* and *Mesolenellus* therefore must also be elevated to subfamilial status. Walcott (1890) originally proposed the family group name Olenellidae, but rejected it because it was a homophone of Olenidae Burmeister 1843. In its stead he established the Mesonacidae (as Mesonacidiae), and continued its use in several important papers (e.g., Walcott 1910). As discussed in Whittington (1989), homophony is not grounds to reject a family group name, and Whittington (1989) rightly stated that a family group name must be based on a genus contained within the taxon. Whittington (1989) further stated that Resser (1928) showed the difficulties of distinguishing between species referred to under *Mesonacis* or *Olenellus,* and Whittington used this to argue that *Mesonacis* is a synonym of the former (because the establishment of *Olenellus* predates the establishment of *Mesonacis*). In reality, Resser (1928) did not show the difficulties of distinguishing between *Mesonacis* and *Olenellus,* but gave clear criteria for differentiating between them (Resser 1928:3–4)! Resser (1928) stated that both *Mesonacis* and *Olenellus* are good genera and can be consistently distinguished by several characters, including the condition of the pleurae on the opisthothoracic segments, the relative position of the ocular lobes and the position of the genal spine angle. However, Resser and Howell (1938) retreated somewhat from this position, and claimed that generic differences do not exist between *Olenellus thompsoni* and *M. vermontanus.* They further claimed that some of the differences elucidated in Resser (1928) were still valid, but "not believed to be of generic importance" (Resser and Howell 1938:217). Subsequent commentaries on the taxonomy of the olenellids (e.g., Harrington et al. 1959) treated *Mesonacis* as a synonym of *Olenellus.* Palmer and Repina (1993) treated *Mesonacis* (and also *Mesolenellus*) as a subgenus of *Olenellus* on the grounds that species within these genera could not always be easily distinguished (Palmer, pers. comm. 1996). However, once clear diagnostic characters for these genera were formulated, it became possible to elevate them to full generic status. Diagnostic characters for both *Mesolenellus* and *Mesonacis* are given below under their respective generic headings and clear means of distinguishing between these taxa and *Olenellus* are provided.

Because it is clear that *Mesonacis* and *Mesolenellus* represent a good clade, and because this clade is of equal rank to the Olenellinae, an appropriate subfamilial name for them is needed. Hence, the taxon Mesonacinae of Walcott (1890) is re-established, as the subfamily is based around *M. vermontanus,* the type of the genus *Mesonacis.*

The Mesonacinae can be defined by the possession of the following diagnostic characters in combination (thoracic and pygidial characters are not preserved in all species assigned to the Mesonacinae): 1. anterior part of ocular lobe close to L4; 2. ocular lobe with prominent furrow; 3. width (tr.) of interocular area approximately equal to width of ocular

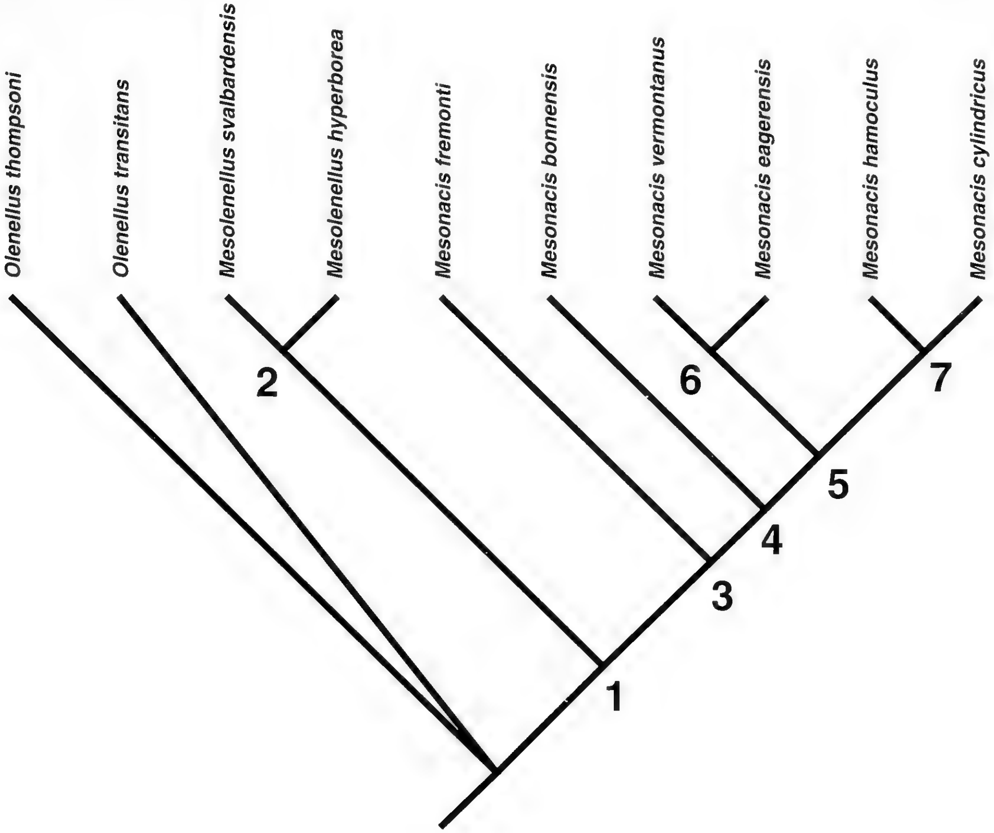

Figure 7.
The most parsimonious tree of length 60 steps produced from analysis of character data in Table 4 with PAUP v. 3.1.1 (Swofford 1993). The cladogram is constructed using an exhaustive search. The retention index is 0.57, and the consistency index is 0.57. The value of the g1 statistic is –0.59. The following nodes in the text were supported by the following bootstrap confidence values (see text for bootstrapping procedure used): Node *1* = 0.49; Node *2* = 0.92; Node *3* = 0.40; Node *4* = 0.45; Node *5* = 0.28; Node *6* = 0.55; Node *7* = 0.29. The following branch support values (Bremer 1994) were recovered for the following nodes: Node *1* = 1; Node *2* = 3; Node *6* = 1. Total tree support (Bremer 1994) is 0.10. Character states are placed at nodes, using MacClade v. 3.04 (Maddison and Maddison 1992), with the characters given in Table 3. The apomorphic state is given in parentheses. Square parentheses indicate equivocal character states that are ambiguous because of missing data or multiple equally parsimonious resolutions. Equivocal characters are placed only at their basal phylogenetic position, and only unambiguous reversals are shown. Node *1,* 3[0, 1], 11(1), 12(1), 14[0, 1], 16(1), 17(1), 19(1); Node *2,* 3(1), 5[0, 1, 2], 6(1), 8(1), 14(0), 21(1), 24(1); Node *3,* 2(1), 7(1), 14(1); Node *4,* 1[0, 1], 11[1, 2], 15(1), 18(1), 20(1), 25(1); Node *5,* 5[0, 2], 10[0, 1], 14[1, 2], 22(2); Node *6,* 5(2), 6(2), 10(1), 12(2), 14(2); Node *7,* 3(1), 13(1), 21(1).

lobe; 4. axial part of L0 with node; 5. extraocular area flattened, lacking prominent anastomosing ridges (except in *M. svalbardensis*); 6. extraocular region opposite L1 40% to 50% width (tr.) of glabella at L1 (except in *M. fremonti*); 7. intergenal angle directed anteriorly at angle greater than or equal to 30 degrees relative to transverse line; 8. anterior margin of thoracic pleural furrow on third segment parallels a transverse line before flexing strongly posteriorly when proceeding from proximal to distal edge; 9. width (tr.) of thoracic pleural spines T5 to T8 at spine midlength less than or equal to half length (exsag.) of corresponding segment between spine and axis; 10. segments of opisthothorax with prominent pleurae (except in *M. fremonti*); 11. pygidium length (sag.) 1.5 times width (tr.). None of these

Table 3.
Description of characters and character states used in phylogenetic analysis of Mesonacinae. (0) represents the primitive state and (1) and (2) are derived states.

	Primitive state	Derived states
1. Anterior margin of third thoracic segment (T3) relative to transverse line	(0) parallel or flexing no more than 5° anteriorly	(1) flexing at least 20° anteriorly
2. Posterior margins of ocular lobes opposite	(0) medial part of distal margin of L0	(1) medial part of distal margin of L1
3. Anterior part of frontal lobe	(0) intersects anterior border furrow	(1) does not intersect anterior border furrow
4. Length (exsag.) of medial part of thoracic pleural furrows	(0) long, 1.5 times as long as posterior pleural band	(1) short, equal to length of posterior pleural band
5. Medialmost part of intergenal angle arches anteriorly	(0) three-fourths of way between point behind distal tip of ocular lobe and genal spine angle	(1) behind distal tip of ocular lobe (2) at a point midway between point behind distal tip of ocular lobe and genal spine angle
6. Length (exsag.) of genal spine	(0) approximately equal to 4–5 times the length (sag.) of L0	(1) approximately equal to 8–10 times the length (sag.) of L0 (2) approximately equal to 2 times the length (sag.) of L0
7. S2	(0) not conjoined medially	(1) conjoined medially (2) very faintly incised medially
8. Lateral margins of glabella opposite L2, when proceeding anteriorly	(0) diverging such that glabella expands laterally	(1) not diverging such that glabella does not expand laterally
9. Plectrum	(0) absent	(1) present
10. Thoracic pleural spines behind T3–T4 extend back roughly	(0) 4–7 segments	(1) 1–2 segments
11. Angle intergenal angle forms with transverse line approximately	(0) 5°–15°	(1) 30°–35° (2) 45°–50°

Continued

Table 3 continued.

	Primitive state	Derived states
12. Length (exsag.) of anterior cephalic border between frontal lobe and genal spine angle	(0) 1.3–1.5 times length (exsag.) of L2 at distal tip	(1) roughly 0.75 times length (exsag.) of L2 at distal tip (2) roughly 0.40 length (exsag.) of L2 at distal tip
13. S2	(0) medial tip behind distal tip such that inner edge is inclined posteriorly	(1) medial and distal tip as far forward, transverse (2) very faintly incised medially
14. Third thoracic pleural spine extends back	(0) 6–8 thoracic segments	(1) length of entire thorax (2) 3–4 thoracic segments
15. Medial part of cephalic posterior border between lateral margins of L0 and intergenal angle	(0) posteriorly directed	(1) parallels transverse line
16. Lateral margins of frontal lobe	(0) distal to lateral margins of L0	(1) directly anterior to lateral margins of L0
17. Lateral margins of glabella between posterior margin of L0 and point midway forward on distal tip of L1	(0) converging, such that glabella contracts	(1) subparallel, such that glabella is of constant width
18. Line from posterior tip of ocular lobe to junction of posterior margin of ocular lobe with glabella forms roughly	(0) 0°–5° angle with sagittal line	(1) 15°–20° angle with sagittal line
19. Width (tr.) of axis relative to width of pleural segment for T3 excluding spine	(0) 60%–70%	(1) 100%–105%
20. Anterior cephalic border	(0) elevates anteriorly from anterior border furrow at approximately 45° angle relative to a dorsal, flat plane, then dorsally flattened, such that border is broadly convex	(1) elevates anteriorly from anterior border furrow at approximately 90° angle relative to dorsal plane, then flattened, such that border is developed as raised ridge

Continued

Table 3 continued.

	Primitive state	Derived states
21. S0	(0) not conjoined medially	(1) conjoined medially
22. Genal spine angle opposite	(0) medial part of margin of L0	(1) distal edge of S0 (2) medial part of margin of L1 (3) medial part of margin of L2
23. S2	(0) does not contact axial furrows	(1) contacts axial furrows
24. Glabellar furrows	(0) prominently incised	(1) faintly incised
25. Thoracic pleural spines on all segments but T3, at medial part of spine	(0) width (tr.) equal to half length (exsag.) of corresponding pleural segment at medial part between spine and axis	(1) width (tr.) roughly equal to one quarter length (exag.) of corresponding pleural segment at medial part between spine and axis

characters are unique to the Mesonacinae, meaning they all show some homoplasy or are symplesiomorphic within the Olenelloidea.

Included Taxa

GENUS *MESOLENELLUS* PALMER AND REPINA 1993

Type species: *Holmia hyperborea* Poulsen 1974.
Assigned taxa: *Olenellus svalbardensis* Kielan 1960.
Diagnosis: Anterior cephalic border anterolateral of frontal lobe length (exsag.) 0.75 times length (exsag.) of L2 at distal tip; anterior cephalic border elevates from anterior border furrow at approximately 45 degree angle relative to dorsal flat plane, then intersects raised lineament, anterior of this point, border lies in flattened dorsal plane before deflecting ventrally; anterior part of frontal lobe does not intersect anterior border furrow; lateral margins of frontal lobe deflected as far laterally as lateral margins of L0; distal margins of glabella opposite L2 subparallel; S2 straight, not conjoined medially; lateral margins of glabella between posterior margin of L0 and point midway forward on distal tip of L1 subparallel; line from posterior tip of ocular lobe to junction of ocular lobes with glabella forms roughly 5 degree angle with sagittal line; S0 conjoined medially; lateral lobes present on L0; posterior margin of ocular lobes opposite medial part of distal margin of L0;

glabellar furrows faintly incised; intergenal angle forms 30 to 35 degree angle with transverse line; genal spine length (exsag.) approximately length (sag.) of 8 to 10 thoracic segments; pleural spine of T3 extends back 6 to 8 thoracic segments; anterior margin of T3 roughly parallels a transverse line medially; posterior margin of pleural furrow of T3 parallels transverse line before flexing posterolaterally; thoracic pleural spines behind T3 extend back 4 to 7 segments posteriorly; spines wide (tr.), one-half length (exsag.) of corresponding pleural segment at its medial part; width (tr.) of thoracic axis 100% of width of pleural field excluding spines; base of large axial spine on T15 less than half width (tr.) of axis of segment.

Discussion: Originally Palmer and Repina (1993) treated *Mesolenellus* as a subgenus of *Olenellus.* However, based on the phylogeny of the Olenelloidea in Lieberman (1998) this would necessitate lumping both *Mesonacis* and *Mesolenellus* within the genus *Olenellus.* Palmer (pers. comm. 1996) now believes that the differences among the taxa *Mesonacis, Mesolenellus* and *Olenellus* are sufficient to warrant generic status, and recommends treatment as separate genera. His recommendation is followed here, as clear diagnostic characters exist for *Mesolenellus* and indeed all of the Mesonacinae, such that it can be discriminated from *Olenellus.* In particular, *Mesolenellus* differs from *Olenellus* (which includes what was formerly referred to as *O.* [*Paedeumias*]) in the condition of the following characters: the anterolateral parts of the glabella are more prominently separated from the extraocular area in *Mesolenellus* than in *Olenellus* (not considering the anterior border furrow); in *Mesolenellus* the posterior margins of L4 are subparallel, in *Olenellus* they are divergent anteriorly; in *Mesolenellus* the lateral margins of the glabella opposite L2 are subparallel, in *Olenellus* they are divergent; in *Mesolenellus* the lateral margins of the glabella between the posterior margin of L0 and a point midway forward on the distal tip of L1 are subparallel, in *Olenellus* they are convergent; in *Mesolenellus* S0 is conjoined medially, in *Olenellus* it is not; in *Mesolenellus* the lateral lobes on L0 are present, in *Olenellus* they are absent; in *Mesolenellus* the glabellar furrows are faintly incised, in *Olenellus* they are prominently incised; in *Mesolenellus* the extraocular area is relatively narrower than it is in *Olenellus*; in *Mesolenellus* the length (exsag.) of the genal spine is equal to the length (sag.) of the first 8 to 10 thoracic segments, in *Olenellus* it is equal to the length of the first 4 to 5 segments; in *Mesolenellus* the intergenal angle is developed posterior of the lateral margins of the ocular lobes, or at a point halfway between the ocular lobes and the genal spine angle, whereas in *Olenellus* it is developed adjacent to the genal spine angle; in *Mesolenellus* the integenal angle has a distinct dorsal swelling, whereas in *Olenellus* it has a spine; in *Mesolenellus* the intergenal angle is directed anteriorly at a roughly 30 to 35 degree angle relative to a transverse line, whereas in *Olenellus* it is directed anteriorly at a roughly 5 to 10 degree angle; in *Mesolenellus* the posterior margin of the thoracic pleural furrow of T3 has the medial part parallel to a transverse line with the lateral part deflected weakly posteriorly, whereas in *Olenellus* it is directed evenly posterolaterally; in *Mesolenellus* the width (tr.) of the thoracic axis on segments 5 to 8 is equal to the width of the pleural segment excluding the spine, in *Olenellus* the axis is 60% to 70% of the width of the pleurae excluding the spine; in *Mesolenellus* the width (tr.) of the thoracic pleural spines on segments 5 to 8 at the spine midlength is less than half the length (exsag.) of the medial part of the inner pleural region, while in *Olenellus* they are relatively broader, more than two thirds the length of the medial part of the inner pleural region; in *Mesolenellus* the base of the spine on T15 is less than half the width (tr.) of the axis of the segment, in *Olenellus* it is nearly as wide as the segment; and in *Mesolenellus* the

Table 4.
Character state distributions for Mesonacinae and outgroups used in phylogenetic parsimony analysis. Characters and alternative states are as listed in Table 3. Missing data are indicated by ?.

	1	1 1 1 1 1 1 1 1 1 2	2 2 2 2 2
	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5
Olenellus thompsoni	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
Olenellus transitans	0 0 1 0 0 0 0 0 1 0	0 1 0 1 0 1 0 0 0 1	0 0 0 0 0
Mesolenellus svalbardensis	0 0 1 0 2 1 0 1 1 0	1 1 0 0 0 1 1 0 1 0	1 0 0 1 0
Mesolenellus hyperborea	0 0 1 1 1 1 0 1 0 0	1 1 0 0 1 1 1 0 1 0	1 3 1 1 0
Mesonacis vermontanus	1 1 0 0 2 2 0 0 0 1	2 2 0 2 1 1 1 1 1 1	0 2 0 0 1
Mesonacis bonnensis	1 1 0 1 0 0 2 0 1 0	2 1 2 1 1 1 1 1 1 1	0 0 0 1 1
Mesonacis fremonti	0 1 0 0 0 0 1 0 0 0	1 0 0 1 0 0 1 0 1 0	0 0 0 0 0
Mesonacis eagerensis	0 1 0 0 2 2 1 0 0 1	1 2 0 2 1 0 0 1 1 1	0 1 0 0 1
Mesonacis hamoculus	? 1 1 ? 2 0 1 0 0 ?	1 1 1 ? 1 1 0 1 ? 0	1 2 1 0 ?
Mesonacis cylindricus	? 1 1 ? 0 ? 1 0 ? ?	2 0 1 ? 0 0 1 1 ? 1	1 2 0 0 ?

opisthothorax has prominent pleurae, in *Olenellus* it does not (not all thoracic characters can be discerned in both species of *Mesolenellus*).

This genus occurs in strata either assigned to the "*Nevadella*" zone or the lower middle *Olenellus* zone.

MESOLENELLUS HYPERBOREA (POULSEN 1974)

Holmia hyperborea; Poulsen 1974:84, pl. 1, figs. 4–7, pl. 2, figs. 1–6, pl. 3, figs. 1–8; Palmer and Peel 1979:33, fig. 3.

Olenellus (*Mesolenellus*) *hyperborea* (Poulsen); Palmer and Repina 1993:22, fig. 3.7; Palmer and Repina 1997:408, fig. 255.4.

Mesolenellus hyperborea (Poulsen); Lieberman 1998:70.

Types: Holotype, MGUH 13008, see Poulsen (1974).

Discussion: All specimens of this species, except MGUH 13945, have the genal spine angle opposite the medial part of the distal margin of L2. In this one specimen the genal spine angle is opposite the medial part of the distal margin of L1. However, in MGUH 13945 the posterior part of the cephalon is also superimposed over the last two thoracic segments, and the intergenal angle appears to be deformed, with a concomitant displacement of the genal spine posteriorly. Because the condition of the genal spine angle in this specimen appears to be affected by deformation, this character (character 22), was coded with the state it has in all the other specimens of the species.

Poulsen (1974) suggested that this species was closely related to *Holmia mirabilis* Poulsen 1958, here assigned to the genus *Elliptocephala*, and presented some statistical evidence as support. He calculated regression lines for measurements of log glabellar length versus several variables including log intergenal width and log border width. In some cases

Poulsen (1974) recovered regression lines with similar slopes across what he regarded as highly divergent taxa (e.g., *Olenellus gilberti* and *Holmia kjerulfi* Linnarsson 1871); in other cases he found divergent slopes across what he believed to be closely related taxa, and finally he found similar slopes across what he believed to be closely related taxa (e.g., *Elliptocephala mirabilis* and *Mesolenellus hyperborea*).

First, there is insufficient taxonomic sampling to determine whether this statistical criteria for recognizing taxonomic entities has any validity. There is also a strong circular element to his reasoning that *E. mirabilis* and *M. hyperborea* are closely related. Thus, although the results of his analysis are interesting, it is hard to determine their broader significance for classification within the Olenelloidea. Moreover, based on phylogenetic analysis of the Olenelloidea in Lieberman (1998), *M. hyperborea* is distantly related to *Holmia* and *Elliptocephala,* and the close relationship of *M. hyperborea* to *H. kjerulfi* or *E. mirabilis* suggested by Poulsen (1974) cannot be accepted at this time.

Differences between *M. hyperborea* and *H. kjerulfi* include (the asterisk denotes genus-level apomorphy of *Mesolenellus*): in *M. hyperborea* the anterior cephalic border near but not directly anterior of L4 has a length (exsag.) less than half the length of L0 (sag.), in *H. kjerulfi* it is equal to the length of L0; in *M. hyperborea* the anterior cephalic border is prominently separated from the extraocular area by a furrow, and in *H. kjerulfi* it is not; in *M. hyperborea** L4 does not contact the anterior border furrow, in *H. kjerulfi* it does; in *M. hyperborea* L4 does not expand prominently dorsally, in *H. kjerulfi* it does; in *M. hyperborea* the lateral margins of L4 are proximal to the lateral margins of L0, in *H. kjerulfi* they are distal; in *M. hyperborea* the posterior margins of L4 are subparallel, in *H. kjerulfi* they are divergent anteriorly; in *M. hyperborea* the ocular lobes are flattened in transverse profile, in *H. kjerulfi* they are convex; in *M. hyperborea* S3 is not conjoined medially, in *H. kjerulfi* it is; in *M. hyperborea* a line between the ends of S2 is directed inward and posteriorly at a roughly 45 degree angle relative to a transverse line, in *H. kjerulfi* such a line parallels a transverse line; in *M. hyperborea* L2 and L3 merge distally, in *H. kjerulfi* they do not; in *M. hyperborea* S2 is straight, in *H. kjerulfi* it is convex anteriorly; in *M. hyperborea* the distal sector of S0 is straight, in *H. kjerulfi* it is convex anteriorly; in *M. hyperborea* S0 is conjoined medially, in *H. kjerulfi* it is not; in *M. hyperborea* the posterior margin of L0 is roughly transverse, in *H. kjerulfi* it is convex posteriorly; in *M. hyperborea* the extraocular area is flattened, in *H. kjerulfi* it is prominently vaulted; in *M. hyperborea* the genal spine near where it hits the cephalic border is directed posterolaterally at a roughly 30 to 35 degree angle relative to a sagittal line, in *H. kjerulfi* it is directed posterolaterally at a roughly 10 to 20 degree angle; in *M. hyperborea** the genal spine is relatively much longer (exsag.) than it is in *H. kjerulfi*; in *M. hyperborea* the genal spine angle is further anterior than it is in *H. kjerulfi*; in *M. hyperborea* the intergenal spine is represented by a distinct dorsal swelling or node, in *H. kjerulfi* it is a small pointed spine; in *M. hyperborea* the posterior border between the intergenal angle and L0 is transverse, in *H. kjerulfi* it flexes posteriorly; in *M. hyperborea* T3 (third thoracic segment) is macropleural, in *H. kjerulfi* it is not; in *M. hyperborea** the anterior and posterior margins of the thoracic pleural furrow on the third segment proceeding from the proximal to distal edge parallels a transverse line before flexing strongly posteriorly, while in *H. kjerulfi* they are directed weakly posteriorly before flexing more strongly posteriorly; in *M. hyperborea** the pleural spines on segments 5 to 8 are relatively much longer (exsag.) and broader (tr.) than they are in *H. kjerulfi*; in *M. hyperborea* the prothoracic axial rings lack lateral furrows, whereas they have two prominent anterolateral lobes in *H. kjerulfi*; in *M. hyperborea* the thoracic pleural furrows extend onto the spines, in *H. kjerulfi* they do not; in *M. hyperborea* the boundary between the thoracic pleural furrow and the anterior band is sharp, in *H. kjerulfi* it is gradational; and the axial spine on T15 is relatively much longer (sag.) in *M. hyperborea* than it is in *H. kjerulfi.* Many of these character states are present in other olenelloids, but the extensive differences between the two species suggests that assignment of *M. hyperborea* to *Holmia* is untenable.

Material examined: MGUH 13008, the holotype, 13011, 13017, 13020, 13021, 13945.

Occurrence: Denmark, Greenland: the upper part of the Buen Formation, above Brillesø, 1.5 km E of Børglum Elv, Peary Land, northeastern end of the island, treated as in the "*Nevadella*" zone by Palmer and Peel (1979), and in the lower middle *Olenellus* zone by Palmer and Repina (1993).

MESOLENELLUS SVALBARDENSIS (KIELAN 1960)

Olenellus svalbardensis; Kielan 1960:84, pl. 1, figs. 1–3, pl. 2, figs. 2, 4, 5, non 1, 3, pl. 3, figs. 2, 3, 5, non 1, 4, pl. 4, figs. 1, 2.

Olenellus cf. *svalbardensis;* Kielan 1960; Poulsen 1974:82, pl. 1, figs. 1–3.

Types: Holotype, Laboratory of Geology, Polish Academy of Sciences, Cracow, Sv-I/14, see Kielan (1960).

Diagnosis: Plectrum present; medial part of intergenal angle arches anteriorly at point midway between distal tip of ocular lobe and genal spine angle; S2 does not contact axial furrows; medial part of cephalic posterior border flexes posteriorly; genal spine angle developed opposite medial part of distal margin of L0; length (exsag.) of medial part of thoracic pleural furrows approximately 1.5 times length (exsag.) posterior pleural band.

Description: Length (exsag.) of anterior cephalic border length at point between lateral margin of L4 and genal spine angle equal to 75% length (exsag.) L2 at distal tip; anterior cephalic border declined at 45 degree angle relative to dorsal plane, before becoming dorsally flattened in region of anterior border furrow; plectrum present; frontal lobe does not contact anterior border furrow; anterior margin of frontal lobe roughly transverse; lateral margins of frontal lobe deflected as far laterally as lateral margins of L0; lateral margins of glabella opposite margin of L2 are subparallel; glabellar furrows faintly incised; S2 transverse, medial edge declined posteriorly, not conjoined medially; L2 and L3 typically merge distally; line from posterior edge of ocular lobe to junction of posterior margin of lobe with glabella roughly forms 10 degree angle relative to sagittal line; S0 transverse, S1 convex anteriorly, both contact axial furrows, with medial edges declined posteriorly; lateral margins of glabella subparallel between L0 and point midway forward on distal tip of L1; posterior edge of ocular lobe opposite medial part of distal tip of S0; S1 conjoined medially; lateral lobes present on L0; posterior margin of L0 weakly convex posteriorly, with faint axial node; genal spines developed as long projections, length (exsag.) of 8 to 10 thoracic segments (sag.), sweeping backward at roughly 20 degree angle relative to sagittal line; genal spine angle opposite medial part of distal margin of L0; intergenal angle prominently developed, without spine, inclined at 30 to 35 degree angle relative to transverse line; extraocular region width (tr.) approximately 40% to 50% width between distal-most tips of ocular lobes; prominent anastomosing ridges visible on extraocular region; faint intergenal and genal ridges visible; posterior margin of cephalic posterior border between L0 and intergenal angle flexing posterolaterally.

Thorax divided into pro- and opisthothorax; faint axial nodes present on medial part of thoracic axial rings; axial rings at fourth segment 30% width (tr.) of pleural field, excluding spines; spines of T3 macropleural, extend as far posteriorly as T6 to T8; medially, anterior margin of T3 parallels transverse line; spines of T3 deflected posteriorly at roughly 30 degree angle relative to sagittal line; anterior margin of pleural furrow of T3 parallels transverse line before flexing posterolaterally; posterior margin of pleural furrow of T3 parallels transverse line before flexing posterolaterally; anterior margins of thoracic pleural furrows prominently separated from anterior band by distinct change in slope; thoracic pleural furrows extend onto spines; thoracic pleural spines behind T4 extend three to four thoracic segments back, lie in roughly same dorso-ventral plane as pleural segments; prominent spine on axial ring of T15, length (sag.) approximately equal length of entire thorax.

Pygidium not sufficiently preserved.

Discussion: Kielan (1960) figured a series of specimens from the Slakli Series of West Spitsbergen that she assigned to *Olenellus svalbardensis.* Her sample appears to contain two distinct morphotypes. One of these, which includes the specimen she designated the holotype of the species, is characterized by the following features: the anterior cephalic border is declined at a 45 degree angle relative to a dorsal plane before becoming dorsally flattened in the region of the anterior border furrow; anterolateral margins of the frontal lobe are directed posteriorly at a roughly 10 degree angle relative to a transverse line; the lateral margins of L4 are deflected as far laterally as the lateral margins of L0; the sides of the glabella opposite L2 and L3 are subparallel; lateral lobes are present on L0; the posterior margins of the ocular lobes extend back to the medial part of L0; and the posterior border of the cephalon parallels a transverse line medially and then distal of a point midway between the distal tip of the ocular lobe and the genal spine it flexes anteriorly such that the intergenal angle forms a roughly 30 to 35 degree angle with a transverse line.

The second morphotype is characterized by the following morphology: the anterior cephalic border, when proceeding anteriorly, elevates from the anterior border furrow at a 90 degree angle relative to a dorsal plane, then is dorsally flattened; the anterolateral margins of the frontal lobe are directed posterolaterally at a roughly 40 degree angle relative to a transverse line; the lateral margins of L4 are distal to the lateral margins of L0; the lateral margins of the glabella opposite L2 are deflected laterally such that the width (tr.) of the glabella expands, opposite L3 they are deflected medially such that the width (tr.) of the glabella contracts; lateral lobes are absent from L0; the posterior margins of the ocular lobes extend back to S0; and the posterior border of the cephalon parallels a transverse line before weakly curving anteriorly distally.

The second morphotype, which does not include the holotype of Kielan's (1960) species, may represent a new species of *Olenellus,* based on the state of some of its characters, including: the anterior margins of the frontal lobe are directed posteriorly at a roughly 40 degree angle relative to a transverse line; the posterior edge of the ocular lobe extends back to the medial part of the distal margin of L0; the lateral margins of L4 are distal to the lateral margins of L0; the ocular lobes smoothly merge with the extraocular area; the anterolateral margins of the frontal lobe of the glabella are not prominently separated from the extraocular area; the surface of the interocular area is developed as a flattened shelf; the cephalic posterior border flexes weakly posterolaterally between L0 and the intergenal angle; L2 and L3 merge laterally; the anterior cephalic border is developed as a narrow flattened ridge; the lateral margins of the glabella bulge laterally at L2; the genal spine angle is opposite L0; there is an axial node on L0; the posterior margin of L0 is relatively transverse.

This taxonomic assignment will remain tentative until all the material for this species can be considered in greater detail.

The other morphotype within Kielan's (1960) *O. svalbardensis,* which includes the holotype, represents a species of *Mesolenellus,* based on its possession of the characters diagnostic for the Mesonacinae and *Mesolenellus* elucidated in this analysis and recovered from Lieberman (1998). In addition, the phylogenetic analysis of the Mesonacinae conducted here suggests that this species is sister to *Mesolenellus hyperborea,* so it is henceforth treated as a species of *Mesolenellus.*

Kielan (1960) originally suggested that this species was closely related to *Fritzolenellus truemani* (Walcott 1913). As mentioned above, Kielan's (1960) species consisted of two distinct taxa. The one treated as *Mesolenellus svalbardensis* is distantly related to *Fritzolenellus,* based on phylogenetic topology within the Olenelloidea from Lieberman (1998), and any similarities between the two taxa must be viewed as primitive retentions or convergences (see Lieberman [1998] for character evidence separating *Fritzolenellus* from *Mesolenellus*). One of the few characters that both *M. hyperborea* and *F. truemani* share in common is the presence of lateral lobes on L0. The other specimens of Kielan's (1960) that are referable to *Olenellus* do appear to match the diagnostic characters of the genus *Olenellus* rather than *Fritzolenellus,* as mentioned above.

Most of the specimens that belong to *M. svalbardensis* have faintly incised glabellar furrows, but the holotype and another specimen illustrated in Kielan (1960) do show faint traces of the glabellar furrows. Thus, these specimens were used for the purpose of coding the characters that describe the glabellar furrows.

Poulsen (1974:82, pl. 1, figs. 1–3) figured specimens from the Schley Fjord Formation, Peary Land, in eastern North Greenland, which he referred to as *O.* cf. *svalbardensis.* The specimens illustrated appear similar if not conspecific with Kielan's (1960) *O. svalbardensis,* and are provisionally assigned here to that species. One possible difference between the Greenland and Spitsbergen material is that, in the specimens Poulsen (1974) illustrated, the lateral margins of the glabella appear to be diverging somewhat more strongly anteriorly than they do in the Spitsbergen material. Knoll and Swett (1987) and Knoll et al. (1989) commented on the close relationship between faunas in Spitsbergen and Greenland, and thus it is not surprising that some species might be distributed in both regions.

Occurrence: Norway: Spitsbergen, the lower part of the Slakli Series, Sofiekammen Formation, on the northern side of Hornsund, West Spitsbergen, co-occurring with a probable specimen of *Nevadella* Raw 1936, though this requires further analysis. This species either occurs in the *Olenellus* zone or the "*Nevadella*" zone, congruent with the first appearance of *M. hyperborea.*

GENUS *MESONACIS* WALCOTT 1885

Type species: *Olenus vermontanus* Hall 1859.

Assigned taxa: *Olenellus fremonti* Walcott 1910; *O. bonnensis* Resser and Howell 1938; *O. eagerensis* Best 1952; *O. hamoculus* Cowie and McNamara 1978; *O. cylindricus* Palmer in Palmer and Halley 1979.

Diagnosis: Anterolateral margins of frontal lobe of glabella not prominently separated from extraocular area by furrow; posterior margins of frontal lobe expanding where ocular lobes intersect with it; anterior portions of posterior margins of ocular lobes opposite medial part of distal margins of L1; posterodistal margins of L3 formed by ocular lobes; length (exsag.) of genal spine less than or equal to length (sag.) of first four thoracic segments; lateral lobes absent from L0; intergenal angle forms 30 to 50 degree angle with transverse line; lateral margins of each prosomal thoracic axial ring converging when proceeding from anterior to posterior edges; field of thoracic pleural furrows at medial portion long (exsag.), equal to approximately 1.3 times length of posterior pleural band; anterior margin of T3 medially flexes anteriorly; posterior margin of thoracic pleural furrow on T3 directed evenly posteriorly laterally; width (tr.) of thoracic axis 100% width of pleural field excluding spines.

Discussion: This genus is distributed throughout Laurentia, from the Great Basin to Vermont, Newfoundland and Scotland, in strata of the *Olenellus* zone. As discussed above under the heading Mesonacinae, there is strong character evidence to support a separation of the genus *Mesonacis* (as well as *Mesolenellus*) from the genus *Olenellus,* including what was formerly referred to as *O.* (*Paedeumias*), and here it is treated as distinct. Character differences between the genus *Mesonacis* and *Olenellus* include: 1. in *Mesonacis* the transverse profile of the ocular lobes is convex dorsally, whereas it is flattened dorsally in *Olenellus*; 2. in *Mesonacis* the posterior tips of the ocular lobes are developed opposite the medial part of the distal margin of L1, in *Olenellus* they are developed opposite the medial part of the distal margin of L0; 3. in *Mesonacis* a line from the posterior tip of the ocular lobe to the junction of the posterior margin of the lobe with the glabella forms a 15 to 20 degree angle with a sagittal line (except in *M. fremonti*), whereas in *Olenellus* it forms a 0 to 5 degree angle; 4. in *Mesonacis* the intergenal angle is directed anteriorly at least 30 degrees relative to a transverse line, whereas in *Olenellus* it is directed anteriorly about 10 degrees; 5. in *Mesonacis* the thoracic pleural spines on all segments but the third are narrow (tr.), roughly one quarter of the length (exsag.) of the corresponding pleural segment at its medial part between the spine and axis (except in *M. fremonti*), whereas in *Olenellus* they are relatively broader, about half the width of the corresponding pleural segment at its medial part between the spine and axis; 6. in *Mesonacis* the width (tr.) of the axis is 100% to 105% the width of T3, excluding the spine, while in *Olenellus* it is 60% to 70%; 7. and in *Mesonacis* the base of the spine on T15 is narrow (tr.), less than half the width of the axis (except in *M. fremonti*), whereas in *Olenellus* it is equal to the width of the axis.

It is clear from this character list that species of *Mesonacis* can now be clearly distinguished from specimens of *Olenellus.* The only species that shows any variability in the development of characters typical of *Mesonacis* is *M. fremonti.* This is not surprising, as this species is a near basal member of the *Mesonacis* clade (obviously the causal relationship is uncertain here because the relationships among species of *Mesonacis* were at least partly determined by reference to the characters given above). Thus, the contention of Resser and Howell (1938), Harrington et al. (1959), Whittington (1989) and Palmer and Repina (1993) that species of *Mesonacis* cannot clearly be distinguished from species of *Olenellus* no longer appears valid.

Resser (1928) described *Mesonacis bristolensis.* Harrington (1956) made this species the type of his genus *Bristolia.* There are many character differences between *Mesonacis* and *Bristolia,* elucidated below under the latter genus, and it is clear that *B. bristolensis* can no longer be assigned to *Mesonacis.*

Best (1952) illustrated the species *O. schofieldi* Best 1952, which bears some similarity to species of *Mesonacis.* However, it lacks the diagnostic characteristics of that genus that differentiate it from members of the genus *Olenellus,* and at this time it is excluded from *Mesonacis.* In particular, in *O. schofieldi* the intergenal angle deflects anteriorly at a 10 to 15 degree angle relative to a transverse line; a line from the posterior tip of the ocular lobe to the junction of the posterior margin of the lobe with the glabella forms a 0 to 5 degree angle with a sagittal line; the ocular lobe is dorsally flattened; and the width (tr.) of the thoracic axis on the third segment is 60% to 70% of the width of the third pleural segment, excluding the spine. The position of the posterior tips of the ocular lobes in *O. schofieldi* is variably developed. In some specimens, including the holotype, they extend back to S0, is more typical of *Olenellus.* However, in one small, incomplete specimen

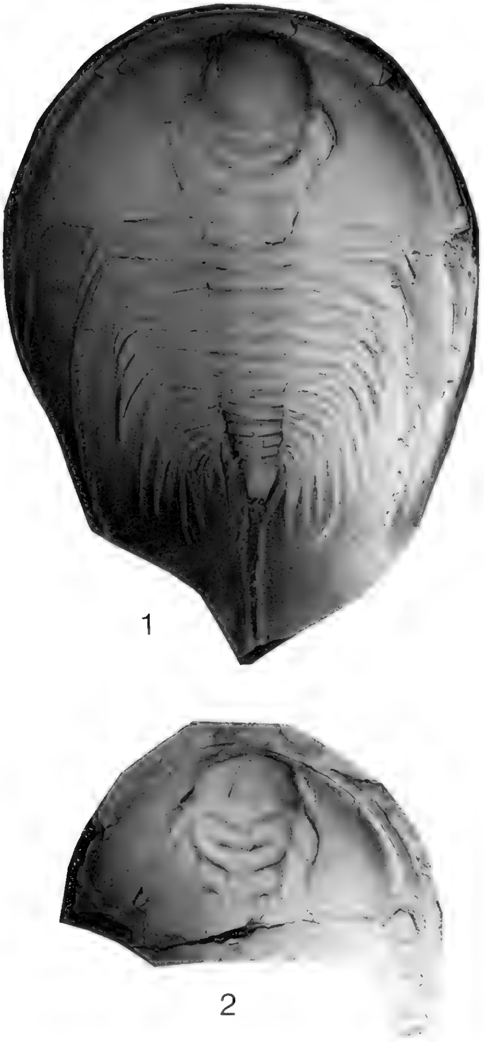

Figure 8.
1, 2. *Mesonacis fremonti* (Walcott), Latham Shale, San Bernardino Co., California. 1. S end of Marble Mtns., near Cadiz (loc. 3376, LACMIP), LACMIP 34973, ×0.8. locality is the same as Figure 3.4, UCR 10, ×0.9.

(Best 1952, pl. 1, fig. 4) they may extend back only to the medial part of the distal margin of L1, which is typical of *Mesonacis.* Because this specimen is poorly preserved, and represents a small individual, the ocular lobes are treated as extending back to S0, but it is important to mention that there is some potential variation here. The thoracic pleural spines are too poorly preserved in *O. schofieldi* to determine whether or not their condition matches that typically found in species of *Mesonacis.* On the basis of these character differences *O. schofieldi* must be excluded from the genus *Mesonacis,* and instead probably belongs within the genus *Olenellus.* It will be treated in greater detail in the analysis of the genus *Olenellus* being undertaken.

Some specimens of *Mesonacis* (e.g., *M. bonnensis* and *M. eagerensis*) have a raised transverse line that extends from the interocular area to the posterior cephalic border. This character was assumed to have little phylogenetic significance, and was instead treated as reflecting some taphonomic factor.

MESONACIS VERMONTANUS (HALL 1859)

Olenellus vermontanus (Hall); Resser and Howell 1938:220, pl. 4, figs. 15, 16; Shaw 1955:793, pl. 75, fig. 10 (see for more complete synonymy); Whittington 1989:120, figs. 14, 16, 18.
Olenellus (*Mesonacis*) *vermontanus* (Hall); Palmer and Repina 1993:22, fig. 3.2; Palmer and Repina 1997:408, fig. 255.2.
Mesonacis vermontanus (Hall); Lieberman 1998:67.
Olenellus georgiensis; Resser and Howell 1938:220, pl. 5, fig. 7, non fig. 6.

Types: Hall's (1859) original type of the species, AMNH 230, was reported lost by Resser and Howell (1938) and Whittington (1989). Thorough additional examination of the collections of the AMNH failed to produce the specimen. Therefore, a new type is needed. Walcott specimen from the type locality (1910, pl. 26, fig. 3), also illustrated by Resser and Howell (1938, pl. 4, fig. 16), is complete and beautifully preserved. That specimen, USNM 15399a, is designated the **neotype** of the species. Resser and Howell (1938) referred to this specimen as a plesiotype.
Material examined: MCZ 2434, and possibly 108662, which is incompletely preserved.
Discussion: The holotype of *Olenellus georgiensis* Resser and Howell bears strong similarity to *M. vermontanus* and, although deformed, appears to be morphologically indistinguishable from that species, as Shaw (1955) recognized. Henceforth it is treated as a junior subjective synonym of *M. vermontanus*. However, the specimen illustrated as *O. georgiensis* (Resser and Howell 1938, pl. 5, fig. 6) is not conspecific with *M. vermontanus* and instead appears to be a specimen of *O. thompsoni* (Hall). In particular, the pleural spines of T3, and the other thoracic pleural spines, are much longer than those in *M. vermontanus* and match the condition found in *O. thompsoni*. Further characters indicating that this specimen belongs to *O. thompsoni* rather than *M. vermontanus* include: the ocular lobes extend back to the medial part of the distal margin of L0 rather than the medial part of the distal margin of L1; the intergenal angle forms approximately a 0 to 10 degree angle with a transverse line, rather than a 30 to 35 degree angle; the extraocular area is relatively broad; and the lateral margins of the glabella between the posterior margin of L0 and the distal tip of S1 converge.
Occurrence: Vermont: Parker Slate, Parker's Quarry, Georgia, middle upper *Olenellus* zone, according to Palmer and Repina (1993).

MESONACIS FREMONTI (WALCOTT 1910)
Figures 8.1, 8.2, 9.1

Olenellus fremonti; Walcott 1910:320, pl. 37, figs. 1, 2; Riccio 1952:30, pl. 7, fig. 6; Mount 1976:176, fig. 7; Palmer in Palmer and Halley 1979:70, pl. 3, figs. 14–17; Mount 1980:22, fig. 7.
Olenellus (*Fremontia*) *fremonti* Walcott; Lochman in Cooper et al. 1952:91, pl. 18, figs. 4, 5.
Mesonacis fremonti (Walcott); Resser 1928:6, pl. 1, figs. 3–9, pl. 2, fig. 9, pl. 3, fig. 8.
Fremontia fremonti (Walcott); Harrington 1956:57, text fig. 1b, non pl. 15, fig. 6.
Fremontia sp.; Nelson 1976:31, pl. 8 (left side of plate).

Types: Lectotype, USNM 56819a. Walcott (1910) figured and assigned several specimens to his new species *O. fremonti* and gave as the type locality for this species his locality 52, Prospect Peak, Eureka District, Nevada. Resser (1928) excluded all but one of the specimens from Walcott's (1910) type locality from his *M. fremonti* (Walcott 1910, pl. 37, fig. 2). None of the other specimens from Walcott's (1910) locality 52 were assigned to any other species by Resser (1928), nor were grounds for removing these specimens from *fremonti* given. Subsequently Harrington (1956) designated USNM 56819a as lectotype for the species. (Lochman in Cooper et al. 1952 suggested that this specimen could potentially be the type for the species.) This was necessary to insure taxonomic stability. Conceivably, any one of the specimens from the type locality not treated as new taxa and described, or lumped with previously described taxa, could serve as the type specimen of *M. fremonti.* Harrington (1956) gave good grounds for the designation of his lectotype and provided justification for excluding most of Walcott's (1910) other specimens of *fremonti* from that species. Unfortunately, the specimen he chose to illustrate as representative of *Fremontia fremonti,* USNM 56819n (Walcott 1910, pl. 37, fig. 18) from the type locality of *fremonti,* is actually a species of *Bristolia,* closely related or perhaps conspecific to *B. fragilis* Palmer (Palmer and Halley [1979]) (see the discussion of characters separating *Bristolia* from *Mesonacis* under the genus *Bristolia,* below). Palmer, in Palmer and Halley (1979), for some unspecified reason ignored Harrington's (1956) lectotype designation and mistakenly asserted that Resser (1928), by removing all but one of the specimens from the type locality from his *M. fremonti,* had automatically designated that specimen (Walcott 1910, pl. 37, fig. 2; USNM 56819a) the holotype of the species. This is incorrect, as there were several specimens from the type locality whose taxonomic affinities had not been established. In addition, Resser (1928) had designated no type specimen. Harrington's (1956) definition serves as the establishment of the lectotype of the species. If Resser (1928) had designated that specimen as a type, he would have validly designated a lectotype for *O. fremonti.*

Discussion: Raw (1936) treated *O. fremonti* as the type of the genus *Fremontia* Raw 1936, and Harrington (1956) elaborated on this. It is conceivable that *Fremontia* could remain a valid genus; however, there are several arguments against this. First, based on phylogenetic topology within the genus *Mesonacis* (Figure 7), the type of the genus *Mesonacis, M. vermontanus,* is nested within a clade that is sister to *M. fremonti.* If *M. fremonti* were to be treated as part of *Fremontia,* then either *M. bonnensis* would have to be assigned to a paraphyletic "*Fremontia,*" or it would need to be treated as a monotypic genus. This of course assumes that it is desirable for the genus *Mesonacis* to remain a valid taxonomic concept, that is, monophyletic. Establishing evolutionary patterns within the genus *Mesonacis* was one of the goals of this analysis, and thus it is essential that *Mesonacis* be monophyletic. In order to avoid naming new monotypic genera, for purposes of taxonomic stability and to avoid establishing paraphyletic genera, *M. fremonti* is lumped within the rest of the genus *Mesonacis.* It is conceivable that the genus *Mesonacis* could be lumped within a *Fremontia* that included *F. fremonti.* However, since *Mesonacis* is a more established name, has precedence and is most frequently used in the literature, it seems preferable to retain that name rather than *Fremontia.*

In the phylogeny of the genus *Mesonacis, M. fremonti* maps as a near basal species within that genus, and characters separating the other species of *Mesonacis* from this species can be seen in Figure 7, and in Tables 3 and 4. Not surprisingly, primitive retentions found in *M. fremonti* are also common to species of *Olenellus.* Some of these include the relatively broad (tr.) extraocular area; the absence of pleurae of the opisthothorax in *M. fremonti* (admittedly indeterminate in some species of *Mesonacis*); and the relatively long (sag.) axial spine on the 15th segment, which is also quite broad (tr.) near the axis.

Lochman in Cooper et al. (1952) figured a few specimens that she assigned to *Olenellus (Fremontia) fremonti.* One of these (Cooper et al. 1952, pl. 18, fig. 5,) is poorly preserved but appears to possess the diagnostic characters of the species, and is thus here provisionally assigned to *M. fremonti.* Some of the specimens Palmer and Halley (1979) figured as *M. fremonti* are extremely deformed, but appear to bear the diagnostic characteristics of the species and are treated as members of *M. fremonti.*

This species shows some variation in the condition of the posterior cephalic border between L0 and the intergenal angle. In some specimens it is transverse, and in others it is weakly deflecting posteriorly.

Material examined: LACMIP 4908–18, 5870 and 34973 (and large numbers of unnumbered specimens in the general stratigraphic collections); SDSNH 168383, 16874, 16954, 16955, 16974, 19099, 20709 (8 specimens), 20806 (2 specimens), 26220; UCR 10/2004 and a large number of unnumbered specimens in the general stratigraphic and taxonomic collections assigned to lots 10, 7270 and 7271; MCZ 2544, 2545, 7370; USNM 56819i.

Occurrence: California: In the middle part of the Latham Shale, southern end of the Marble Mountains, E slope of hill 1440, 834 ft E and 1999 ft N of the SW corner sec 12, T 5 N, R 14 E, and in the Latham Shale, 190 m W of the limestone quarry, 0.5 mi E of Cadiz, in the Mojave Desert portion of San Bernardino County, possibly equivalent to Hazzard's (1933) locality M-5, treated as in the *Bristolia* zonule, upper *Olenellus* zone; from the upper Poleta and lower Harkless Formations, lower *Olenellus* zone, and the Mule Spring Limestone, upper *Olenellus* zone, White/Inyo Mountains region (Nelson 1976); the Pyramid Shale Member, Carrara Formation, *Olenellus* zone, Funeral Mountains, Resting Springs Range, and Salt Spring Hills, White/Inyo Mountains region (Palmer and Halley 1979). Nevada: In arenaceous shales at the summit of Prospect Mountain, Eureka County.

MESONACIS BONNENSIS (RESSER AND HOWELL 1938)

Olenellus bonnensis; Resser and Howell 1938:222, pl. 7, fig. 3.
Olenellus terranovicus; Resser and Howell 1938:222, pl. 6, fig. 8.
Olenellus brevoculus; Resser and Howell 1938:225, pl. 8, figs. 18, 19; Best 1952:19.

Types: Holotype, USNM 90808, see Resser and Howell (1938).

Discussion: The three separate species that Resser and Howell (1938) figured and described are identical and come from the same locality. Thus, they are treated as belonging to the same species. The name of the species, based on the best preserved material, is retained.

Occurrence: Canada: Newfoundland, Forteau Formation, *Olenellus* zone, E shore of East Arm, Bonne Bay, west coast of Newfoundland.

MESONACIS EAGERENSIS (BEST 1952)

Olenellus eagerensis; Best 1952:19, pl. 1, figs. 5–9.
?*Olenellus eagerensis*; Best 1952:19, pl. 1, figs. 10–12.

Types: Holotype, University of British Columbia GT 101, see Best (1952).

Discussion: Some of the specimens illustrated by Best (1952, pl. 1, figs. 6, 8) appear to be somewhat deformed and crushed sagittally, causing L4 to appear relatively shorter (sag.) than it should. However, the holotype and the other figured specimens of this species have the characteristic long (sag.) L4, circa 1.5 times the length of L0 and L1. Best (1952, pl. 1, figs. 11, 12) figured two specimens that he claimed were closely related varieties of *O. eagerensis.* These specimens have a more dorsally expanded L4, a narrower extraocular area and a genal spine angle further anterior than what is found in the holotype and the

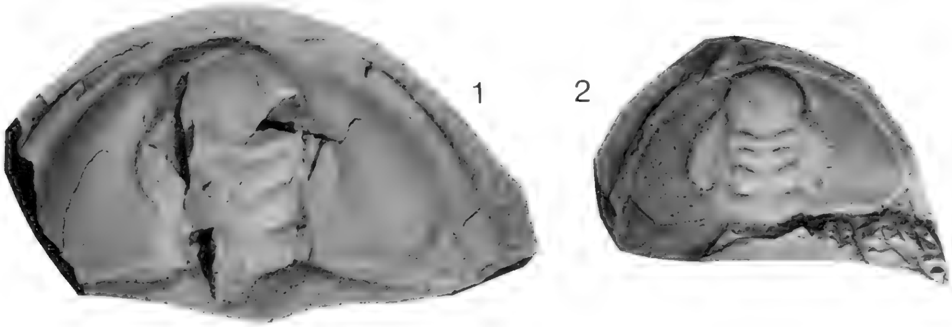

Figure 9.
Mesonacis spp. **1.** *Mesonacis fremonti* (Walcott), Pioche Fm., Prospect Mt., Eureka District, Nevada, USNM 56819i, ×1.5. **2.** *Mesonacis cylindricus* (Palmer in Palmer and Halley 1979), 10 to 10.5 ft above base of Latham Shale, in small NE trending gully on E side of hill 1440 in S end of Marble Mtns., 834 ft. E and 1,999 ft N of SW corner sec 12, T 5 N, R 14 E, San Bernardino Co., California, UCR 7897, ×1.4.

paratypes of the adult specimens of *M. eagerensis.* These specimens appear to be highly deformed and it is hard to determine if they are truly different from *M. eagerensis.* At this time they are questionably assigned to *M. eagerensis.* Similarly, Best (1952, pl. 1, fig. 9) illustrated a small cephalon that shows some morphological similarity to *M. eagerensis,* but may also be similar to the specimens in Best (1952, pl. 1, figs. 10–12) in having a narrow extraocular area and an expanded L4. Again, it is questionably assigned to *M. eagerensis.*
Occurrence: Canada: British Columbia, the Eager Formation, the *Olenellus* zone, just S of the Fort Steele-St. Eugene Mission road, 6 mi NE of Cranbrook.

MESONACIS HAMOCULUS (COWIE AND MCNAMARA 1978)

Olenellus hamoculus; Cowie and McNamara 1978:627, pl. 70, figs. 3–9; McNamara 1978:641, text figs. 4e, f.
Olenellus (*Angustolenellus*) *hamoculus*; Palmer and Repina 1993:22, fig. 3.6.

Types: Holotype, BGS 13302, see Cowie and McNamara (1978).
Discussion: Cowie and McNamara (1978) placed this species in the genus *Olenellus* and considered it closely related to *O. lapworthi* Peach and Horne 1892, *O. reticulatus* Peach 1894, *O. intermedius* Peach 1894 and *Olenelloides armatus* Peach 1894. What Cowie and McNamara (1978) and McNamara (1978) referred to as *Olenellus reticulatus* and *O. lapworthi,* two species from the middle *Olenellus* zone of northwest Scotland, actually appear to belong to the genus *Fritzolenellus* and appear to bear all the diagnostic characters of that genus (see the discussion below under the genus *Fritzolenellus*). *Fritzolenellus* is distantly related to *Mesonacis,* based on the phylogenetic analysis conducted in Lieberman (1998), and thus the contention of Cowie and McNamara (1978) that *M. hamoculus* is closely related to either *F. reticulatus* or *F. lapworthi* must be strongly questioned. Because these Scottish taxa comprise distantly related species that happen to co-occur in rocks of similar age from the same region, the paedomorphic and evolutionary pathway that McNamara (1978) saw connecting these species, as well as *Olenelloides armatus,* cannot be accepted. Similar ages and geographic distributions are not generally accepted as a means of establishing hypotheses of evolutionary relationship. *Olenellus intermedius* Peach was also

placed into the paedomorphic evolutionary pathway with *F. reticulatus, F. lapworthi* and *M. hamoculus* by McNamara (1978). *Olenellus intermedius* is known from two poorly preserved specimens, both early ontogenetic stages; however, these appear to be conspecific with, or belong to, a species closely related to either *F. reticulatus* or *F. lapworthi.* This species is discussed in greater detail under the genus *Fritzolenellus,* below.

Species of *Mesonacis* and *Fritzolenellus* can be distinguished by the following characters: in *Mesonacis* L4 does not expand prominently dorsally, in *Fritzolenellus* it does; in *Mesonacis* the anterolateral margins of the ocular lobes smoothly merge with the extraocular area, in *Fritzolenellus* the anterolateral margins of the ocular lobes are separated from the extraocular area by a furrow; in *Mesonacis* the interocular area is developed as a flattened shelf, in *Fritzolenellus* it is arched; in *Mesonacis* the lateral lobes on L0 are absent, in *Fritzolenellus* they are present (this character is not clearly visible in *F. reticulatus* or *F. lapworthi* as these species are poorly preserved); in *Mesonacis* the intergenal angle is directed anteriorly at least 30 degrees relative to a transverse line, in *Fritzolenellus* it is directed anteriorly only 0 to 10 degrees; in *Mesonacis* the anterior margin of the third thoracic pleural segment is directed anteriorly before flexing posterolaterally, in *Fritzolenellus* it parallels a transverse line; in *Mesonacis* the anterior margin of the thoracic pleural furrow on T3, when proceeding from the proximal to the distal edge, parallels a transverse line, before flexing posterolaterally, while in *Fritzolenellus* it flexes weakly posterolaterally; in *Mesonacis* the length (exsag.) of the thoracic pleural furrows (excluding T3) at the medial part of the segment are equal to 1.5 times the length of the posterior band of the pleural segment, in and *Fritzolenellus* their length is less than or equal to the length of the posterior pleural band; and in *Mesonacis* the base of the spine on the 15th thoracic segment is less than half the width (tr.) of the axis of the segment (except in *M. fremonti*), whereas in *Fritzolenellus* it is nearly as wide (tr.) as the axis of the segment.

Palmer and Repina (1993) made *M. hamoculus* the type of their new subgenus *Olenellus* (*Angustolenellus*), but *M. hamoculus* is nested within a clade of several species assigned to the genus *Mesonacis.* The name *Angustolenellus* could be retained, but this would entail either erecting several new monotypic genera or establishing paraphyletic genera. This is not desirable, and hence *Angustolenellus* is relegated to a synonym of *Mesonacis.*

Material examined: BGS 13302, the holotype, and BGS 13298, a paratype.

Occurrence: Scotland: The "Fucoid" Beds, middle *Olenellus* zone according to Palmer and Repina (1993), from a roadside quarry 170 m E 10 degrees S of NE inlet of Loch Ae, Sutherland, NW Scotland.

MESONACIS CYLINDRICUS (PALMER IN PALMER AND HALLEY 1979)
Figure 9.2

Olenellus cylindricus; Palmer in Palmer and Halley 1979:69, pl. 2, figs. 9, 10, 13 non 14.

Types: Holotype, USNM 177197, see Palmer and Halley (1979).

Discussion: Palmer questionably assigned a specimen to this species (Palmer and Halley 1979, pl. 2, fig. 14) that differs in the condition of several character states from that found in *M. cylindricus.* In particular, this specimen lacks an advanced genal spine angle; has a transverse intergenal angle instead of forming an angle with a transverse line of roughly 50 degrees; has a faintly incised, transverse S2 that is not conjoined, does not contact the axial furrows and has the medial edges directed posteriorly, rather than a convex S2 that is conjoined medially, contacts the axial furrows and has the distal and medial edges as far forward; the cephalic posterior border is transverse between L0 and the intergenal angle rather than being directed posteriorly; and S0 and S1 are not conjoined, rather than being conjoined. On the basis of these character differences this specimen is excluded from *M. cylindricus.* It may instead be referable to *Wanneria humilis* Robison and Hintze 1972.

Material examined: UCR 7897.

Occurrence: California: Eagle Mountain Shale, Carrara Formation, the *Olenellus arcuatus* zonule, upper *Olenellus* zone, Grapevine Mountains, White/Inyo Mountains region, according to Palmer and Halley (1979); and 10 ft to 10.5 ft above base of Latham Shale, upper *Olenellus* zone, in small NE trending gully on E side of hill 1440 in S end of Marble Mountains, 834 ft E and 1999 ft N of SW corner sec 12, T 5 N, R 14 E, San Bernardino County.

• THREE •

Phylogenetic Analysis of *Elliptocephala*

The genus *Elliptocephala* is a moderately diverse clade within the Olenelloidea (see Palmer and Repina 1993; Lieberman 1998). Using the diagnostic characters of *Elliptocephala* recognized by a higher level phylogenetic analysis of the Olenelloidea given in Lieberman (1998), it was possible to recognize 11 previously described species and one new species from the Lower Cambrian *Olenellus* zone of Laurentia and the *Schmidtiellus mickwitzi* zone of Baltica that belong within that genus. Eleven of these species were subjected to a phylogenetic analysis to determine their relationships.

A total of 12 taxa was subjected to phylogenetic analysis, including 11 ingroup taxa. All available adequately preserved species within the genus were analyzed. Additional species possibly referable to *Elliptocephala* are discussed below. *Wanneria walcottana* was used as the outgroup taxon in phylogenetic analysis, based on phylogenetic topology within the Olenelloidea determined in Lieberman (1998). According to Lieberman (1998), *Elliptocephala* and *Wanneria* are very closely related, though not sister taxa, and fewer character differences separate *Wanneria* from *Elliptocephala* than separate *Elliptocephala* from any other taxon considered in Lieberman's (1998) analysis.

Evolutionary relationships within *Elliptocephala* were determined by parsimony analysis of 20 exoskeletal characters (Tables 5 and 6). Unfortunately, only cephalic characters could be used because of the dearth of thoracopygidia known for species of *Elliptocephala.* These data were subjected to an exhaustive search using PAUP v. 3.1.1. All characters were treated as unordered. Two most parsimonious trees of length 53 steps were recovered. These trees differed solely in the relative placement of *Elliptocephala parvifrons* (Fritz 1972) and *E. logani*, and a strict consensus of these two trees is shown in Figure 10. The retention index is 0.53 and the consistency index is 0.43. The g_1 statistic was –0.33. This value differs significantly ($p<0.05$) from values derived from distributions using random data (Hillis 1991) and suggests a strong and robust phylogenetic signal in the character data given in Table 6. Confidence values for the nodes of the consensus tree duplicated in the bootstrap analysis are given in Figure 10.

Thirty-six trees of length less than or equal to 54 steps were recovered before the analysis of Bremer (1994) was terminated because the consensus cladogram was a complete polytomy. Thus, the total support index (Bremer 1994) for the tree is very low.

Lieberman (1998) suggested that there might be some incongruence between phylogenetic position and stratigraphic occurrence, particularly centered around the phylogenetic placement of the genera *Elliptocephala, Wanneria* (assigned in Lieberman [1998] to the paraphyletic "Wanneriidae") and the Holmiidae. The latter comprises several genera, including *Holmia, Kjerulfia, Esmeraldina, Schmidtiellus* and *Holmiella,* relative to the Olenellidae. The Holmiidae in Lieberman (1998) are derived within the Olenelloidea relative to several taxa, including the Olenellidae, *Elliptocephala* and *Wanneria.* Past studies (e.g., Palmer and Repina 1993) have suggested that the Olenellidae do not appear until the subsequent *Olenellus* zone, with *Elliptocephala* and *Wanneria* not appearing until the lower

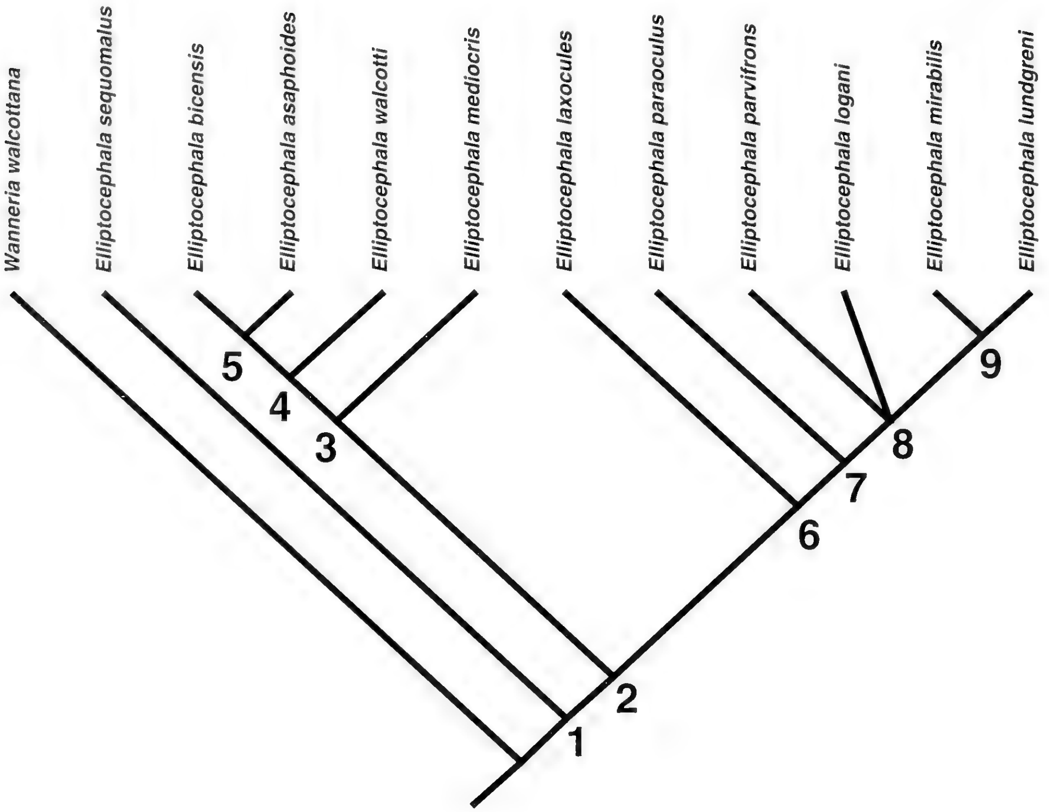

Figure 10.
A strict consensus of two most parsimonious trees of length 53 steps produced from analysis of character data in Table 6 with PAUP v. 3.1.1 (Swofford 1993). The cladogram is constructed using an exhaustive search. All characters were treated as unordered. The retention index is 0.53 and the consistency index is 0.43. The following nodes in the text were supported by the following bootstrap confidence values (see text for bootstrapping procedure used): Node *1* = 1.00; Node *2* = 0.37; Node *5* = 0.26; Node *6* = 0.13; Node *8* = 0.38; Node *9* = 0.50. Character states are placed at nodes, using MacClade v. 3.04 (Maddison and Maddison 1992), with the characters given in Table 5. The apomorphic state is given in parentheses. Brackets indicate equivocal character states that are ambiguous because of missing data, polymorphisms or multiple equally parsimonious resolutions. Equivocal characters are placed only at their basal phylogenetic position, and only unambiguous reversals are shown. Node *1*, 1(1), 3[0, 1], 5[0, 1], 9[0, 1, 2], 19(1); Node *2*, 9(1), 11(1), 14(1), 16(1); Node *3*, 3(0), 4(1), 10(1); Node *4*, 2(1), 5(1), 18(1), 19[0, 1]; Node *5*, 9(2), 14(0), 20(1); Node *6*, 3(1), 12(1), 15(1); Node *7*, 5(0), 13(1), 17(1); Node *8*, 2(1), 4(1), 8(1), 14[0, 1], 16[0, 1], 19(0); Node *9*, 1(0), 10(1), 14(0), 15(0), 16(1).

middle *Olenellus* zone; however, the holmiids appear early in the fossil record, in the "*Nevadella*" zone in Laurentia and in the *Schmidtiellus mickwitzi* through *H. kjerulfi* zones in Baltica. These studies were based on a rigid belief in the accuracy of the western Laurentian fossil record. However, based on character evidence (discussed below), *Elliptocephala lundgreni* (Moberg 1892) is clearly a member of the genus *Elliptocephala* and the species appears in the earliest part of the trilobitic fossil record in Baltica, in strata assigned to the *Schmidtiellus mickwitzi* zone (Ahlberg et al. 1986; Ahlberg 1991). Thus, the earliest members of the genus *Elliptocephala* appear at the same time in the fossil record as do species within the Holmiidae. This obviates most of the gap between stratigraphic first occurrence and phylogenetic position originally inherent in the phylogeny of the Olenelloidea presented in Lieberman (1998), and suggests that evolutionary position of genera within the Olenelloidea is actually nearly completely in accord with the relative ages of taxa, except for the Olenellidae.

Based on phylogenetic patterns within the genus *Elliptocephala* presented here, *E. lundgreni* is a derived member of the genus, indicating that the entire clade must have diversified by the *Schmidtiellus mickwitzi* zone, if not earlier. If the phylogeny in Figure 10 accurately reflects true evolutionary topology within the genus *Elliptocephala,* we must conclude that there is a substantial gap in the history of the genus *Elliptocephala* since more basal members of the clade first appear in the lower and middle *Olenellus* zone of Laurentia.

Systematic Paleontology

Superfamily Olenelloidea Walcott 1890
Family "Wanneriidae" Hupé 1953

Included Taxa

Genus *Wanneria* Walcott 1910

Type species: *Olenellus* (*Holmia*) *walcottanus* Wanner 1901
Assigned taxa: Monotypic.
Diagnosis: Length (exsag.) anterior cephalic border near but not directly anterior to frontal lobe equal to length (sag.) of L0; cephalic anterior border not prominently separated from extraocular area by furrow; frontal lobe of glabella contacts anterior border furrow; length of L4 (sag.) equal to length (sag.) of L0 and L1; posterolateral margins of L4 divergent anteriorly, distal to lateral margins of L0; anterodistal margins of L3 formed by ocular lobes; distal margin of L3 convex outward; S3 carat shaped, not conjoined medially; distal margins of L2 diverge anteriorly; posterior tips of ocular lobes developed opposite medial part of distal margin of L1; L0 with lateral lobes absent, node present; line between ends of S2 transverse; S0, S2 convex anteriorly; length (exsag.) of genal spine equal to length (sag.) of first four to five thoracic segments; intergenal spine faintly developed; intergenal angle developed posterior to point half way between ocular lobes and genal spine; anterior margin of thoracic pleural furrow on third segment parallels transverse line axially, abaxially flexes strongly posteriorly; thoracic pleural furrows extend only half width of inner pleural region; prominent spine of length (sag.) five thoracic segments present on 15th axial ring, width (tr.) of base of spine nearly as wide as axis of segment; length (sag.) of pygidium equal to width (tr.).

Wanneria walcottana (Wanner 1901)
Figures 11.1, 11.2

Wanneria walcottana (Wanner); Resser and Howell 1938:228, pl. 9, figs. 9, 10, pl. 10, figs. 8–10, pl. 11 (see for more complete synonymy); Harrington 1956:59, text fig. 1e; Harrington et al. 1959:O197, fig. 139; Whittington 1989:125, figs. 24, 30, 32, 33, 35–38; Palmer and Repina 1993:25, fig. 5; Palmer and Repina 1997:414, fig. 260; Lieberman 1998:67.

Types: Holotype, USNM 56807e, see Resser and Howell (1938) for elaboration.
Material examined: AMNH 24212, 24214, 24264, 24265; MCZ 2514, 2515; YPM 9295, 9296,

Table 5.
Description of characters and character states used in phylogenetic analysis of *Elliptocephala*; (0) represents the primitive state, (1) and (2) represent derived states.

	Primitive state	Derived states
1. Length (exsag.) of anterior cephalic border between lateral margins of frontal lobe and genal spine angle equal to length (sag.) of	(0) L0	(1) 50%–60% length of L0
2. Prominent parafrontal band	(0) not visible in dorsal view	(1) visible in dorsal view
3. Ocular lobe	(0) only faintly separated from extraocular area by small vertical wall	(1) prominently separated from extraocular area by vertical wall
4. S0	(0) not conjoined medially	(1) conjoined medially
5. Frontal lobe	(0) contacts anterior border furrow	(1) does not contact anterior border furrow
6. Cephalic posterior border between intergenal angle and genal spine	(0) transverse or weakly bending anteriorly	(1) bending posteriorly (2) flexing strongly anteriorly
7. Plectrum	(0) not visible	(1) visible
8. Extraocular region opposite L1	(0) width (tr.) greater than or equal to 70%–100% width of the glabella at L1	(1) width (tr.) 50%–55% width of glabella at L1
9. Posterior end of ocular lobes extend back to	(0) medial part of margin of L1	(1) distal tip of S0 (2) medial part of margin of L0
10. S2	(0) not conjoined medially	(1) conjoined medially
11. S1	(0) not conjoined medially	(1) conjoined medially
12. Intergenal spine represented by	(0) distinct dorsal swelling or node	(1) small pointed spine or faint, posteriorly directed swelling
13. Frontal lobe	(0) does not expand prominently dorsally	(1) expands prominently dorsally

Continued

Table 5 continued.

	Primitive state	Derived states
14. Surface of interocular area	(0) developed as flattened shelf	(1) slopes evenly from tip of ocular lobe to glabella
15. S3	(0) jaggedly convex[a]	(1) gently convex
16. S3	(0) not conjoined medially	(1) conjoined medially
17. S0	(0) convex	(1) straight
18. Prominent anastomosing ridges	(0) absent on extraocular area	(1) present on extraocular area
19. S2, S3	(0) prominently incised	(1) very faintly incised
20. Distal margins of glabella at L1 relative to L0	(0) constricting	(1) displaced as far laterally

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[a] Jaggedly convex is equivalent to carat shaped.

14345, 29269, 35853, 35855–35858, 61513, 94089, 94169.
Discussion: Character differences separating this species from members of the genus *Elliptocephala* were determined in the phylogenetic analysis of the Olenelloidea conducted in Lieberman (1998). These characters pulled *Wanneria* up the olenelloid tree relative to the two species of *Elliptocephala* considered in that analysis: *E. logani* and *E. asaphoides* Emmons 1844. In particular, *Wanneria* grouped as the sister taxon to a large clade that includes the Holmiidae and the genera *Fritzolenellus, Mummaspis, Laudonia, Bristolia, Lochmanolenellus, Fremontella, Nephrolenellus, Bolbolenellus, Olenelloides, Peachella* and *Biceratops.* The character differences excluding *Wanneria* from a sister group relationship with the two members of *Elliptocephala* discovered in Lieberman (1998) include: 1. the length (exsag.) of the anterior cephalic border near but not directly in front of the frontal lobe, which in *W. walcottana* the length is equal to the length (sag.) of L0 while in *E. asaphoides* and *E. logani* the length is equal to approximately half the length of L0; 2. in *W. walcottana* the parafrontal band is not visible, whereas in both *E. asaphoides* and *E. logani* it is prominently developed; 3. in *W. walcottana* the posterior tips of the ocular lobes are developed opposite the medial part of the distal margin of L1, whereas in *E. asaphoides* and *E. logani* they extend further posteriorly; and 4. the pygidium of *W. walcottana* is relatively broader than that of *E. asaphoides* (pygidium of *E. logani* not known). Consideration of

Table 6.
Character state distributions for *Elliptocephala* and outgroup used in phylogenetic analysis. Characters and alternative states are as listed in Table 5. Missing data are indicated by ?. Character states listed as X are polymorphic, where X=(0&1).

										1	1	1	1	1	1	1	1	1	1	2
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0
Wanneria walcottana	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Elliptocephala asaphoides	1	1	0	1	1	0	1	0	2	X	0	1	0	0	0	1	0	1	1	1
Elliptocephala sequomalus	1	1	1	0	1	1	1	0	2	0	0	0	0	0	0	0	0	0	1	0
Elliptocephala mediocris	1	0	0	1	0	1	0	0	1	1	1	0	0	1	0	1	0	0	1	0
Elliptocephala walcotti	1	1	0	1	1	0	0	0	1	1	1	0	0	1	0	1	1	1	0	0
Elliptocephala bicensis	1	1	0	1	1	0	0	1	2	1	1	?	0	0	1	1	0	?	0	1
Elliptocephala laxocules	1	0	1	0	1	0	1	0	1	0	1	1	0	1	1	1	0	1	1	0
Elliptocephala paraoculus	1	0	1	0	0	0	0	0	1	0	1	1	1	1	1	1	1	0	1	0
Elliptocephala parvifrons	1	1	1	1	0	0	0	1	1	0	1	1	1	0	1	0	1	0	0	0
Elliptocephala logani	1	1	1	1	0	1	0	1	1	0	0	1	1	1	1	0	1	0	0	0
Elliptocephala mirabilis	0	1	1	1	0	2	0	1	1	1	1	?	1	0	0	1	1	?	0	0
Elliptocephala lundgreni	0	1	?	1	0	0	0	1	2	1	1	?	1	0	0	1	?	?	0	1

additional species of *Elliptocephala* in this analysis reveals that characters 3 and 4 still reliably distinguish *Wanneria* from all members of *Elliptocephala,* though admittedly no pygidial remains for this genus are known aside from the type of the genus. However, the two most derived species of *Elliptocephala* relative to *Wanneria, E. mirabilis* (Poulsen 1958) and *E. lundgreni* do possess a relatively broad anterior cephalic border (character 1). In addition, three species of *Elliptocephala* considered here, *E. paraoculus* (Fritz 1972), *E. laxocules* (Fritz 1972) and *E. mediocris* (Poulsen 1958), do not have a prominently developed parafrontal band (character 2). This indicates that some of the characters separating *Wanneria* from *Elliptocephala* do show homoplasy, and this underscores the contention of Lieberman (1998) that the branch separating *Wanneria* and *Elliptocephala* from one another in the phylogeny of the Olenelloidea is a short one. This matches the conclusion of Bergström (1973) and Ahlberg et al. (1986), who suggested that *Elliptocephala* and *Wanneria* were closely related.

However, one of these two characters reliably distinguishes *Wanneria* from *E. logani*: the relative position of the posterior margin of the ocular lobe may show ontogenetic variation (Westrop, pers. comm. 1998). Specifically, during the ontogeny of some olenelloids the ocular lobes become progressively shortened (see Fritz 1972, pl. 9, figs. 1, 5, 6, 12). Specimens of *W. walcottana* are typically much larger than specimens of *E. logani.* This size difference, and thus the relative position of the posterior margin of the ocular lobes, might be related to taphonomic factors. For example, perhaps large specimens of *W. walcottana* are more likely to be found than large specimens of *E. logani* because the habitat that large specimens of *W. walcottana* occupied is easily sampled for fossils, and in reality both taxa show similar size distributions (with size being a proxy for age). If this is in fact the case, then these taxa would be differentiated on spurious characteristics. On the other hand, the differences in size could reflect true, evolutionary differences between *W. walcottana* and *E. logani* since two closely related taxa are likely to differ in minor features, such as overall size, with only a simple heterochronic shift involved in producing the morphological differences. Because these two taxa come from geographically disparate regions that have been extensively sampled for fossils, and because the *W. walcottana* morphotype is not known from the localities where *E. logani* is found, and vice versa, the position put forward here is that the size related differences between the two taxa are evolutionary, and not taphonomic.

Additional cephalic characters distinguish *Wanneria* from all members of the genus *Elliptocephala.* Specifically, the anterior margins of the frontal lobe at each side of the midline are deflected posteriorly relative to a transverse line at a larger angle in *Elliptocephala* than in *Wanneria,* and the posterior margin of L0 is of greater convexity in *Elliptocephala* than in *Wanneria.* Thoracic characters separating *Wanneria* from *Elliptocephala* (only preserved in *E. asaphoides* and *E. bicensis* [Walcott 1910]) include: the distal part of the posterior margin of the pleural furrow of T3 is directed weakly anterolaterally in *Wanneria,* whereas it is directed posterolaterally in *Elliptocephala*; pleural spines T5 to T8 sweep roughly four segments back in *Wanneria* as opposed to roughly one to two segments back in *Elliptocephala*; the pleural furrows extend only half the width of the inner pleural region in *Wanneria,* whereas they extend onto the spine in *Elliptocephala*; the thoracic pleural furrows (excluding T3) at the medial portion of the segment relative to the length (exsag.) of the posterior band of the pleural segment are long in *Wanneria,* 1.3 to 1.5 times the length of the posterior band, whereas they are short, equal to the length of the posterior band, in *Elliptocephala*; and the spine on the 15th thoracic segment is relatively much longer in *Elliptocephala* (only known in *E. asaphoides*) than it is in *Wanneria.* A pygidial character separating *Wanneria* from *Elliptocephala* (only preserved in *E. asaphoides*) is the condition of the posterior margin, which is weakly convex in *Elliptocephala* and bifurcated with a median notch in *Wanneria.* Thus, based on all this character evidence, and following Lieberman (1998), the genus *Wanneria* is still considered to be closely related to *Elliptocephala,* but the two do not share a sister group relationship. As the branch between *Elliptocephala* and *Wanneria* is a short one, these two genera were placed within a single paraphyletic family, the "Wanneriidae," rather than erecting monotypic families for each of them.
Occurrence: Pennsylvania: the Kinzers Formation, Lancaster County, treated as in the middle upper *Olenellus* zone, following Palmer and Repina (1993).

GENUS *ELLIPTOCEPHALA* EMMONS 1844

Type species: *Elliptocephala asaphoides* Emmons 1844
Assigned taxa: *Olenellus sequomalus* Fritz 1972; *Wanneria mediocris* Poulsen 1958; *Elliptocephala walcotti* n. sp.; *Callavia bicensis* Walcott 1910; *Olenellus laxocules* Fritz 1972; *Olenellus paraoculus* Fritz 1972; *Wanneria parvifrons* Fritz 1972; *Olenellus logani* Walcott 1910; *Holmia mirabilis* Poulsen 1958; *Olenellus praenuntius* Cowie 1968; *Olenellus lundgreni* Moberg 1892.
Diagnosis: Length (sag.) of L4 equal to roughly 1.5 times length of L0 and L1 (sag.); anterior margins of frontal lobe at each side of midline deflected posteriorly at roughly 40 degree angle relative to transverse line; lateral margins of L4 distal to lateral margins of L0;

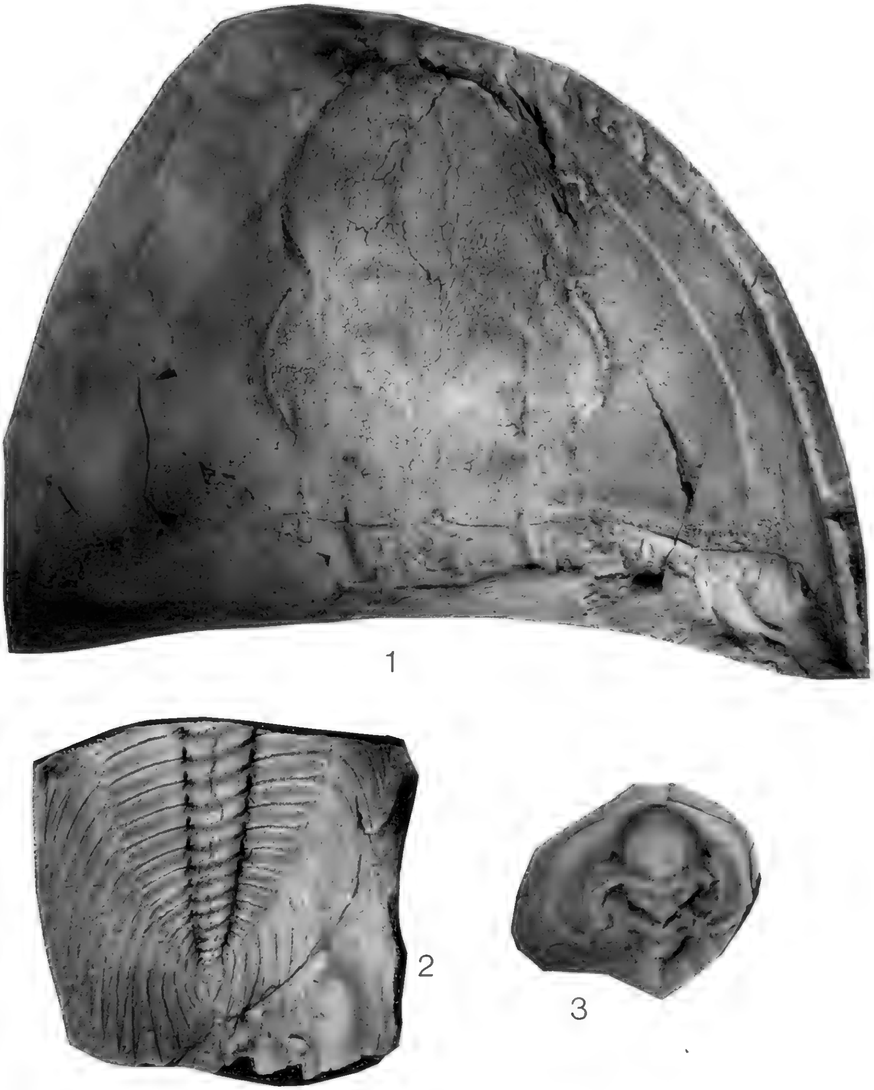


Figure 11.
1, 2. *Wanneria walcottana* (Wanner), Kinzers Shale, Pennsylvania. 1. near Lancaster, YPM 9295, ×0.9. 2. locality is the same as Figure 3.8, YPM 29269, ×1.1. 3. *Holmia kjerulfi* (Linnarsson) Tømten, Ringsaker, Norway, PIL Lo 4456t, ×1.4.

preocular furrow on L4 directed inward and forward from glabellar margin; posterior margins of L4 divergent anteriorly; distal margins of L3 convex outward; middle sector of S3 convex anteriorly; L2 and L3 do not merge; distal margins of L2 diverging anteriorly; line between ends of S2 transverse; S2 convex anteriorly; ocular lobe with prominent ocular furrow; line from posterior tip of ocular lobe to junction of posterior margin of lobe with glabella forms 10 to 20 degree angle with sagittal line; anterodistal margins of L3 formed by ocular lobes; intergenal angle developed posterior of point halfway between ocular lobes and genal spine angle; genal and intergenal ridges prominently developed; distal sector of S0 with proximal end well posterior of distal end; axial part of L0 with node;

posterior margin of L0 convex posteriorly; lateral lobes on L0 absent; thoracic pleural furrows extend onto spines; length (exsag.) of furrows equal to length of posterior band; anterior margin of thoracic pleural furrow on T3 parallels a transverse line before flexing strongly posteriorly; long spine on 15th thoracic segment, spine broad (tr.) at its base; pygidium twice as broad as long, posterior margin weakly convex.

Discussion: This genus is widespread, distributed throughout eastern (New York State, Quebec, Labrador and Greenland) and western Laurentia (Northwest Territories), and into Baltica as well. Thus it occurs in the Acado-Baltic and Pacific Provinces of the Olenellid Realm (sensu Cowie and McNamara 1978), in strata assigned to the lower and middle *Olenellus* zone in Laurentia and in strata assigned to the *Schmidtiellus mickwitzi* zone, the basal trilobitic strata, in Baltica. As discussed above under *Wanneria, Elliptocephala* is closely related to *Wanneria* but does not share a sister taxon relationship with it.

As mentioned above under the genus *Olenellus,* Rasetti (1966, 1967) assigned several specimens to the genera *Olenellus* and *Paedeumias.* However, these specimens instead appear referable to the genus *Elliptocephala* since they have many of the characters diagnostic of that taxon. In particular, the anterior margins of frontal lobe at each side of midline are deflected posteriorly at roughly 40 degree angle relative to transverse line; the preocular furrow on L4 is directed inward and forward from the glabellar margin; the distal margins of L3 are convex outward; the middle sector of S3 is convex anteriorly; L2 and L3 do not merge; the distal margins of L2 are diverging anteriorly; a line between the ends of S2 is transverse; S2 is convex anteriorly; the ocular lobe has a prominent ocular furrow; a line from the posterior tip of the ocular lobe to the junction of the posterior margin of the lobe with the glabella forms a 10 to 20 degree angle with a sagittal line; the anterodistal margins of L3 are formed by the ocular lobes; the distal sector of S0 has the proximal end well posterior of the distal end; the axial part of L0 has a node; the posterior margin of L0 is convex posteriorly; and the lateral lobes on L0 are absent. These specimens are probably closely related to *Elliptocephala asaphoides.*

Fritz (1991) figured a partial cephalon, which he referred to as *Wanneria* sp. 1, that appears to satisfy all the diagnostic characteristics of *Elliptocephala* and belong to *E. parvifrons,* though it does show subtle differences from this taxon (discussed below under the species). However, since it is from an early ontogenetic stage and poorly preserved, it is not treated as distinct at this time.

ELLIPTOCEPHALA ASAPHOIDES EMMONS 1844
Figure 12.1

Elliptocephala asaphoides Emmons; Walcott 1910:269, pl. 24, figs. 1–10, pl. 25, figs. 1–18, pl. 44, fig. 3 (see for more complete synonymy); Tasch 1952:486, figs. 1a–d; Lochman 1956:1376, pl. 6, figs. 2–21; Whittington 1957:935, pl. 115, figs. 1–6; Harrington et al. 1959:O194, fig. 135.1; Bergström 1973:307; Whittington 1989:128, figs. 45, 46, 48, 50, 51; Palmer and Repina 1993:26, fig. 6.7; Palmer and Repina 1997:414, fig. 262.4; Lieberman 1998:67.

Types: Lectotype, USNM 18350a, designated by Palmer and Repina (1993).

Material examined: AMNH 222; USNM 18350a, the lectotype; YPM 8190, 35863.

Occurrence: New York: the Greenwich Formation, eastern New York State, within the middle *Olenellus* zone, following Palmer and Repina (1993), detailed locality information given in Landing and Bartowski (1996) and references therein.

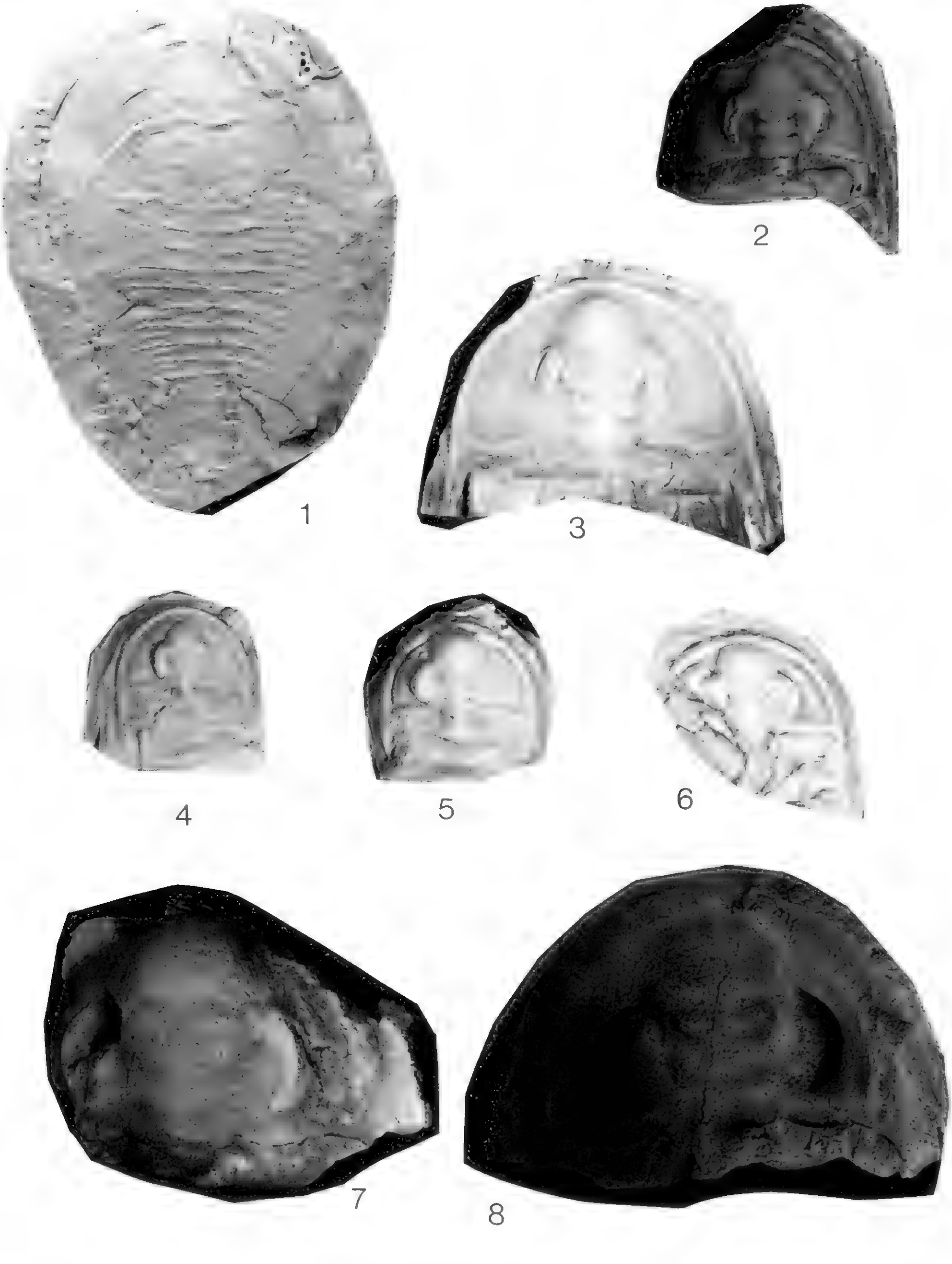


Figure 12.
Elliptocephala spp. **1.** *Elliptocephala asaphoides* Emmons, Greenwich Fm., Greenwich, Washington Co., New York, YPM 8190, ×0.7. **2–6.** Sekwi Fm. type section, 0.2 mi SE of June Lake, Mackenzie Mtns., District of Mackenzie, Canada. **2.** *Elliptocephala sequomalus* (Fritz), GSC 27352, the holotype, ×1.6. **3.** *Elliptocephala walcotti,* new species, GSC 27291, the holotype, ×1.6. **4.** *Elliptocephala laxocules* (Fritz), GSC 27333, the paratype, ×1.6. **5.** *Elliptocephala logani* (Walcott), GSC 27376, ×1.6. **6.** *Elliptocephala parvifrons* (Fritz), GSC 27355, the holotype, ×1.7. **7, 8.** *Elliptocephala lundgreni* (Moberg), Norretorp Fm. at Tunbyholm, east Scania, Sweden, PIL Lo 1398t internal and external molds, ×1.6.

Elliptocephala sequomalus (Fritz 1972)
Figure 12.2

Olenellus sequomalus; Fritz 1972:15, pl. 12, figs. 14–25.

Types: Holotype, GSC 27352, see Fritz (1972).
Discussion: Fritz (1972) treated this species as belonging to the genus *Olenellus*. However, it lacks some of the diagnostic characteristics of that genus, and instead appears to bear the hallmark characteristics of the genus *Elliptocephala*. In particular, the lateral margins of L4 are distal to the lateral margins of L0; the preocular furrow on L4 is directed inward and forward from the glabellar margin; the middle sector of S3 is convex anteriorly; L2 and L3 do not merge; a line between the ends of S2 is transverse; S2 is convex anteriorly; the intergenal angle is developed posterior of a point halfway between the ocular lobes and the genal spine angle; and the posterior margin of L0 is strongly convex posteriorly. Thus, because of the possession of these characters, and the absence of other characters diagnostic of *Olenellus*, it must be excluded from that genus and instead assigned to *Elliptocephala*.
Material examined: GSC 27352, the holotype.
Occurrence: Canada, Northwest Territories: the type section of the Sekwi Formation (Handfield 1968), 0.2 mi SE of June Lake, 1668 ft above the base of the formation, middle *Olenellus* zone, following Fritz (1972), south end of the Sekwi Range, Mackenzie Mountains, District of Mackenzie.

Elliptocephala mediocris (Poulsen 1958)

Wanneria mediocris; Poulsen 1958:18, pl. 5, figs. 1–5.
Wanneria troelseni; Poulsen 1958:21, pl. 5, figs. 6–9.
Wanneria ruginosa; Poulsen 1958:19, pl. 6, figs. 1–5.
Wanneria subglabra; Poulsen 1958:20, pl. 6, figs. 6–8.

Types: Holotype, MUGH 10696, see Poulsen (1958).
Discussion: Poulsen (1958) was correct in recognizing the close relationship between this species and *W. walcottana*. However, *E. mediocris* is more closely related to, and better fits the diagnostic characters of, the genus *Elliptocephala* rather than those of the genus *Wanneria*, and thus it is treated as belonging to *Elliptocephala*.

Poulsen (1958) recognized several species of *Wanneria* from northwestern Greenland; specifically, his *W. troelseni*, *W. ruginosa* and *W. subglabra* in the collections of the MUGH. On re-examination these appear to be identical to *E. mediocris*. This material consists of variably preserved cephala, and most of the differences between these "species" seem to center around the fact that they represent substantially different ontogenetic stages. Even then, prominent similarities emerge in the condition of the posterior cephalic border, which lateral to the intergenal angle flexes posterolaterally; the jaggedly convex S2 and S3; the conjoined S0, S1, S2 and S3; the rounded and broad (tr.) L4; and in the relative position of the posterior margins of the ocular lobes. Some differences can be seen between *E. mediocris* and *W. ruginosa*, particularly in the latter's relatively slightly longer (exsag.) anterior cephalic border and more prominently incised S2 and S3. However, these characters vary even within the two illustrated specimens of *W. ruginosa*. The specimens of *W. ruginosa* are half the size of *E. mediocris* and from a presumably much earlier ontogenetic stage. Because these character differences seemed insignificant, all these species

were treated as conspecific and the specimens of *E. mediocris* were used for coding characters, as these appear to come from the latest ontogenetic stages available for this taxon.
Material examined: MUGH 10696, the holotype; MUGH 10698, holotype of *W. troelseni*; MUGH 10699, holotype of *W. ruginosa*.
Occurrence: Denmark: Greenland, W of Blomsterbaekken, Kap Leiper, and Marshall Bugt, Inglefield Land, NW Greenland, Lower Cambrian Wulff River Formation, questionably placed somewhere within the *Olenellus* zone.

ELLIPTOCEPHALA WALCOTTI LIEBERMAN NEW SPECIES
Figure 12.3

Olenellus truemani Walcott; Fritz 1972:16, pl. 9, figs. 1–14.

Types: Holotype, GSC 27291, designated here, the best specimen of Fritz's (1972) material housed in the GSC.
Diagnosis: Length (exsag.) of anterior cephalic border between lateral margins of L4 and genal spine angle equal to 50% to 60% length (sag.) of L0; L4 does not contact anterior border furrow and does not expand prominently dorsally; plectrum not visible in dorsal view; prominent parafrontal band visible, width (tr.) near ocular lobes equal to length (sag.) medially; ocular lobe only subtly separated from extraocular area by shelf; posterior end of ocular lobes extend back to S0; S3 jaggedly convex; S3, S2, S1 and S0 conjoined medially; S2 and S3 prominently incised; S1 transverse; intergenal angle represented by distinct dorsal swelling; posterior cephalic border between intergenal angle and genal spine transverse.
Description: Anterior cephalic border narrow, flattened ledge, length (exsag.) between lateral margins of L4 and genal spine angle equal to 50% to 60% length (sag.) of L0; frontal lobe does not contact anterior border furrow; prominent parafrontal band visible in dorsal view; plectrum not visible; anterior margin of frontal lobe at each side of midline deflected posteriorly at roughly 40 degree angle relative to a transverse line; lateral margins of frontal lobe distal to lateral margins of L0; lateral margins of L4.divergent anteriorly; anterodistal margins of L3 formed by ocular lobes, distal margins of L3 convex outward; S3 jaggedly convex, conjoined medially; S2 convex anteriorly, conjoined medially; L2 and L3 do not merge distally; line from anterior to posterior edge of ocular lobe forms roughly 10 degree angle relative to sagittal line; S0, S1 transverse, contact axial furrows, medial edges declined posteriorly, conjoined medially; width (tr.) of glabella opposite margins of L1 constricted slightly relative to width at lateral margins of L0; posterior edge of ocular lobe opposite distal tip of S0; ocular lobes weakly elevated from extraocular area; posterior margin of L0 convex posteriorly, with axial node medially; genal spines of length (exsag.) approximately 4 to 5 times length (sag.) of L0, sweeping posterolaterally at roughly 15 degree angle relative to sagittal line; genal spine angle opposite L0; intergenal angle developed as faint dorsal projection, inclined at 10 to 15 degree angle relative to transverse line; extraocular area opposite L1 broad, width (tr.) approximately 75% width of glabella at L1; faint anastomosing ridges visible on extraocular area; faint intergenal and genal ridges visible; posterior margin of cephalic posterior border between L0 and intergenal angle weakly flexing posterolaterally.
Discussion: Originally Fritz (1972) treated this species as conspecific with *O. truemani*. However, Fritz (1992) recognized that this identification was no longer tenable, though he still treated this species as belonging to the genus *Olenellus*. First, *Olenellus truemani*

belongs to *Fritzolenellus* and differs in a large number of characters from members of the genus *Olenellus* (characters elucidated in Lieberman [1998]) so that generic assignment can no longer be upheld. In addition, what Fritz (1972) identified as *O. truemani* lacks some of the diagnostic characters of *Fritzolenellus* and instead matches those diagnostic of the genus *Elliptocephala* (given above). In particular, this new species, *E. walcotti,* differs from the type of *Fritzolenellus, F. truemani,* in the condition of the following characters: *E. walcotti* has the length (exsag.) of the anterior cephalic border near but not directly in front of L4 equal to 50% to 60% length (sag.) of L0, while in *F. truemani* it is equal to the length of L0; *E. walcotti* has a prominent parafrontal band, *F. truemani* does not; the posterior tips of the ocular lobes extend back to S0 in *E. walcotti,* in *F. truemani* they extend back to the medial part of the distal margin of L1; *E. walcotti* lacks lateral lobes on L0, *F. truemani* has these lobes; *E. walcotti* has the interocular area sloping evenly from the tip of the ocular lobe to the glabella, in *F. truemani* the interocular area is somewhat arched or swollen; *E. walcotti* has S0 conjoined, in *F. truemani* S0 is not conjoined; and *E. walcotti* has a more prominently developed genal ridge than does *F. truemani.* These and other characters mark *E. walcotti* as distinct from *F. truemani* and group it with species of the genus *Elliptocephala* rather than with *Fritzolenellus* or *Olenellus.*
Material examined: GSC 27291, the holotype.
Occurrence: Canada: Northwest territories, the type section of the Sekwi Formation (Handfield 1968), 0.2 mi SE of June Lake, 1271 ft above the base of the formation, lower *Olenellus* zone, following Fritz (1972), S end of the Sekwi Range, Mackenzie Mountains, District of Mackenzie.

ELLIPTOCEPHALA PRAENUNTIUS (COWIE 1968)

Olenellus praenuntius; Cowie 1968:9, pl. 1, figs. 1–10; Fritz 1972:17.

Types: Holotype, GSC 18040, see Cowie (1968).
Discussion: This species is nearly identical to *E. walcotti,* new species. It differs from that species solely in the relative placement of the posterior tip of the ocular lobes, which is opposite the medial part of the distal margin of L0 in *Elliptocephala praenuntius,* whereas it is opposite S0 in *E. walcotti.* These character states do not seem to vary meaningfully within either species. Because *E. praenuntius* is poorly preserved and because the original material could not be obtained for study, it was not subjected to phylogenetic analysis, but instead simply placed within *Elliptocephala* and considered to be closely related to *E. walcotti.*
Occurrence: Canada: 430 ft above the base of the Kane Basin Formation, possibly the lower *Olenellus* zone, 6 mi NW of the head of Scoresby Bay, eastern Ellesmere Island.

ELLIPTOCEPHALA BICENSIS (WALCOTT 1910)

Callavia bicensis; Walcott 1910:277, pl. 41, figs. 9, 9a; Rasetti 1948:10, pl. 2, figs. 1–3.

Types: Holotype, USNM 56794, see Walcott (1910) and Rasetti (1948).
Discussion: Originally, this species was assigned to the genus *Callavia.* However, the type species of *Callavia* lacks the diagnostic characteristics of the superfamily Olenelloidea and must henceforth be excluded from that superfamily (Lieberman 1998). In contrast, *E. bicensis* clearly bears the hallmark characteristics of the Olenelloidea: the ocular lobes merge with the posterior margin of L4, and the length (sag.) of L4 is equal to the length of L0 and L1. In addition, although poorly preserved, the species appears to have all the diagnostic

characters outlined above of the genus *Elliptocephala,* based on higher level phylogenetic analysis of the Olenelloidea, and thus can be treated as belonging to that genus. The age of this species is difficult to determine, as it comes from a limestone boulder within a conglomerate, and the boulder can no longer be definitively ascertained (Rasetti 1948). However, all limestone boulders subsequently collected from near this Bic, Quebec locality all contain ptychoparids that probably correlate with the *Olenellus* zone. Thus, *E. bicensis* is provisionally placed within that zone in the Early Cambrian.
Occurrence: Canada: Quebec, limestone boulder believed to be from the Early Cambrian *Olenellus* zone, in ?Lower Ordovician conglomerate, from near Bic (Rasetti 1948).

ELLIPTOCEPHALA LAXOCULES (FRITZ 1972)
Figure 12.4

Olenellus laxocules; Fritz 1972:13, pl. 11, figs. 7–21.

Types: Holotype, GSC 27335, see Fritz (1972).
Discussion: Based on the character evidence discussed above under *E. sequomalus,* although originally assigned to *Olenellus E. laxocules* must henceforth be assigned to *Elliptocephala.*
Material examined: GSC 27333, a paratype.
Occurrence: Canada: Northwest Territories, the type section of the Sekwi Formation (Handfield 1968), 0.2 mi SE of June Lake, 1668 ft above the base of the formation, middle *Olenellus* zone, following Fritz (1972), S end of the Sekwi Range, Mackenzie Mountains, District of Mackenzie.

ELLIPTOCEPHALA PARAOCULUS (FRITZ 1972)

Olenellus paraoculus; Fritz 1972:14, pl. 15, figs. 8–22.

Types: Holotype, GSC 27394, see Fritz (1972).
Discussion: Based on the character evidence discussed above under *E. sequomalus,* although originally assigned to *Olenellus, E. paraoculus* must henceforth be assigned to *Elliptocephala.*
Occurrence: Canada: Northwest Territories, the type section of the Sekwi Formation (Handfield 1968), 0.2 mi SE of June Lake, 1746 ft to 1945 ft above the base of the formation, middle *Olenellus* zone, following Fritz (1972), S end of the Sekwi Range, Mackenzie Mountains, District of Mackenzie.

ELLIPTOCEPHALA PARVIFRONS (FRITZ 1972)
Figure 12.6

Wanneria parvifrons; Fritz 1972:30, pl. 13, figs. 1–5.
?*Wanneria* sp. 1; Fritz 1991:18, pl. 3, fig. 2.

Types: Holotype, GSC 27355, see Fritz (1972).
Discussion: Fritz (1972) originally assigned this species to the genus *Wanneria.* Although *Wanneria* is closely related to *Elliptocephala, Elliptocephala parvifrons* actually appears to be more closely related to the genus *Elliptocephala* than to *Wanneria* since it bears the diagnostic characteristics of *Elliptocephala* and lacks some of the diagnostic characteristics of *Wanneria.* In particular, *E. parvifrons* does not have the length (exsag.)

of the anterior cephalic border between the lateral margins of the frontal lobe and the genal spine angle equal to the length (sag.) of L0 (the condition in *W. walcottana*), but rather the length is equal to about half the length of L0; the parafrontal band is prominently visible in *E. parvifrons,* whereas it is not visible in *W. walcottana*; the ocular lobes in *E. parvifrons* extend back to S0 rather than the medial part of the distal margin of L1; the anterior margins of the frontal lobe at each side of the midline in *E. parvifrons* are deflected posteriorly at a roughly 40 degree angle relative to transverse line, rather than at a roughly 10 degree angle as in *W. walcottana*; the ocular lobe is separated from the extraocular area by a shelf in *E. parvifrons,* whereas it smoothly merges with the extraocular area in *W. walcottana*; and the posterior margin of L0 is convex posteriorly in *E. parvifrons,* whereas it is roughly transverse in *W. walcottana.* Thus, based on this character evidence, henceforth this species is assigned to the genus *Elliptocephala* and excluded from *Wanneria.*

Fritz (1991) figured a partial cephalon, referred to as *Wanneria* sp. 1, that appears to satisfy all the diagnostic characteristics of *Elliptocephala.* Although from an early ontogenetic stage, and poorly preserved, it appears to show no differences from *E. parvifrons.* Although Fritz (1991) claimed that there were differences between his *Wanneria* sp. 1 and *E. parvifrons,* when material from similar ontogenetic stages are compared these differences do not appear to be valid. Thus, at this time his *Wanneria* sp. 1 is treated as conspecific with *E. parvifrons.*

Material examined: GSC 27355, the holotype.

Occurrence: Canada: Northwest Territories, the type section of the Sekwi Formation (Handfield 1968), 0.2 mi SE of June Lake, 1668 ft above the base of the formation, middle *Olenellus* zone, following Fritz (1972), S end of the Sekwi Range, Mackenzie Mountains, District of Mackenzie. Yukon Territory, the Illtyd Formation, Fritz's (1991) Unit 3, *Olenellus* zone, Early Cambrian, Wernecke Mountains.

ELLIPTOCEPHALA LOGANI (WALCOTT 1910)

Figure 12.5

Olenellus logani; Walcott 1910:333, pl. 41, figs. 5, 6.

Wanneria logani (Walcott); Poulsen 1958:16; Fritz 1972:29, pl. 14, figs. 1–14, pl. 16, figs. 1–7; Fritz 1991:17, pl. 3, figs. 16–17; Lieberman 1998:70.

Types: Walcott (1910) figured two USNM specimens that were casts of GSC 414d and 414e. These specimens serve as Walcott's (1910) original syntype material. The better of these specimens (Walcott 1910, pl. 41, fig. 5), GSC 414d, is here designated the **lectotype.** The other specimen, GSC 414e, is the paralectotype.

Discussion: Fritz (1972) concluded that this species belonged to the genus *Wanneria.* However, on the basis of character evidence identical to that given above under *E. parvifrons,* it is clear that this species must henceforth be assigned to the genus *Elliptocephala. Elliptocephala logani* has a larger geographic range than any other species of olenelloid considered in this study.

Material examined: GSC 27376.

Occurrence: Canada: Northwest Territories, the type section of the Sekwi Formation (Handfield 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, Mackenzie Mountains, District of Mackenzie; Yukon Territory, the Illtyd Formation, Fritz's (1991) Unit

3, *Olenellus* zone, Early Cambrian, Wernecke Mountains; Newfoundland, the Forteau Formation, *Olenellus* zone, Early Cambrian, L'Anse au Loup, straits of Belle Isle, Labrador.

ELLIPTOCEPHALA MIRABILIS (POULSEN 1958)

Holmia mirabilis; Poulsen 1958:15, pl. 3, figs. 5–8; Bergström 1973:309.
Wanneria? *mirabilis* (Poulsen); Fritz 1973:13.

Types: Holotype, MUGH 10691, designated in Poulsen (1958).
Discussion: Poulsen (1958) assigned this species to the genus *Holmia*. This species is only known from cephalic remains, but there are some cephalic characters that differentiate members of the genus *Elliptocephala* from the type species of the genus *Holmia, H. kjerulfi*. The condition of these characters indicates that Poulsen's (1958) species should be assigned to the genus *Elliptocephala*. In particular, in *E. mirabilis* the anterior cephalic border is prominently separated from the extraocular area by a furrow and in *H. kjerulfi* such a furrow is not prominently developed; in *E. mirabilis* the parafrontal band is much more prominently developed in dorsal view than it is in *H. kjerulfi*; in *E. mirabilis* the pre-ocular furrow on L4 is directed inward and forward from the glabellar margin, in *H. kjerulfi* it is not prominently developed; in *E. mirabilis* the ocular lobe is separated from the extraocular area by a prominent shelf, whereas the ocular lobe smoothly merges with the extraocular area in *H. kjerulfi*; in *E. mirabilis* S0 is prominently conjoined medially, in *H. kjerulfi* it is not; in *E. mirabilis,* lateral lobes on L0 are absent, in *H. kjerulfi* they are present; and in *E. mirabilis* the intergenal angle is developed posterior of a point halfway between the ocular lobes and the genal spine, while in *H. kjerulfi* it is developed directly posterior of the lateral margins of the ocular lobe. These characters indicate that *E. mirabilis* should be assigned to the genus *Elliptocephala*. However, it is not that easy to distinguish every species of *Elliptocephala* from *H. kjerulfi,* particularly on the basis of cephalic material. Following the phylogenetic topology within the Olenelloidea from Lieberman (1998), the genus *Elliptocephala* is not that distantly related from the Holmiidae. This agrees with the conclusions of Ahlberg et al. (1986), though the two are not sister taxa. Therefore, based on the material that he had available to him, Poulsen's (1958) assignment is not that far off. Bergström (1973) asserted that this species probably belonged with *Wanneria,* which he considered to be closely related to *Elliptocephala*. Again, this analysis suggests that his taxonomic assignment was fairly accurate.

In addition, it so happens that all of the characters elucidated in Lieberman (1998) that distinguish the entire family Holmiidae from members of the genus *Elliptocephala* are characters of the thorax. These are of no assistance when trying to demonstrate that the cephalon Poulsen (1958) referred to as *H. mirabilis* should be excluded from the Holmiidae. However, the close match between the diagnostic characters of *Elliptocephala* and the characters of *E. mirabilis,* as well as the failure of that species to adequately match the diagnoses of any of the genera within the Holmiidae, suggest that this species belongs to the genus *Elliptocephala*.

Fritz (1973) suggested that this species belonged within the genus *Wanneria*. As discussed above, the genus *Elliptocephala* is closely related to *Wanneria,* though they are not sister taxa. Species of these genera can clearly be distinguished by the characters given above.
Material examined: MUGH 10691, the holotype.
Occurrence: Denmark: Greenland, Marshall Bugt, Inglefield Land, NW Greenland, Lower Cambrian Wulff River Formation, questionably placed somewhere within the *Olenellus* zone.

ELLIPTOCEPHALA LUNDGRENI (MOBERG 1892)

Figures 12.7, 12.8

Wanneria? *lundgreni*; Bergström 1973:304, figs. 17, 18, 19a (see for more complete synonymy).
Kjerulfia? *lundgreni*; Ahlberg, Bergström and Johansson 1986:52.
Holmia lundgreni; Fritz 1973:13.
Holmia? *lundgreni*; Fritz 1995:714.

Types: Lectotype, PIL LO 1398T, designated in Bergström (1973).
Discussion: This species has an autapomorphy that easily distinguishes it from other members of the genus *Elliptocephala*: near the ocular lobe, the width (tr.) of the parafrontal band on L4 is twice the length (sag.) of the parafrontal band at the anterior end of the glabella. In all other species of *Elliptocephala* the width of the parafrontal band is approximately equal to the length of the parafrontal band. Bergström (1973) questionably assigned this species to the genus *Wanneria.* However, he recognized (as did Ahlberg et al. 1986), the close relationship between *Elliptocephala* and *Wanneria* and concluded that either one of these generic assignments could hold for his *W.*? *lundgreni.* In fact, he suggested that his *W.*? *lundgreni* might actually share more features with *E. asaphoides* than it does with *W. walcottana.* This analysis and the analysis of Lieberman (1998) are essentially concordant with his conclusion. As discussed above, *Elliptocephala* and *Wanneria* are closely related, though not sister taxa. On the basis of the character evidence presented under *E. parvifrons,* this species is assigned to *Elliptocephala* rather than to *Wanneria.* Bergström (1973) figured additional thoracic material, which he also assigned to this species. This material is not articulated with the cephalic material, and thus at this time it is not treated as conspecific with *E. lundgreni.* In addition, it is rather poorly preserved, making any conclusions on this material and its affinities difficult.

Ahlberg et al. (1986) questionably assigned this species to the genus *Kjerulfia.* As discussed above under *E. mirabilis,* only thoracic characters unequivocally distinguish members of the genus *Elliptocephala* from the family Holmiidae, and *E. lundgreni* is only definitely known from cephalic material. However, several cephalic characters make it possible to distinguish *E. lundgreni* from the type of the genus *Kjerulfia, K. lata* Kiaer 1917. In particular: 1. in *E. lundgreni* the anterior cephalic border between the lateral margins of the frontal lobe and the genal spine angle is short, with the length (exsag.) equal to one-half the length (sag.) of L0, in *K. lata* the length is equal to the length of L0; 2. in *E. lundgreni* the anterior border is prominently separated from the extraocular area by a furrow, in *K. lata* such a furrow is not prominently developed; 3. in *E. lundgreni* the parafrontal band is much more prominently developed in dorsal view than it is in *K. lata*; 4. in *E. lundgreni* the lateral margins of L4 are distal to the lateral margins of L0, in *K. lata* they are proximal to the lateral margins of L0; 5. in *E. lundgreni* the ocular lobe is separated from the extraocular area by a prominent shelf, whereas the ocular lobe smoothly merges with the extraocular area in *K. lata*; 6. in *E. lundgreni* the distal margins of L3 are convex outward, whereas in *K. lata* they are straight; 7. in *E. lundgreni* a line between the ends of S2 is transverse, whereas in *K. lata* a line between the ends of S2 is directed inward and posteriorly at a roughly 45 degree angle relative to a transverse line; 8. in *E. lundgreni* a node is present on the axial part of L0, in *K. lata* a spine is present; 9. in *E. lundgreni,* lateral lobes on L0 are absent, in *K. lata* they are present; 10. in *E. lundgreni* the extraocular area is prominently vaulted, whereas in *K. lata* it is gently convex. On the basis of these character differences *E.*

lundgreni must be excluded from the genus *Kjerulfia.*

Similar character differences emerge between *E. lundgreni* and *H. kjerulfi,* except for 4, 6, 7 and 10. These taxa also differ in the condition of the following: in *E. lundgreni* S0 is conjoined medially, in *H. kjerulfi* it is not; in *E. lundgreni* the intergenal angle forms a roughly 10 degree angle relative to a transverse line, in *H. kjerulfi* it forms a roughly 45 degree angle; and in *E. lundgreni* the posterior tips of the ocular lobes extend back to the medial part of the distal margin of L0, while in *H. kjerulfi* they extend back to the distal tips of S0. A similar set of characters discriminate this species from other holmiids.

Based on the phylogeny in Figure 10 this species appears to be a derived member of the genus *Elliptocephala,* though it appears early in the fossil record. Indeed, it is one of the earliest trilobites in the fossil record of Baltica (Ahlberg et al. 1986; Ahlberg 1991). All other members of the genus *Elliptocephala* do not appear before strata equivalent with the lower middle *Olenellus* zone. In conjunction with phylogenetic topology within the genus, this suggests that there is a substantial gap in the history of *Elliptocephala,* with the implication that a large portion of the Cambrian Radiation may be missing from the fossil record.

Material examined: PIL LO 1398T, the lectotype.

Occurrence: Sweden: The upper part of the Norretorp Formation, Lower Cambrian, at Tunbyholm, Flagabro, Gladsax, and S of Brantevik in eastern Scania. Trollskogen at Hällestad in central Scania. All treated as in the *Schmidtiellus mickwitzi* zone, following Ahlberg et al. (1986) and Ahlberg (1991).

Phylogenetic Analysis of the Holmiidae

The Holmiidae is a diverse family of seven genera and at least 17 species, some of which are the earliest trilobite species to appear in the fossil record of Baltica. It includes taxa distributed throughout Baltica and Western Laurentia (in the Great Basin and northwestern Canada), and also in Morocco. The family and the genera within it are revised, and one new genus is diagnosed, "*Baltobergstroemia.*" The bearing of taxonomy within the family on stratigraphic boundaries in Baltica is also discussed.

A total of 18 taxa was subjected to phylogenetic analysis. This includes all species that in past studies have been assigned to the genera *Esmeraldina, Kjerulfia, Holmia, Holmiella, Palmettaspis* and *Schmidtiellus.* It also includes one outgroup taxon, *Wanneria walcottana.* This taxon is an appropriate outgroup to these genera, based on the higher level phylogenetic analysis presented in Lieberman (1998). Phylogenetic patterns were determined by parsimony analysis of 35 holaspid exoskeletal characters. These are given in Table 7. The codings for the taxa analyzed are given in Table 8. All characters were treated as unordered (nonadditive). These data were subjected to a heuristic search on PAUP v. 3.1.1 (Swofford 1993). The six most parsimonious trees of length 90 steps were recovered, with a consistency index of 0.52 and a retention index of 0.69. A strict consensus of these trees is shown in Figure 13. The bootstrap confidence values for the nodes of the consensus tree duplicated in the bootstrap analysis are given in Figure 13. Almost all of the nodes have bootstrap support, but the value of this support varies depending on which node is being considered. Using the method of Bremer (1994), 156 trees of length less than or equal to 91 steps, 1,790 trees of length less than or equal to 92 steps and 8,600 trees of length less than or equal to 93 steps were recovered before the analysis was terminated because of insufficient computer memory. Only one of the nodes received any branch support (see Figure 13). It is conceivable that this node had even greater support, but because of insufficient computer memory this could not be determined. The total support index (Bremer 1994) for the tree is at least 0.03, a low value according to the examples given in Bremer (1994). Most of the uncertainty in the tree centers around the poorly known "*Baltobergstroemia*" sp. from Morocco. To determine which of the six most parsimonious trees is best supported by the data, a weighting procedure was used on PAUP v. 3.1.1 (Swofford 1993), with characters reweighted according to the rescaled consistency index, with the maximum value (best fit) used and a base weight of 1,000 assigned (standard protocol in PAUP). A single most parsimonious tree of length 32,490 steps was recovered (shown in Figure 14).

There is some incongruence between stratigraphic and phylogenetic patterns in the phylogeny presented in Figure 14, particularly in the timing of relative appearance of some of the Baltic species. The basal taxa within the Holmiidae, members of the genus "*Holmia,*" appear relatively late in the stratigraphic column, in the *Holmia kjerulfi* group zone, relative to their phylogenetic position. By contrast, species of the genera *Schmidtiellus* and "*Baltobergstroemia,*" which are derived relative to species of the genus "*Holmia,*" appear in the first trilobite bearing beds in Baltica, in the *Schmidtiellus mickwitzi* zone. The Laurentian taxa,

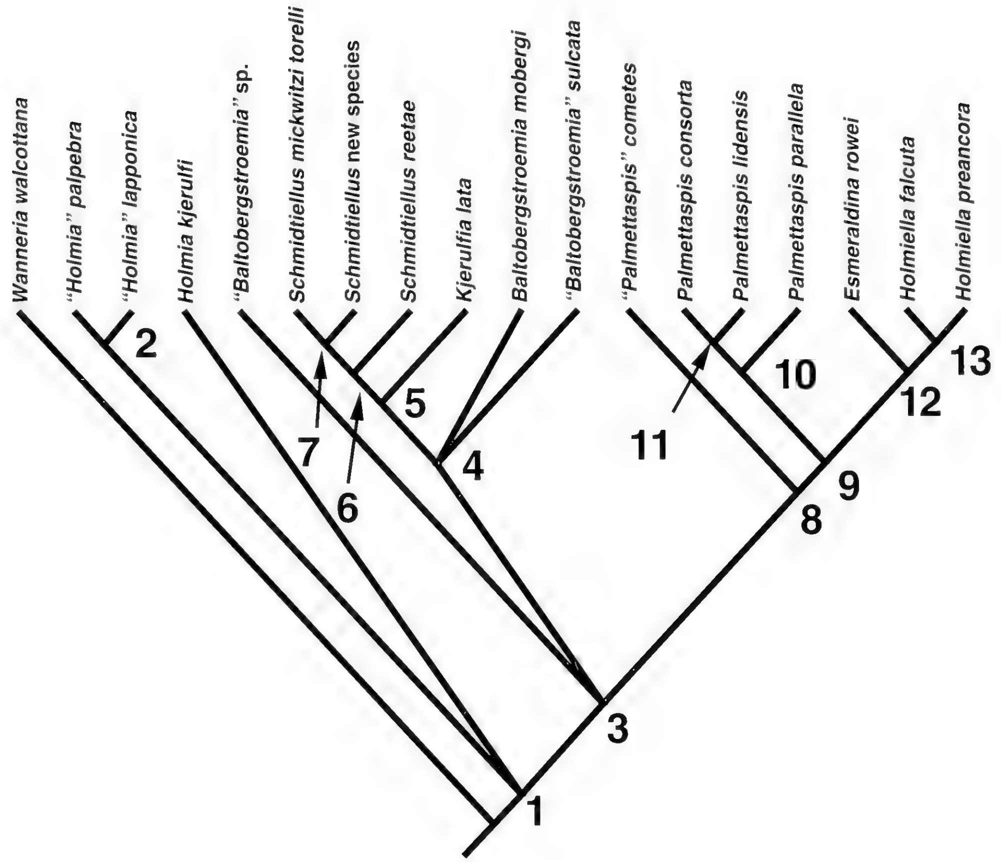


Figure 13.
A strict consensus of the six most parsimonious trees of length 90 steps produced from analysis of character data in Table 8 with PAUP v. 3.1.1 (Swofford 1993). The cladogram is constructed using a heuristic search with a stepwise addition sequence and 100 random replications. The retention index is 0.69, and the consistency index is 0.52. The following nodes in the text were supported by the following bootstrap confidence values (see text for bootstrapping procedure used): Node *2* = 0.67; Node *3* = 0.52; Node *4* = 0.41; Node *5* = 0.49; Node *6* = 0.61; Node *7* = 0.58; Node *8* = 0.68, Node *9* = 0.49; Node *10* = 0.34; Node *11* = 0.46; Node *13* = 1.00. The following branch support value (Bremer 1994) was recovered for Node *13* = 3+. Total tree support (Bremer 1994) is 0.03. Character states are placed at nodes, using MacClade v. 3.04 (Maddison and Maddison 1992), with the characters given in Table 7. The apomorphic state is given in parentheses. Square parentheses indicate equivocal character states that are ambiguous because of missing data, polymorphisms or multiple equally parsimonious resolutions. Equivocal characters are placed only at their basal phylogenetic position, and only unambiguous reversals are shown. Node *1*, 4[0, 1], 5[0, 1, 2], 9(1), 12(1), 19[0, 1], 23[0, 1], 24(1), 25[0, 1], 29[0, 1], 33(1), 34[0, 2]; Node *2*, 5(1), 18(1), 25(1), 26(1); Node *3*, 2[0, 1], 6(1), 18(1), 19(1), 22[0, 1, 2], 23(1), 28(1), 34(2); Node *4*, 4(1), 5(2), 8(1), 12(2), 22(2), 25(1); Node *5*, 26(1), 31(1), 34[1, 2]; Node 6, 3(1), 13(1), 29(0), 34(1), 35(1); Node *7*, 2(1), 19[1, 3], 23(0); Node *8*, 2(1), 5[1, 2], 13(1), 14(1), 15(1), 21(1), 22(2), 25(1), 27(1); Node 9, 1(1), 17(1), 20[0, 1]; Node *10*, 7(1), 8(1), 29(0); Node *11*, 5(1), 10(1), 11(1), 20(1); Node *12*, 5(1), 16(1), 20[0, 1, 2]; Node *13*, 3(1), 4(1), 10(2), 11(2), 18(0), 19(2), 20(2), 23(0), 24(0), 27(0), 32(1), 33(0).

sister to the clade containing the genera *Schmidtiellus* and "*Baltobergstroemia*," appear in the basal "*Nevadella*" zone. The precise correlation between the North American and Baltic sections is not clear, but these zones may both correlate with the upper part of the Atdabanian Stage according to Palmer and Repina (1993) and Geyer and Palmer (1995), implying reasonable concordance in this section of the tree. However, some caution must be exercised in extrapolating too much from these general stratigraphic patterns to the phylogenetic patterns, because stratigraphic correlations for the Early Cambrian, particularly those of Palmer and Repina (1993), are based on the presumed phylogenetic position of the taxa contained within those strata. This may create some circularity.

Systematic Paleontology

SUPERFAMILY Olenelloidea Walcott 1890
FAMILY Holmiidae Hupé 1953

The Holmiidae has been defined in several ways over the years, and it is worth briefly presenting this taxonomic history here to show the areas of congruence between this study and past studies, while also highlighting incongruence and its potential source. Hupé (1953) defined the Holmiidae as a subfamily (Holmiinae) within the Olenellidae and specified that it definitively contained the genera *Holmia, Kjerulfia* and *Bondonella* Hupé 1953. Lieberman (1998) excluded *Bondonella* from the Olenelloidea as it lacked some of the diagnostic characteristics of that superfamily. In particular, in *Bondonella* the posterior part of L3 does not bulge laterally relative to L1, and the ocular lobes merge with the entire lateral margin of the frontal lobe, rather than just with the posterolateral part of L4. Lieberman (1998) placed this taxon within the Judomioidea Repina, a superfamily sister to the Olenelloidea. On this basis, that taxon must be excluded from the Holmiidae, which is nested within the Olenelloidea. The other genera listed appear correctly assigned to the Holmiidae. Harrington et al. (1959) partly retained Hupe's (1953) taxonomy, but excluded *Kjerulfia* from the Holmiidae while assigning *Schmidtiellus* to it. Character evidence suggests that *Kjerulfia* should be included within the Holmiidae, but *Schmidtiellus* belongs there as well. Bergström (1973) treated the Holmiidae as a family containing the genera *Holmia, Elliptocephala, Esmeraldina, Schmidtiellus* and *Wanneria.*

Elliptocephala and *Wanneria* are closely related but are not sister taxa, according to the phylogeny of the Olenelloidea in Lieberman (1998) (and also discussed in greater detail above). These two genera are in turn closely related to the Holmiidae, but do not share a sister group relationship with that family. Conceivably they could be placed within the Holmiidae, but this would entail either making the Holmiidae paraphyletic or placing all olenelloid taxa outside the Olenellidae within that family. The former is not advocated because the Holmiidae as defined here is a good clade. The latter taxonomic decision was not followed because it is believed that additional families within the Olenelloidea can be recognized, and thus a more informative classification can potentially be made. This analysis and that of Lieberman (1998) are in accord with the other genera Bergström (1973) assigned to the Homiidae.

Repina (1979) assigned the genera *Holmia, Schmidtiellus, Kjerulfia, Elliptocephala, Bondonella, Andalusiana* and, questionably, *Holmiella* to the Holmiinae, one of two subfamilies she assigned to the Holmiidae. To the other subfamily, the Callaviinae (Poulsen in Harrington et al. 1959), she assigned the genus *Callavia.* Grounds for exclusion of some of these genera from the Holmiidae have already been presented above. This study and that of

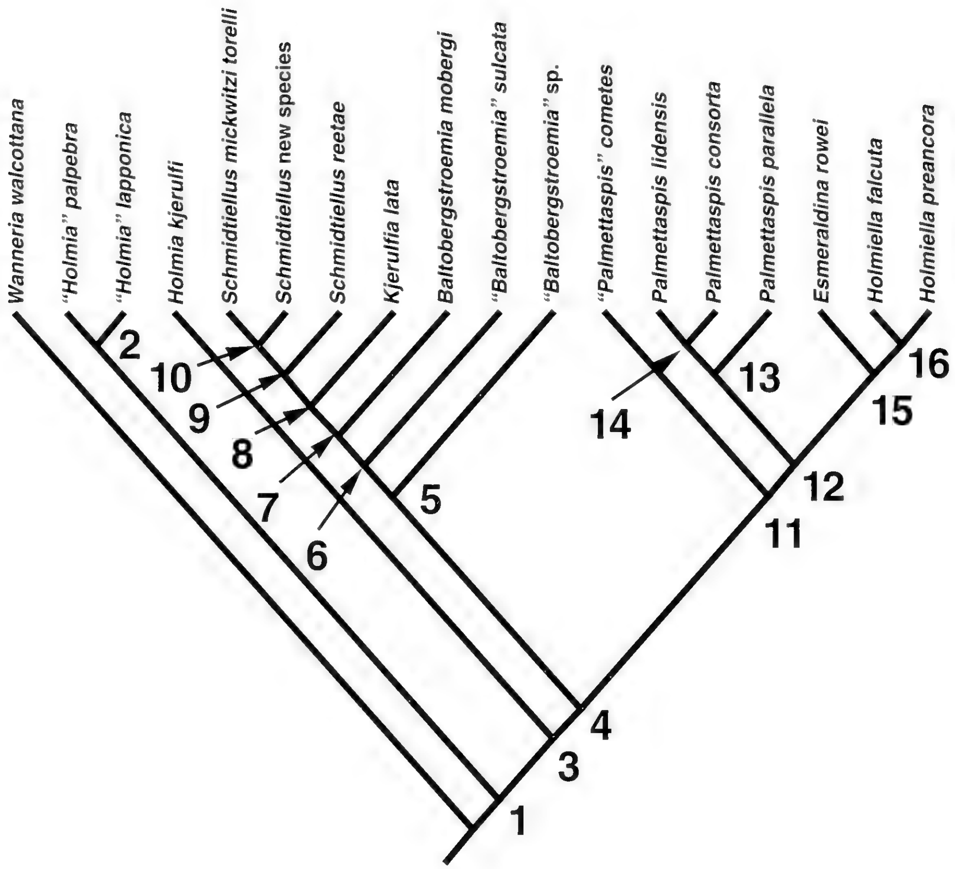


Figure 14.
The weighted tree of length 32,490 steps, with the same topology as one of the most parsimonious trees used to derive the consensus tree shown in Figure 13. Characters were reweighted according to the rescaled consistency index with a base weight of 1,000 steps, and the maximum value was used (standard protocol of PAUP v. 3.1.1 [Swofford 1993]). Then a heuristic search with a stepwise addition sequence and 100 random replications was used to construct the tree. Character states were placed at nodes, using MacClade v. 3.04 (Maddison and Maddison 1992), with the characters given in Table 7. Only differences from the cladogram in Figure 13 are shown: Node *1*, 4(1), 5(1), 9(1), 12(1), 18[0, 1], 19(1), 23(1), 24(1), 25(1), 29(1), 33(1), 34(2); Node *3*, 22[0, 1, 2], 28(1); Node *4*, 2[0, 1], 5[1, 2], 6(1), 18(1), 22(2); Node *5*, 5(2), 12(2); Node *6*, 8(1), 25(0); Node *7*, 26(1); Node *8*, 29[0, 1], 31(1), 34[1, 2]; Node *11*, 2(1), 4[0, 1], 13(1), 14(1), 15(1), 21(1), 27(1).

Lieberman (1998) support the contention that *Holmiella,* as well as *Schmidtiellus* and *Kjerulfia,* belong with the Holmiidae.

Andalusiana is known from poorly preserved material; however, it appears to lack some of the diagnostic characters of the Olenelloidea. In particular, the ocular lobes contact but do not merge with the ocular lobe; the ocular lobe is in contact with the entire lateral margin of the frontal lobe; and the dorso-ventral elevation of the ocular lobes gradually decreases between the distal most tip of the ocular lobe and the point where the ocular lobes contact the frontal lobe. However, one diagnostic character of the Olenelloidea this genus possesses is the condition of L3, which bulges laterally relative to L1. On the basis of these character differences, this genus is excluded from the Olenelloidea, and thus is also excluded from the Holmiidae. Its relationships to the other superfamilies within the Olenellina—the

Nevadioidea Hupé 1953, the Judomioidea, the Olenelloidea and the paraphyletic "Fallotaspidoidea" Hupé 1953—will be considered in a subsequent paper.

The type of the genus *Callavia, C. broeggeri* (Walcott), also lacks some of the diagnostic characters of the Olenelloidea. In particular, the ocular lobes merge with the entire margin of the frontal lobe, L3 does not bulge laterally relative to L1, and the length (sag.) of the frontal lobe is less than the total (sag.) length of L0 and L1. Lieberman (1998) therefore excluded it from the Olenelloidea and provisionally assigned it to the Judomioidea. Because its propinquity does not lie with the Olenelloidea, it will be discussed in a later paper, along with *Andalusiana* and several other taxa.

Ahlberg et al. (1986) correctly recognized that the Callaviinae could not be related to the Holmiidae. They assigned the four genera *Holmia, Andalusiana, Kjerulfia* and *Schmidtiellus* to the Holmiidae. The status of these genera have been evaluated above.

Palmer and Repina's (1993) classification was discussed in detail in Lieberman (1998). They assigned two subfamilies, Holmiinae and Callaviinae, to the Holmiidae, following Repina (1979). To the Holmiinae they assigned *Holmia, Andalusiana, Elliptocephala, Holmiella* and *Schmitdiellus.* Palmer and Repina (1993) also assigned *Kjerulfia* to the Callaviinae. As mentioned above, *Callavia* needs to be excluded from the Olenelloidea. By contrast, *Kjerulfia* is a bona fide member of the Holmiidae. Inexplicably, Palmer and Repina (1993) omitted *Esmeraldina* from their concept of the Holmiidae and, indeed, did not even discuss it in their paper on the Olenellina. However, this was rectified in Palmer and Repina (1997). *Esmeraldina* is a member of the Olenelloidea and the Holmiidae, and evidence for this is presented below.

Geyer and Palmer (1995) incorrectly assigned two taxa to the Holmiidae that appear not to belong within the Olenelloidea. *Iyouella* Geyer and Palmer 1995 lacks the defining characters of the Olenelloidea. In particular, L3 does not bulge laterally relative to L1, the ocular lobe contacts but does not merge with the lateral margins of the frontal lobe, and L4 is very short (sag.), roughly two-thirds the length (sag.) of L0 and L1. It instead belongs within the paraphyletic "Fallotaspidoidea." Geyer and Palmer (1995) also assigned the genus *Cambropallas* Geyer 1993 to the Holmiidae. As discussed in Lieberman (1998), species of this genus lack some of the diagnostic characters of the Olenelloidea, and *Cambropallas* must be excluded from the Olenelloidea because the ocular lobes fuse with the entire lateral margin of the frontal lobe. Lieberman (1998) placed this genus within the Judomioidea. Interestingly, Geyer (1993) also had suggested that this genus sat outside the Olenelloidea, though his position changed in subsequent publications.

Lieberman (1998) recently defined the Holmiidae as a clade including, but not restricted to, the genera *Holmia, Kjerulfia, Esmeraldina* and *Holmiella.* This analysis extends the character analysis of Lieberman (1998), presents characters diagnostic for the Holmiidae and discusses all of the genera and species within the family. Characters diagnostic of the Holmiidae include: 1. anterior cephalic border between the genal spine angle and the anterolateral margins of the frontal lobe with length (exsag.) equal to length (sag.) of L0; 2. plectrum absent; 3. pre-ocular furrow on frontal lobe when visible directed inward and forward from glabellar margin; 4. line from posterior tip of ocular lobe to junction of posterior margin of lobe with glabella forms 0 to 25 degree angle with sagittal line; 5. posterior tips of ocular lobes developed opposite S0 or medial part of distal margin of L0; 6. width (tr.) of interocular area greater than or equal to width of ocular lobe; 7. S3 gently or jaggedly convex; 8. L2 and L3 do not merge; 9. S2 convex; 10. distal margins of L2 when proceeding anteriorly either diverging or subparallel; 11. distal sector of S0 convex or sinuous, with proximal end well posterior of distal end; 12. axial part of L0 with node or spine present;

Table 7.
Description of characters and character states used in phylogenetic analysis of Holmiinae; (0) represents the primitive state, (1), (2) and (3) represent derived states.

	Primitive state	Derived states
1. Abrupt dorsal notch-like truncation of ocular lobes at margins of L4	(0) absent	(1) present
2. S3	(0) jaggedly convex or carat shaped	(1) evenly convex
3. Lateral margins of glabella opposite L2, when proceeding anteriorly	(0) diverging	(1) subparallel
4. Lateral lobes on L0	(0) absent	(1) present
5. Posterior margin of ocular lobe opposite	(0) medial part of margin of L1	(1) distal tip of S0 (2) medial part of margin of L0
6. Ornamentation on L0	(0) node	(1) spine
7. Frontal lobe	(0) contacts anterior border furrow	(1) does not contact anterior border furrow
8. Lateral margins of frontal lobe	(0) distal to lateral margins of L0	(1) anterior of lateral margins of L0
9. Intergenal angle developed	(0) midway between ocular lobe and genal spine	(1) directly behind distal tip of ocular lobe
10. Angle intergenal angle forms with transverse line	(0) 0° to 15°	(1) 35° to 45° (2) 80° to 90°
11. Genal spine angle opposite	(0) medial part of margin of L0	(1) medial part of margin of L1 (2) medial part of margin of L3 or medial part of frontal lobe
12. Extraocular region	(0) flattened	(1) prominently vaulted (2) gently sloping from ocular lobe to lateral border furrow

Continued

Table 7 continued.

	Primitive state	Derived states
13. Anterior cephalic border	(0) not prominently separated from extraocular area by furrow	(1) prominently separated by furrow
14. Anterolateral margins of frontal lobe	(0) not prominently separated from anterior extraocular area by furrow	(1) prominently separated from anterior extraocular area by furrow
15. Length (sag.) of frontal lobe	(0) equal to 1.5 times length (sag.) of L0 and L1	(1) equal to 1 to 1.1 times length (sag.) of L0 and L1
16. Anterodistal margins of L3 formed by	(0) ocular lobes	(1) axial furrows
17. Distal margins of L3	(0) convex outward	(1) straight
18. S1	(0) not conjoined medially	(1) conjoined medially
19. Extraocular region opposite of L1	(0) broad, width approximately 75% width of glabella at L1	(1) narrow, width approximately 45% to 55% width of glabella at L1 (2) very narrow, width approximately 10% to 15% width of glabella at L1 (3) very narrow, width approximately 25% width of glabella at L1
20. Orientation of lateral margin of genal spine near spine angle relative to a sagittal line	(0) deflected at roughly 10° to 15°angle	(1) deflected at roughly 30° to 40° angle (2) deflected at roughly 60° to 70° angle
21. Genal spine extends back approximately	(0) first 4 to 5 thoracic segments	(1) at least 8 thoracic segments

Continued

Table 7 continued.

	Primitive state	Derived states
22. Thoracic pleural spines of T1 to T4	(0) sweep back 4 segments	(1) sweep back 2 segments (2) sweep back 1 or no segments
23. S2	(0) not conjoined medially	(1) conjoined medially
24. S3	(0) not conjoined medially	(1) conjoined medially
25. Frontal lobe	(0) does not expand prominently dorsally	(1) expands dorsally at least to level of dorsalmost surface of eyes
26. Line from posterior tip of ocular lobe to junction of posterior margin of lobe with glabella forms	(0) 0° to 15° angle with sagittal line	(1) 20° to 25° angle with sagittal line
27. Anterior cephalic border developed as	(0) flattened plane, angled relative to dorsal plane	(1) rounded ridge
28. Medial part of intergenal angle	(0) with distinct node	(1) with small spine
29. Lateral margins of prothoracic pleural spines inclined at angle relative to sagittal line	(0) 10° to 20°	(1) 40° to 50°
30. Medial and distal tips of S3	(0) as far forward	(1) distal tip further forward than medial tip
31. Medial and distal tips of S2	(0) as far forward	(1) distal tip further forward than medial tip
32. Pygidium	(0) length (sag.) equal to 0.8 to 1 times width (tr.)	(1) broad, twice as wide (tr.) as long (sag.)
33. Posterior margin of pygidium	(0) with median notch	(1) weakly convex
34. Posterior margins of first four thoracic segments near spine bases, relative to orientations of margins on spines	(0) both flexing weakly posteriorly at roughly same angle	(1) roughly transverse (2) flexing slightly anteriorly before flexing posteriorly
35. Ornament on occipital lobe	(0) posterior of midline of L0	(1) anterior of midline of L0

13. posterior margin of L0 convex; 14. glabellar furrows moderately incised; 15. extraocular area gently convex or prominently vaulted; 16. width (tr.) extraocular region opposite L1 equal to 15% to 55% width of glabella at L1; 17. genal spine extends back 4 to 8 thoracic segments; 18. intergenal angle developed posterior of lateral margins of ocular lobes or posterior of point halfway between ocular lobes and genal spine; 19. intergenal spine with distinct node or spine; 20. posterior cephalic border between intergenal angle and L0 flexes posteriorly; 21. thorax broken up into pro- and opisthothorax; 22. anterior margin of T3 medially parallels a transverse line or is very weakly directed posteriorly; 23. T3 normal; 24. anterior margin of thoracic pleural furrow on T3, when proceeding from proximal to distal edge directed weakly posterolaterally before flexing strongly posterolaterally; 25. prothoracic axial rings with two prominent anterolateral lobes; 26. lateral margins of individual prothoracic axial rings prominently converging when proceeding from anterior to posterior edges; 27. single nodes present on medial part of thoracic axial rings; 28. thoracic pleural furrows extend width of inner pleural region; 29. width (tr.) of thoracic pleural spines T5 to T8 at spine midlength less than half length (exsag.) of medial part of inner pleural region; 30. prominent spine at 15th thoracic axial ring or at pro-opisthothoracic boundary; 31. base of spine of width (tr.) roughly half width of axis; and 32. pygidium broad, width (tr.) one to two times length (sag.). On the basis of these characters, all members of the Holmiidae discussed below can be assigned to that family, whereas all other taxa can easily be excluded. Taxa in this family are found in the "*Nevadella*" zone of western Laurentia (the Great Basin), and in the *Schmidtiellus mickwitzi* and the various *Holmia* zones of Baltica. The subfamily Holmiinae is treated as containing the same taxa as does the Holmiidae.

Several Polish taxa that clearly belong to the Holmiidae could not be subjected to phylogenetic analysis as they are poorly preserved and illustrated and were not available for study. The taxonomic status of these species could not be investigated. Included in this group are: *Holmia glabra* Orlowski 1974; *H. orienta* Orlowski 1974; *H. grandis* Kiaer1916; *Schmidtiellus panowi* (Samsonowicz) 1959; *S. nodosus* Orlowski 1985; and *Kjerulfia orcina* Orlowski 1974.

Included Taxa

Subfamily Holmiinae Hupé 1953

Genus *Holmia* Matthew 1890

Type species: *Paradoxides kjerulfi* Linnarsson 1871.
Assigned taxa: *Holmia lapponica* Ahlberg and Bergström 1983; *Kjerulfia*? *palpebra* Ahlberg 1984.
Diagnosis: Anterior cephalic border not prominently separated from extraocular area by furrow; frontal lobe of glabella contacts anterior border furrow; anterolateral parts of glabella not prominently separated from extraocular area by furrow; prominent parafrontal band not visible in dorsal view; anterior margins of frontal lobe at each side of midline deflected posteriorly at roughly 40 degree angle relative to transverse line; length (sag.) of frontal lobe equal to 1.5 times length of L0 and L1 medially; L4 expands dorsally; lateral margins of L4 distal to lateral margins of L0; abrupt dorsal notch-like truncation of ocular lobes at margin of L4 absent; ocular lobe smoothly merges into extraocular area; ocular lobe with prominent furrow; transverse profile of ocular lobes convex dorsally; surface of interocular area developed as flattened shelf; anterodistal margins of L3 formed by

ocular lobes; distal margins of L3 convex outward; S3 conjoined medially, jaggedly convex; medial and distal tips of S3 as far forward; lateral margins of glabella at L2 when proceeding anteriorly diverging; L1 to L3 strongly transversely convex; line between ends of S2 transverse; S0 not conjoined medially; distal sector of S0 convex anteriorly; posterior margin of ocular lobe opposite distal tip of S0; L0 with axial node posterior of midline; lateral lobes present on L0; extraocular region prominently vaulted; genal spine near genal spine angle directed posterolaterally at roughly 10 to 20 degree angle relative to sagittal line; genal spine extends back four to five thoracic segments; genal spine angle opposite medial part of distal margin of L0; intergenal angle posterior of lateral margins of ocular lobes; posterior margin of thoracic pleural furrow on T3 directed evenly posterolaterally; lateral margins of prothoracic pleural spines inclined at roughly 45 degree angle relative to sagittal line; posterior margins of first four thoracic segments near spine bases flex slightly anteriorly before flexing posteriorly; boundary between thoracic pleural furrow and anterior band gradational; length (exsag.) of thoracic pleural furrows at medial part of thoracic segment 1 to 1.3 times length of pleural furrows on distal part of segment; length (exsag.) of thoracic pleural furrows at medial part of segment equal to length (exsag.) of posterior band; spine on 15th thoracic segment short, length (sag.) of two thoracic segments; opisthothorax with prominent pleurae which continue orientation of prothoracic segments; pygidium with length (sag.) equal to width (tr.); posterior margin of pygidium weakly convex.

Discussion: Several taxa that in the past have been assigned to this genus must on the basis of this analysis be excluded. In particular, *Baltobergstroemia mobergi* (Bergström 1973) and "*B.*" *sulcata* (Bergström 1973) must be excluded from the genus *Holmia* because of the condition of the following characters: the posterior margin of the ocular lobe is opposite the medial part of the distal margin of L0 instead of opposite the distal tip of S0; the lateral margins of L4 are directly anterior to the lateral margins of L0 instead of distal to them; the extraocular region is less prominently vaulted; and the frontal lobe does not expand prominently dorsally.

An apparently new *Schmitdiellus* species (formerly *H.* cf. *mobergi* in Ahlberg et al. 1986) must be excluded from *Holmia* because of the condition of the following characters, in addition to the ones listed above for the genus "*Baltobergstroemia*": the anterior cephalic border is prominently separated from the extraocular area by a furrow; S3 is evenly, rather than jaggedly, convex; the distal tip of S2 is further forward than the medial tip, instead of being at the same position; the lateral margins of the glabella opposite L2 are subparallel rather than diverging anteriorly; and the axial node on L0 is anterior of the midline of L0 rather than posterior of the midline. All these species are discussed in greater detail below.

What was formerly referred to as *Holmia mirabilis* by Poulsen (1958) also must be excluded from the genus *Holmia*. This species is discussed in detail above under the genus *Elliptocephala*, to which it is assigned, and character evidence for this exclusion is also provided there.

As construed here, *Holmia* is defined as a paraphyletic clade centered around the type of the genus, *H. kjerulfi*. This was done rather than erecting a new paraphyletic genus, or two monotypic genera, because the morphological differences separating these species from one another seemed slight. Moreover, the nodes separating these species are not extremely resilient, according to tests done on the cladistic analysis conducted here. Thus, it seemed prudent to lump these two species into the genus *Holmia* even though that makes the genus paraphyletic. The shuttermark convention of Wiley (1979) is used to designate the paraphyly of *Holmia*.

HOLMIA KJERULFI (LINNARSSON 1871)
Figure 11.3

Holmia kjerulfi (Linnarsson); Bergström 1973:287, fig. 2 (see for more complete synonymy); Ahlberg 1984:256; Whittington 1988:579, figs. 2, 3; Whittington 1990:37, figs. 13–19; Palmer and Repina 1993:25, fig. 6.1; Palmer and Repina 1997:414, fig. 261.1; Lieberman 1998:67.

Types: Lectotype, Swedish Geological Survey, Uppsala, Sweden, 5329a, b, see Bergström (1973).
Discussion: *Holmia kjerulfi marginata* Orlowski 1974, treated as a distinct species by Orlowski (1985), is closely related to *H. kjerulfi,* as Ahlberg et al. (1986) argued. However, this material is so poorly preserved that at this time it is hard to ascertain whether or not it is conspecific with *H. kjerulfi,* represents a distinct subspecies, or rather deserves full specific status. One potential difference between this Polish material and the Norwegian material is that in the former the extraocular region is relatively narrower. Ahlberg and Bergström (1983) illustrate a small internal mold that they questionably referred to *H. kjerulfi.* It is difficult to tell the veracity of this assignment because of the state of the material.
Material examined: MCZ 2524; PIL Lo4456t.
Occurrence: Norway: The *Holmia* shale, in the *Holmia kjerulfi* zone, Tømten Farm, Ringsaker (Ahlberg 1985).

"*HOLMIA*" *LAPPONICA* AHLBERG AND BERGSTRÖM 1983

Holmia lapponica; Ahlberg and Bergström 1983:242, fig. 2; Ahlberg 1985 fig. 3; Ahlberg et al. 1986:47, fig. 5.

Types: Holotype, Swedish Geological Survey, Uppsala, Sweden, 1231, see Ahlberg and Bergström (1983).
Discussion: This species is assigned to a paraphyletic "*Holmia*" because it differs from the type of that genus in the condition of characters 18, 26 and 28, listed in Tables 5 and 6.
Occurrence: Sweden: Grammajukku Formation, in the *Holmia kjerulfi* zone, on the NE shore of Lake Langvattnet near Langsjoby, 10 km W of the village of Storuman, county of Vasterbotten, southern Swedish Lapland (Ahlberg and Bergström 1983).

"*HOLMIA*" *PALPEBRA* (AHLBERG 1984)

Kjerulfia? *palpebra*; Ahlberg 1984:257, figs. 6, 7; Ahlberg et al. 1986:41, fig. 1.
Holmia? sp.; Ahlberg 1984:256, figs. 4, 5.

Types: Holotype, Swedish Geological Survey, Uppsala, Sweden, 3916, see Ahlberg (1984).
Discussion: Ahlberg's (1984) *Holmia* sp. appears to be identical to the type of his *K.*? *palpebra,* and the specimens hail from the same locality and horizon. Because of this, they are treated as conspecific. This species can no longer be assigned to the genus *Kjerulfia* because it differs from the type of that species in the condition of several characters, including: the anterior cephalic border is developed as a rounded ridge, rather than as a flattened, inclined plane; the lateral margins of L4 are deflected further laterally than the lateral margins of L0, rather than being directly anterior of the lateral margins of L0; the frontal lobe expands more

Table 8.
Character state distributions for Holmiinae and outgroup used in phylogenetic analysis. Characters and alternative states are as listed in Table 7. Missing data are indicated by ?. Character states listed as X are polymorphic, where X=(0&1).

										1	1	1	1	1	1	1	1	1	1	2
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0
Wanneria walcottana	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Holmia kjerulfi	0	0	0	1	1	0	0	0	1	1	0	1	0	0	0	0	0	0	1	0
"Holmia" lapponica	0	0	0	1	1	0	0	0	1	0	0	1	0	0	0	0	0	1	1	0
"Holmia" palpebra	0	0	0	?	1	0	0	0	1	0	0	1	0	0	0	0	0	1	3	0
Baltobergstroemia mobergi	0	0	0	1	2	1	0	1	1	0	0	2	0	0	0	0	0	1	1	0
"Baltobergstroemia" sulcata	0	0	0	1	2	1	0	1	1	0	0	2	0	0	0	0	0	1	3	?
"Baltobergstroemia" sp.	0	1	0	1	2	?	0	0	1	0	0	2	0	0	0	0	0	1	1	0
Kjerulfia lata	0	1	0	1	1	1	0	1	0	0	0	2	0	0	0	0	1	1	1	0
Schmidtiellus mickwitzi torelli	0	1	1	1	2	1	0	1	?	?	?	?	1	?	0	0	0	0	?	?
Schmidtiellus sp.	0	1	1	1	2	1	0	1	1	0	0	2	1	0	1	0	1	1	3	0
Schmidtiellus reetae	0	0	1	1	2	1	0	1	1	0	0	2	1	0	0	0	0	1	1	0
Palmettaspis consorta	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1	1
Palmettaspis parallela	1	1	?	?	2	1	1	1	1	0	0	1	1	1	1	0	1	1	1	0
Palmettaspis lidensis	1	1	0	1	1	1	1	X	1	1	1	1	1	1	1	1	1	1	1	1
"Palmettaspis" cometes	0	1	0	0	2	1	X	0	1	0	0	1	1	1	1	0	0	1	1	0
Esmeraldina rowei	1	1	0	0	1	1	0	0	1	0	0	1	1	1	1	1	1	1	1	1
Holmiella preancora	1	1	1	1	1	0	0	0	1	2	2	1	1	1	1	1	1	0	2	2
Holmiella falcuta	1	1	1	1	1	1	0	0	1	2	2	1	1	1	1	1	1	0	2	2

Continued

prominently dorsally; the medial and distal tips of S2 are as far forward instead of having the distal tip further forward than the medial tip; the extraocular region is more prominently vaulted; the extraocular region is relatively narrower; and the intergenal angle lacks a small spine. This species is assigned to a paraphyletic "*Holmia*" because it differs from the type of that genus in the condition of characters 18, 26 and 28, listed in Tables 5 and 6.
Occurrence: Sweden: Upper part of the Grammajukku Formation, in the *Holmia kjerulfi* zone, E bank of the Torbacken rivulet, about 600 m SSW of Delliknas, the Laisvall area, central Swedish Lapland (Ahlberg 1984).

GENUS *BALTOBERGSTROEMIA* LIEBERMAN NEW GENUS

Type species: *Holmia mobergi* Bergström 1973.
Assigned taxa: *Holmia sulcata* Bergström 1973; *Holmia inusitata* Ahlberg and Bergström in Ahlberg et al. (1986); *Holmia*? sp. in Geyer and Palmer 1995.

Table 8 continued.

	2	2	2	2	2	2	2	2	2	3	3	3	3	3	3
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5
Wanneria walcottana	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Holmia kjerulfi	0	1	X	1	1	0	0	1	1	0	0	0	1	2	0
"Holmia" lapponica	0	0	1	1	1	1	0	0	1	0	0	0	1	2	0
"Holmia" palpebra	?	?	1	1	1	1	1	0	?	0	0	?	?	?	0
Baltobergstroemia mobergi	?	2	1	1	0	1	0	1	1	0	0	?	?	2	0
"Baltobergstroemia" sulcata	?	?	1	1	0	0	1	1	?	0	0	?	?	?	0
"Baltobergstroemia" sp.	?	?	1	?	1	0	0	?	?	0	0	?	?	?	0
Kjerulfia lata	0	?	1	1	0	1	0	1	?	1	1	?	?	?	0
Schmidtiellus mickwitzi torelli	?	2	0	1	0	1	0	?	0	0	1	0	1	1	1
Schmidtiellus sp.	?	?	0	1	0	1	1	?	?	1	1	?	?	?	1
Schmidtiellus reetae	0	2	1	1	0	1	0	1	0	0	1	?	?	1	1
Palmettaspis consorta	1	2	1	1	1	0	1	1	0	1	1	?	?	2	0
Palmettaspis parallela	1	2	1	1	?	0	1	1	0	0	0	?	?	1	0
Palmettaspis lidensis	1	?	1	1	1	0	1	1	?	0	0	0	1	?	0
"Palmettaspis" cometes	1	?	1	1	1	0	1	1	?	0	0	?	?	?	0
Esmeraldina rowei	1	2	1	1	1	0	1	1	1	0	0	0	1	2	0
Holmiella preancora	?	?	0	0	1	0	0	1	?	0	0	1	0	?	0
Holmiella falcuta	?	?	0	0	1	0	0	1	?	0	0	1	0	?	0

Diagnosis: Anterior cephalic border not prominently separated from extraocular area by furrow; frontal lobe contacts anterior border furrow, not expanding prominently dorsally; distal margins of L4 deflected as far or farther laterally than distal margins of L0; length (sag.) of frontal lobe 1.5 times length of L0 and L1; anterodistal margins of L3 formed by ocular lobes; lateral margins of L3 convex outward; S3 and S2 with medial and distal tips as far forward; lateral margins of glabella opposite L2 diverging when proceeding anteriorly; S1, S2 and S3 conjoined medially; posterior margin of ocular lobe opposite medial part of distal margin of L0; lateral lobes on L0 present; L0 with node or spine posterior of midline of L0; intergenal angle directly behind distal tip of ocular lobe; intergenal angle forms 0 to 15 degree angle with transverse line; intergenal angle with small spine; extraocular region gently sloping from eye to lateral border furrow; genal spine angle opposite medial part of distal margin of L0.

Discussion: In the most parsimonious consensus cladogram (Figure 13) two of the species in this genus, *B. mobergi* and *"B." sulcata*, sit in a polytomy that is sister to a clade con-

taining the genera *Kjerulfia* and *Schmidtiellus.* The poorly preserved "*B.*" sp. was variably placed in the six most parsimonious trees (consensus in Figure 13) either sister to the clade including the Great Basin taxa and the genera *Kjerulfia, Schmitdiellus* and the rest of "*Baltobergstroemia*"; sister solely to the clade of Great Basin taxa; or sister solely to the clade comprising the genera *Kjerulfia, Schmitdiellus* and the rest of "*Baltobergstroemia.*" However, in the weighted tree (Figure 14), this species is one node down the tree from "*B.*" *sulcata,* which is in turn sister to a clade consisting of *B. mobergi* and the genera *Kjerulfia* and *Schmidtiellus.* These species could have been treated as three monotypic genera, but because the differences separating them were slight, they are known from relatively limited material and the nodes separating them are not particularly resilient, according to tests of the cladogram in Figure 13, it seemed most prudent to lump these taxa into a single genus, even though that makes the genus paraphyletic (according to the weighted tree) or even polyphyletic (according to some of the unweighted equally most parsimonious trees).
Etymology: The genus is named by combining "Balto" for Baltica, the region where two of these species are found, with the latinized "bergstroem," for Jan Bergström, whose research has significantly increased our knowledge of Cambrian trilobites.

BALTOBERGSTROEMIA MOBERGI (BERGSTRÖM 1973)

Holmia mobergi; Bergström 1973:288, figs. 3–6 (see for more complete synonymy); Ahlberg et al. 1986:48, fig. 1.
?*Holmia inusitata*; Ahlberg and Bergström in Ahlberg et al. 1986:43, fig. 3.

Types: Holotype Palaeontological Institute, University of Lund (PIL), Lund, Sweden, LO 4457T, see Bergström (1973).
Discussion: *Baltobergstroemia inusitata* (Ahlberg and Bergström) appears almost identical to *B. mobergi,* though both species, particularly the former, are known from extremely limited material. The only difference between these taxa is the condition of the occipital spine, whose base appears somewhat broader in *B. inusitata* than in *B. mobergi. Baltobergstroemia inusitata* was not incorporated into phylogenetic analysis because its character codings were identical to those given for *B. mobergi* in Table 8 (the difference in the condition of the occipital spine was not coded because it would have been an autapomorphy). Additional differences may emerge in the condition of the anterior cephalic border, not preserved in *B. inusitata,* and also in the condition of the extraocular area. Therefore, at this time, these two species are not synonymized. If these species are identical, it would imply that the *Holmia inusitata* zone that Ahlberg et al. (1986) established would not be valid. Instead, it would be indistinguishable from the underlying *Schmidtiellus mickwitzi* zone, from which *B. mobergi* is known.

This species is excluded from the genus *Holmia* because of the condition of the following characters: 1. the lateral margins of L4 are anterior of the lateral margins of L0, rather than being deflected distal to the lateral margins of L0; 2. L4 is less prominently expanded dorsally; 3. S1 is conjoined medially; 4. a line from the posterior margin of the ocular lobe to the junction of the posterior margin of the lobe with the glabella forms a larger angle with a sagittal line than it does in *H. kjerulfi*; 5. the posterior margin of the ocular lobe is opposite the medial part of the distal margin of L0 rather than the distal tip of S0; 6. there is a spine rather than a node on L0; 7. the extraocular area is gently sloping from the eye to the lateral border furrow, rather than being prominently vaulted; 8. the thoracic

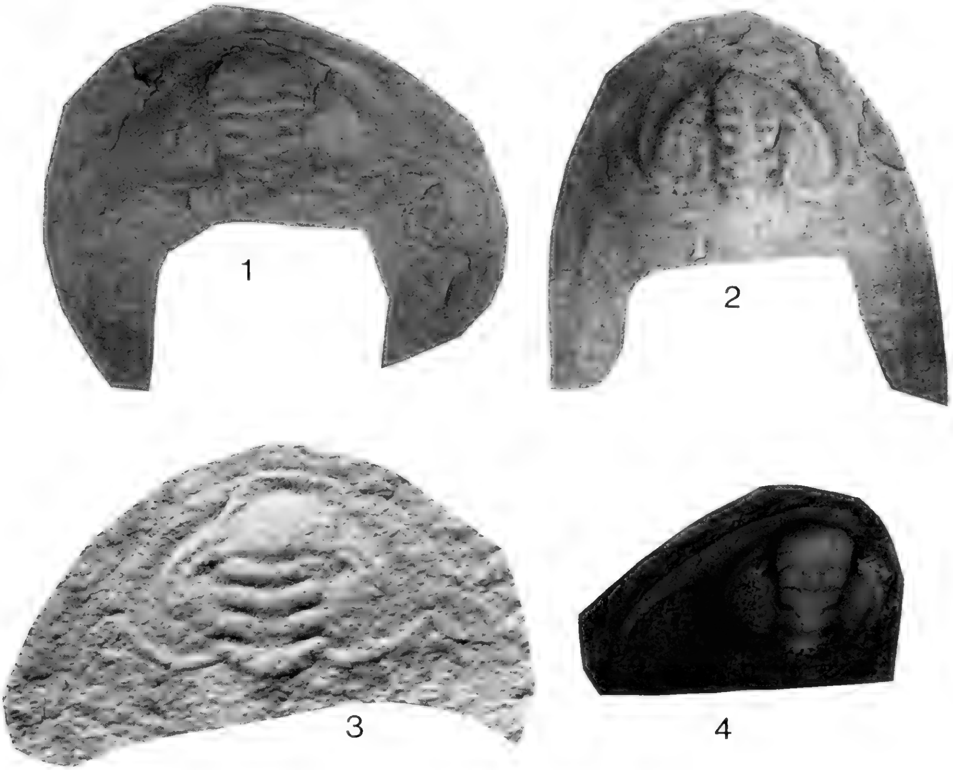


Figure 15.
1–3. Base of the Montenegro Mbr., Campito Fm., Barrel Springs, Silver Peak Range, Nevada. 1, 3. *Esmeraldina rowei* (Walcott). 1. YPM 72929, ×1.6. 3. YPM 35865, ×2.3. 2. *Palmettaspis consorta* Fritz, YPM 72908, ×1.7. 4. *Holmiella falcuta* Fritz, locality is the same as Figure 12.2, GSC 27273, the paratype, ×1.5.

pleural spines are relatively slightly shorter than those found in *H. kjerulfi*.
Occurrence: Sweden: Norretorp Formation, *Schmidtiellus mickwitzi* zone, Early Cambrian, on the shore between Brantevik and Gislovshammar, eastern Scania.

“*Baltobergstroemia*” *sulcata* (Bergström 1973)

Holmia sulcata; Bergström 1973:292, figs. 7, 8; Ahlberg et al. 1986:41, fig. 41.

Types: Holotype, Palaeontological Institute, University of Lund, Lund, Sweden (PIL), LO 4462T, see Bergström (1973).
Discussion: The generic name of this species is placed within paraphyletic shuttermarks because it differs from the type of the genus in the condition of only one character, part of the reason why the two species were placed within the same genus: the condition of the posterior margin of the ocular lobe relative to the junction of the posterior margin of the lobe with the glabella. In *B. mobergi* the posterior margin of the lobe is rotated outward about 10 degrees relative to its condition in “*B.*” *sulcata*. This species is excluded from the genus *Holmia* because of the condition of characters 1 to 3, 5 and 6, listed above under *B. mobergi*.
Occurrence: Sweden: Believed to be in the *Holmia kjerulfi* zone, from Forsemolla in Andrarum and Brantevik-Gislovshammar, eastern Scania.

"*BALTOBERGSTROEMIA*" SP.

Holmia? sp.; Geyer and Palmer 1995:468, fig. 3.10.

Discussion: This species is assigned to the paraphyletic genus "*Baltobergstroemia*" because it differs from *B. mobergi* in the condition of the following characters: the lateral margins of L4 are distal to the lateral margins of L0; L4 expands more prominently dorsally; and the posterior margin of the lobe is rotated inward about 10 degrees relative to its condition in *B. mobergi*. This species is excluded from the genus *Holmia* because of the condition of characters 3 and 5, listed above under *B. mobergi*. It was not described as a new species because of its poor state of preservation and because it is known from limited material. However, it was included in this phylogenetic analysis due to its relevance to Cambrian biogeography.
Occurrence: Morocco: Issafen Formation, *Sectigena* zone, western Anti-Atlas Area, Adai Section (see Geyer and Palmer 1995).

GENUS *KJERULFIA* KIAER 1917

Type species: *Kjerulfia lata* Kiaer 1917.
Assigned taxa: Monotypic.
Diagnosis: Anterior cephalic border not prominently separated from extraocular area by deep furrow, developed as flattened, angled plane; frontal lobe contacts anterior border furrow, does not expand prominently dorsally; lateral margins of L4 directly anterior to lateral margins of L0; anterolateral margins of glabella not prominently separated from extraocular area by furrow; length (sag.) of frontal lobe equal to 1.5 times length (sag.) of L0 and L1; pre-ocular furrow on frontal lobe directed inward and forward from glabellar margin; anterodistal margins of L3 formed by ocular lobes; postero- and anterodistal margins of L3 with same orientation; lateral margins of glabella opposite L2 diverging when proceeding anteriorly; posterior margins of ocular lobes opposite distal tip of S0; line from posterior margin of ocular lobe to junction of posterior margin of lobe with glabella forms 20 to 25 degree angle relative to sagittal line; S3 evenly convex, distal tip further forward than medial tip; distal tip of S2 further forward than medial tip; S0, S1, S2 and S3 conjoined medially; S0 sinuous; L0 with spine posterior of midline of L0; lateral lobes on L0 present; intergenal angle developed midway between ocular lobe and genal spine, with small spine; intergenal angle forms 10 to 15 degree angle with transverse line; extraocular area gently sloping from eye to lateral border furrow, width (tr.) opposite L1 equal to 45% to 55% width of glabella at L1; genal spine angle opposite medial part of distal margin of L0; genal spine close to genal spine angle forms roughly 10 to 15 degree angle relative to sagittal line; genal spine extends back roughly 4 to 5 thoracic segments.
Discussion: As several new characters were discovered in the course of this analysis, a new diagnosis for the genus is presented. Several taxa that in the past have been assigned to this genus must be excluded. In particular, *Kjerulfia*? *palpebra* Ahlberg instead appears to belong in the genus "*Holmia*." Character evidence for its exclusion from the genus *Kjerulfia* is given above under "*H.*" *palpebra*. Geyer and Palmer (1995:472, figs. 5.6, 5.9, 5.12) illustrated four extremely poorly preserved and deformed partial cephala from the Asrir Formation, *Sectigena* zone, in the western Anti-Atlas area of Morocco. Two of these they referred to *Kjerulfia*? sp. and two as Holmiidae? genus and species undetermined. As far as can be determined, these specimens belong to the same species: they are morphologically identical, but are so poorly preserved little more can be said about their relationships. The only conclusive fea-

ture that would group these taxa with *Kjerulfia lata* is the axial spine, posterior of the midline on L0. It is interesting that in addition to "*Baltobergstroemia*" sp. (discussed above) another species belonging to the Holmiidae may be found in Early Cambrian Moroccan strata.

Kjerulfia schwarzbachi Ahlberg and Bergström (Ahlberg et al. 1986) is known from extremely poorly preserved and deformed material, and thus was not considered in phylogenetic analysis. It is difficult to determine its precise generic relationships. One feature it shares with *Kjerulfia lata* is the axial spine, posterior of the midline on L0.

KJERULFIA LATA KIAER 1917

Kjerulfia lata; Kiaer 1917:73, pl. 9–13, 14, figs. 1–2; Nikolaisen and Henningsmoen 1990:62, figs. 3, 7a–c (see for more complete synonymy); Palmer and Repina 1993:27, figs. 6.9, 6.10; Palmer and Repina 1997:416, figs. 2a, b; Lieberman 1998:67.

Types: Lectotype, Paleontologisk Museum Oslo 61376, see Nikolaisen and Henningsmoen (1990).
Discussion: Palmer and Repina (1993, fig. 6.10) figured a partial thorax that they assigned to this species (also illustrated in Palmer and Repina 1997, fig. 2b). Since it is completely disarticulated from any cephalic material it is impossible to determine whether this assignment is correct, and therefore thoracic characters for this taxon were coded as "?" in Table 8.
Occurrence: Norway: Middle part of the massive-bedded quartzite member of the Doulbasgaissa Formation, questionably in the *Holmia kjerulfi* group zone, Digermul peninsula, Tanafjord, Finnmark, and the *Holmia* Shale, questionably in the *Holmia kjerulfi* group zone, Tomten Farm, Ringsaker.

GENUS *SCHMIDTIELLUS* MOBERG IN MOBERG AND SEGERBERG 1906

Type species: *Olenellus mickwitzi* Schmidt 1888.
Assigned taxa: *Olenellus torelli* Moberg 1899; *Schmidtiellus reetae* Bergström 1973; *Schmidtiellus* sp.
Diagnosis: Anterior cephalic border prominently separated from extraocular area by furrow; frontal lobe contacts anterior border furrow, does not expand prominently dorsally; anterolateral margins of glabella not prominently separated from extraocular area by furrow; length (sag.) of frontal lobe roughly 1.5 times length (sag.) of L0 and L1; lateral margins of L4 directly anterior of lateral margins of L0; S3 conjoined medially; lateral margins of glabella opposite L2 subparallel; distal tip of S2 further forward than medial tip; posterior margin of ocular lobe opposite medial part of distal margin of L0; line from posterior margin of ocular lobe to junction of posterior margin of lobe with glabella forms roughly 20 to 25 degree angle with sagittal line; L0 with spine, anterior of midline of L0; lateral lobes on L0 present; intergenal angle developed directly behind distal tip of ocular lobe; intergenal angle forms roughly 10 degree angle with transverse line; extraocular region gently sloping from eye to lateral border furrow; genal spine angle opposite medial part of distal margin of L0; lateral margin of genal spine near spine angle forms roughly 10 to 15 degree angle with sagittal line; posterior margins of first four thoracic segments near spine roughly transverse; thoracic pleural spines on first four segments extend back only one thoracic segment, lateral margins of spines inclined at roughly 10 to 20 degree angle relative to sagittal line.
Discussion: Bergström (1973) gives an excellent discussion of the genus. There he states that the original material of *O. mickwitzi,* which was fragmentary, is now completely lost.

Bergström (1973) went on to demonstrate that subsequent assignments of species to this genus by past authors were incorrect. He further claimed that *S. torelli* is almost indistinguishable from *S. mickwitzi*, although there may be some differences between the two taxa. Bergström (1973) treated these taxa as two varieties of a single species, and his treatment is followed here. *Schmidtiellus*? sp., discussed in Ahlberg et al. (1986), is poorly known and could not be obtained for study in this analysis. If it does indeed belong to this genus, this would extend its range into the *Holmia kjerulfi* zone. Additional species that have been referred to *Schmidtiellus* (such as *S. panowi* [Samsonowicz] and *S. nodosus* Orlowski) are from Polish sections, and are known from extremely limited and poorly illustrated material. These could not be obtained for the purposes of this analysis, and were not considered here.

Species of this genus are, along with *Elliptocephala lundgreni* (discussed above), the earliest undoubted trilobite taxa in the Baltic fossil record, occurring in the *Schmidtiellus mickwitzi* zone. Because additional character evidence bearing on this genus was recovered, a diagnosis for its members is provided.

SCHMIDTIELLUS MICKWITZI TORELLI (MOBERG 1899)

Olenellus torelli; Moberg 1892:3.
Schmidtia? torelli; Moberg 1899:330, pl. 15, figs. 1–17.
Mesonacis torelli (Moberg); Walcott 1910:264, pl. 26, figs. 5–18.
Schmidtiellus mickwitzi torelli; Bergström 1973:296, figs. 9–14; Ahlberg et al. 1986:41, fig. 1; Palmer and Repina 1993:26.

Types: Lectotype, PIL LO 1411T, see Bergström (1973).
Discussion: Bergström's (1973) treatment of this taxon is followed here.
Occurrence: Sweden: Upper part of the Norretorp Formation, *Schmidtiellus mickwitzi* zone, at Hardeberga, South Sandby, E of Lund, and at Bjorkelunda and Brantevik, S of Simrishamn, Scania.

SCHMIDTIELLUS REETAE BERGSTRÖM 1973

Schmidtiellus reetae; Bergström 1973:301, figs. 15, 16; Ahlberg et al. 1986:41, fig. 1; Palmer and Repina 1993, fig. 6.2.

Types: Holotype, Geological Institute of Tallinn, Estonia, Tr 290a.
Occurrence: Estonia: The Lukati Beds, *Volborthella* zone, treated as coeval with the *Schmidtiellus mickwitzi* zone by Ahlberg et al. (1986), at the Saviranna outcrop, 15 km E of Tallinn.

SCHMIDTIELLUS SP.

Holmia cf. *mickwitzi* (Moberg); Skjeseth 1963:40.
Schmidtiellus cf. *mickwitzi* (Moberg); Martinsson 1974:231.
Holmia cf. *mobergi* (Bergström); Ahlberg and Bergström 1978:6; Ahlberg and Bergström in Ahlberg et al. 1986:47, fig. 6, ?fig. 7, non fig. 8, non *Holmia mobergi* Bergström 1973.

Discussion: Because this taxon is known from such limited material (a single, incomplete cephalon) it is not described as a new species; however, its phylogenetic position was evaluated and it was found to be nested within species referable to the genus *Schmidtiellus.* One of the specimens Ahlberg et al. illustrated (1986, fig. 8) as *Holmia* cf. *mobergi* is not conspecific with this new species. Instead, it belongs to *Kjerulfia lata,* as discussed in Nikolaisen and Henningsmoen (1990). Originally, Skjeseth (1963) and Martinsson (1974) held that this specimen was closely related to species of the genus *Schmidtiellus,* and this conclusion is upheld here. However, Ahlberg et al. (1986) treated this taxon as more closely related to species within the genus *Holmia,* commenting on the affinity between this specimen and *H. mobergi,* here treated as the type of the genus *Baltobergstroemia.* An apparently new species of *Schmidtiellus* does bear some affinity to *B. mobergi,* but can be distinguished from that taxon based on the condition of the following characters: 1. the anterior cephalic border is prominently separated from the extraocular area by a furrow; 2. the anterior cephalic border is developed as a rounded ridge, rather than being an angled, flattened plane; 3. the frontal lobe is relatively shorter (sag.); 4. S3 is evenly versus jaggedly convex; 5. the distal margins of L3 are straight, rather than convex outward; 6. the lateral margins of the glabella opposite L2 are subparallel, rather than diverging when proceeding anteriorly; 7. S2 is not conjoined medially; 8. the extraocular area is relatively narrower (tr.); 9. the occipital spine is developed anterior of the midline on L0. Characters 1, 6, 7 and 9 are important in influencing the phylogenetic placement of this specimen within the genus *Schmidtiellus* rather than with *Baltobergstroemia.*

Occurrence: Norway: 1 to 2 m above the top of the Ringsaker Quartzite Member, upper Vangsas Formation, *Schmidtiellus mickwitzi* zone, near Brennsaetersag at the Flagstadelva river, E of Lake Mjosa.

GENUS *PALMETTASPIS* FRITZ 1995

Type species: *Palmettaspis consorta* Fritz 1995.

Assigned taxa: *Palmettaspis parallela* Fritz 1995; *Esmeraldina lidensis* Fritz 1995; *Esmeraldina? cometes* Fritz 1995.

Diagnosis: Anterior cephalic border prominently separated from extraocular area by furrow, border developed as rounded ridge; frontal lobe does not contact anterior cephalic border furrow (variably developed in "*P.*" *cometes*); frontal lobe expands prominently dorsally; anterolateral margins of glabella prominently separated from anterior extraocular area; length (sag.) of frontal lobe equal to 1 to 1.1 times length (sag.) of L0 and L1; S3 evenly convex; notch in ocular lobes where they contact frontal lobe (not in "*P.*" *cometes*); S1, S2 and S3 conjoined medially; posterior margin of ocular lobe opposite distal tip of S0 or medial part of distal margin of L0; line from posterior margin of ocular lobe to junction of posterior margin of lobe with glabella forms roughly 0 to 15 degree angle with sagittal line; L0 with spine, posterior of midline; intergenal angle with small spine directly behind distal tip of ocular lobe; extraocular region prominently vaulted, width (tr.) at L1 45% to 55% width of glabella at L1; genal spine extends back roughly eight thoracic segments; thoracic pleural spines very short (exsag.), extend back only one segment, lateral margins inclined at 10 to 20 degree angle relative to sagittal line (see Fritz 1995 for additional characters).

Discussion: A new diagnosis of this genus is presented, building on that of Fritz (1995), since in the course of this analysis several additional characters were recognized. The genus *Palmettaspis* consists of a clade of three species, plus one species, "*Palmettaspis*" *cometes,* that sits outside of this clade. Although this makes the genus paraphyletic it seemed preferable to erecting a new monotypic genus for this species. This could have been done; however, there were very few characters excluding this species from a monophyletic *Palmettaspis.* In addition, "*P.*" *cometes* is known from relatively limited material. Character differences separating "*P.*" *cometes* from the monophyletic genus *Palmettaspis* include: "*P.*" *cometes* sometimes has the frontal lobe in contact with the anterior border furrow; "*P.*" *cometes* has the lateral margins of L4 distal to the lateral margins of L0 (as does *P. lidensis*); "*P.*" *cometes* does not have a notch in the ocular lobe where it meets the frontal lobe; and it does not have the straight distal margins of L3 (neither does *P. consorta*).

Fritz (1995) suggested that this genus was closely related to either *Mummaspis* or *Schmidtiellus.* Phylogenetic analysis of the Olenelloidea (Lieberman 1998) suggested that this genus is distantly related to *Mummaspis* and is much more closely related to *Schmidtiellus,* though the two do not share a sister group relationship. This analysis predicts that this genus shares a more recent common ancestry with *Esmeraldina* and *Holmiella,* two other taxa known from western Laurentia. Species of this genus are confined to the "*Nevadella*" zone of the Great Basin of western Laurentia.

PALMETTASPIS CONSORTA (FRITZ 1995)

Figure 15.2

Palmettaspis consorta; Fritz 1995:720, figs. 5.4, 8.1–8.6, 10.1, 10.2 (see for more complete synonymy); Palmer and Repina 1997:416, fig. 262.5.

Types: Holotype, USNM 476024, see Fritz (1995).
Material examined: YPM 72908, 72930.
Occurrence: Nevada: near the base of the Montenegro Member, Campito Formation, above the base of the "*Nevadella*" zone, Barrel Spring Section, Lida Wash, Silver Peak Range.

PALMETTASPIS PARALLELA FRITZ 1995

Palmettaspis parallela; Fritz 1995:720, figs. 5.5, 5.6, 9.1–9.5 (see for more complete synonymy).

Types: Holotype, USNM 476027, see Fritz (1995).
Discussion: Fritz (1995) provisionally assigned a partial thorax to this species, and his assignment was accepted for the purposes of coding thoracic characters in this species.
Occurrence: Nevada: near the base of the Montenegro Member, Campito Formation, above the base of the "*Nevadella*" zone, Barrel Spring Section, Lida Wash, Silver Peak Range.

PALMETTASPIS LIDENSIS (FRITZ 1995)

Esmeraldina lidensis; Fritz 1995:716, figs. 5.2, 7.4–7.9.

Types: Holotype, USNM 476020, see Fritz (1995).
Discussion: Fritz (1995) provisionally assigned a lone pygidium to this species, and this assignment was accepted for the purpose of coding pygidial characters for phylogenetic analysis. The posterior pygidial margin was treated as being roughly transverse.

Fritz (1995) assigned this species to the genus Esmeraldina, but phylogenetic analysis indicates it is more closely related to a clade that includes the type of the genus *Palmettaspis* than it is to the type of *Esmeraldina, E. rowei.* Therefore, it is reassigned to the genus *Palmettaspis.* Characters placing this species with *Palmettaspis* rather than with *Esmeraldina* in-

clude: 1. the frontal lobe does not contact the anterior border furrow; 2. the intergenal angle forms a greater angle with a transverse line; and 3. the genal spine angle is opposite the medial part of the distal margin of L1, rather than L0. However, interesting convergences between this species and *E. rowei* include: 1. the anterodistal margins of L3 are formed by the axial furrows; 2. the posterior margin of the ocular lobe is opposite the distal tip of S0; and 3. the genal spine near the spine angle has a similar orientation relative to a sagittal line.
Occurrence: Nevada: near the base of the Montenegro Member, Campito Formation, above the base of the "*Nevadella*" zone, Barrel Spring Section, Lida Wash, Silver Peak Range.

"*PALMETTASPIS*" *COMETES* (FRITZ 1995)

Esmeraldina? *cometes*; Fritz 1995:716, figs. 5.3, 9.8, 10.3–10.5.

Types: Holotype, USNM 479804, see Fritz (1995).
Discussion: Fritz (1995) questionably assigned this species to the genus *Esmeraldina,* but a clade including several species of *Palmettaspis* is more closely related to the type of the genus *Esmeraldina* than is "*P.*" *cometes,* based on phylogenetic analysis of the Holmiidae. Therefore, it cannot be placed within that genus without substantially changing the taxonomy of the family.
Occurrence: Nevada: near the base of the Montenegro Member, Campito Formation, above the base of the "*Nevadella*" zone, Barrel Spring Section, Lida Wash, Silver Peak Range, southern Nevada.

GENUS *ESMERALDINA* RESSER AND HOWELL 1938

Type species: *Holmia rowei* Walcott 1910.
Assigned taxa: *Holmia*? sp. of Fritz (1973).
Diagnosis: Anterior cephalic border developed as rounded ridge, prominently separated by furrow from extraocular area; frontal lobe contacts anterior border furrow, lateral margins distal of lateral margins of L0, expands prominently dorsally; anterolateral margins of frontal lobe prominently separated from extraocular area by furrow (not anterior border furrow); length (sag.) of L4 equal to 1 to 1.1 times length of L0 and L1; dorsal notch in ocular lobe where it contacts lateral margins of frontal lobe; S3 evenly convex, medial and distal tips as far forward; anterodistal margins of L3 formed by axial furrows; distal margin of L3 straight; lateral margins of glabella opposite L2 diverging anteriorly; medial and distal tips of S2 as far forward; S1, S2 and S3 conjoined medially; posterior edge of ocular lobe opposite distal tip of S0; line from posterior margin of ocular lobe to junction of lobe with glabella forms roughly 5 to 15 degree angle relative to sagittal line; L0 with spine posterior of midline; lateral lobes absent from L0; intergenal angle with small spine directly behind distal tip of ocular lobe; intergenal angle forms roughly 10 to 15 degree angle with transverse line; extraocular area prominently vaulted, width (tr.) at L1 45% to 55% width of glabella at L1; genal spine angle opposite distal margin of L0; lateral margin of genal spine near spine angle forms roughly 30 to 40 degree angle with sagittal line; genal spine extends back roughly 8 thoracic segments; thoracic pleural spines on first four segments extend back only one segment; lateral margins of spines inclined at 40 to 50 degree angle relative to sagittal line; posterior margins of first four thoracic segments near spines flex slightly anteriorly; length (sag.) and width (tr.) of pygidium roughly equal; posterior margin of pygidium roughly transverse.
Discussion: Fritz (1995) assigned a few additional taxa to this genus, but these had to be

placed within a revised "*Palmettaspis*." The character evidence for this is discussed above. Resser and Howell (1938) included two taxa in this genus, *Mummaspis occidens* (Walcott) and *M. macer* (Walcott), which also can no longer be considered congeneric with *E. rowei.* Both of these are clearly different from the type of the genus *Esmeraldina,* and character evidence supporting their separation and distinctness from that genus is given below under the genus *Mummaspis.* Fritz (1973) figured a partial cephalon from the Sekwi Formation (probably in the "*Nevadella*" zone) of the Mackenzie Mountains, Northwest Territories, Canada that bears prominent similarity to the type of the genus *Esmeraldina.* For those characters that could be coded, this specimen appears to almost completely match the diagnostic characters of the genus, and thus this species is tentatively placed within *Esmeraldina.* The only significant difference between this species and *E. rowei* is in the condition of S2, which is less prominently incised in the new species. Thus, this genus probably ranges throughout western Laurentia during the "*Nevadella*" zone. Because additional characters of this genus were discovered in the course of this analysis, a revised diagnosis of the genus is presented.

ESMERALDINA ROWEI (WALCOTT 1910)
Figures 15.1, 15.3

Esmeraldina rowei (Walcott); Fritz 1995:714, figs. 5.1, 6.1–6.12, 7.1–7.3, 10.10, 10.11; Palmer and Repina 1997:414, fig. 262.1a, b; Lieberman 1998:71, fig. 3.4 (see for more complete synonymy).

Types: Lectotype, USNM 56801c, see Fritz (1995).
Material examined: LACMIP 6751, 6753, 6756–6758 (all lots containing a total of over 100 individuals); MCZ 2523 (lot containing 4 specimens), 7680; YPM 35865, 72909, 72929.
Occurrence: Nevada: near the base of the Montenegro Member, Campito Formation, above the base of the "*Nevadella*" zone, Barrel Spring Section, Lida Wash, Silver Peak Range.

GENUS *HOLMIELLA* FRITZ 1972

Type species: *Holmiella preancora* Fritz 1972.
Assigned taxa: *Holmiella falcuta* Fritz 1972, and *Holmiella* sp. of Nelson 1976.
Diagnosis: Anterior cephalic border developed as flattened plane, prominently separated from extraocular area by furrow; frontal lobe contacts anterior border furrow, lateral margins distal to lateral margins of L0, expands prominently dorsally; anterolateral margins of glabella prominently separated from extraocular area by furrow; length (sag.) of frontal lobe 1 to 1.1 times length (sag.) of L0 and L1; dorsal notch-like truncation in ocular lobes where they contact frontal lobe of the glabella; anterodistal margins of L3 formed by axial furrows; distal margins of L3 straight; S3 evenly convex, medial and distal tips as far forward; lateral margins of glabella opposite L2 subparallel; S1, S2 and S3 not conjoined medially; medial and distal tips of S2 as far forward; line from posterior edge of ocular lobe to junction of lobe with glabella forms roughly 10 to 15 degree angle with sagittal line; posterior margin of ocular lobe opposite distal tip of S0; lateral lobes present on L0; node or spine on L0 posterior of midline; intergenal angle with small spine directly behind distal tip of ocular lobe; intergenal angle forms 80 to 90 degree angle with transverse line; extraocular region prominently vaulted, very narrow, width (tr.) at L1 10% to 15% width of glabella at L1; genal spine angle opposite distal tip of L3 or L4; lateral margin of genal spine near

spine angle forms roughly 60 to 70 degree angle relative to sagittal line; pygidium twice as wide (tr.) as long (sag.), posterior margin notched.
Discussion: The node including this genus is the most strongly supported in the phylogeny given in Figure 13, and the two taxa definitively assigned to this genus share a large number of synapomorphous traits. We can be extremely confident that these two species are closely related.

Nelson (1976) figured a spectacular, but poorly preserved, specimen from the "*Nevadella*" zone of the Great Basin that he referred to the genus *Holmiella*. This material was examined by the author and Nelson's (1976) generic assignment appears correct. However, it was too poorly preserved to incorporate into phylogenetic analysis. The chief difference between this new species and the taxa from northwestern Canada is that the Laurentian taxon appears to have a somewhat broader extraocular area. Until this new taxon can be studied in detail, the generic diagnosis of *Holmiella* was treated as including a very narrow extraocular area. Including this species, exponents of the genus are known from throughout western Laurentia in the "*Nevadella*" zone. Ahlberg et al. (1986) figured a complete pygidium from the *Holmia kjerulfi* zone of Sweden that they referred to as *Holmiella* sp. It does agree in one important respect with the pygidium of the type of the genus *H. preancora*: the width (tr.) of the pygidium is roughly twice its length (sag.). However, the posterior pygidial margin of Ahlberg et al.'s (1986) *Holmiella* sp. is roughly transverse, or even weakly convex posteriorly, whereas in *H. preancora* it has a median notch. Because pygidial material for all the holmiids is so limited, and only two informative characters of the pygidium could be recognized in this analysis, it cannot be definitively stated whether or not this pygidium belongs to *Holmiella* or to some other holmiid genus. This pygidium differs in as many characters from those known for *Holmiella* as it does from those known for *Esmeraldina, Schmidtiellus, Holmia* and "*Baltobergstroemia*." Therefore, at this time the pygidium is treated as belonging to an indeterminate holmiid. If it does indeed belong to a species of *Holmiella*, it would extend the geographic range of that genus into Baltica.

HOLMIELLA PREANCORA FRITZ 1972

Holmiella preancora; Fritz 1972:25, pl. 4, figs. 1–13; Palmer and Repina 1993:26, figs. 6.4, 6.6; Lieberman 1998:67.

Types: Holotype, GSC 27241, see Fritz (1972).
Material examined: GSC 27240, a paratype.
Occurrence: Canada: Northwest Territories, the type section of the Sekwi Formation (Handfield 1968), 0.2 mi SE of June Lake, 348 ft to 668 ft above the base of the formation, "*Nevadella*" zone, following Fritz (1972), S end of the Sekwi Range, Mackenzie Mountains, District of Mackenzie.

HOLMIELLA FALCUTA FRITZ 1972
Figure 15.4

Holmiella falcuta; Fritz 1972:26, pl. 7, figs. 7–17.

Types: Holotype, GSC 27277, see Fritz (1972).
Material examined: GSC 27273, a paratype.
Occurrence: Canada: Northwest Territories, the type section of the Sekwi Formation

(Handfield 1968), 0.2 mi SE of June Lake, 668 ft to783 ft above the base of the formation, "*Nevadella*" zone, following Fritz (1972), S end of the Sekwi Range, Mackenzie Mountains, District of Mackenzie.

Phylogenetic Analysis of *Fritzolenellus*

Fritzolenellus is a small clade distributed throughout part of Laurentia (northwestern Canada and northwestern Britain) in the lower and middle *Olenellus* zone (according to the stratigraphic correlations of Fritz [1992] and Palmer and Repina [1993]). It includes three species, all of which were subjected to phylogenetic analysis here.

Two outgroup taxa were employed in phylogenetic analysis, *Wanneria walcottana* and *Holmia kjerulfi.* These species are appropriate outgroups to the genus *Fritzolenellus* based on the higher level phylogenetic analysis of the Olenelloidea presented in Lieberman (1998). Phylogenetic patterns were determined by parsimony analysis of four holaspid exoskeletal characters. Only a limited number of characters could be recognized because of the paucity of taxa assigned to the genus, as well as the poor state of preservation of two of the species assigned to *Fritzolenellus.* However, since these characters seemed to contain some phylogenetic information content, cladistic analysis was pursued. These characters and character states are given in Table 9. The codings for the taxa analyzed are given in Table 10. All characters were treated as unordered (nonadditive). These data were subjected to an exhaustive search on PAUP v. 3.1.1 (Swofford 1993). One most parsimonious tree (Figure 16) was recovered of length 5 steps, consistency index = 0.80, and retention index = 0.75 The g_1 statistic, was –0.94, and this value differs from those values derived from distributions using random data at the 0.01 level of confidence (Hillis 1991). This suggests that there is a strong and robust phylogenetic signal to the character data given in Table 10. The bootstrap confidence value for the node of the most parsimonious tree duplicated in the bootstrap analysis is given in Figure 16. Using the method of Bremer (1994), three trees of length less than or equal to 6 steps and eight trees of length less than or equal to 7 steps were recovered before the analysis was terminated because the consensus cladogram was a complete polytomy. The branch support value is given in Figure 16. The total tree support for the cladogram is 0.2, a moderate value according to Bremer (1994).

All the taxa within this genus are known from the lower and middle *Olenellus* zone, implying fairly good concordance between stratigraphic and phylogenetic patterns (according to the correlations of Fritz [1992] and Palmer and Repina [1993]). The species that appears first in the fossil record is cladistically subordinate to the other two species of *Fritzolenellus,* which appear relatively later in the fossil record.

Systematic Paleontology

Family "Laudoniidae" Harrington 1956
Subfamily "Laudoniinae" Harrington 1956

Lieberman (1998) argued for the designation of a paraphyletic family "Laudoniidae" and subfamily "Laudoniinae" (paraphyly designated using the shuttermark convention of Wiley

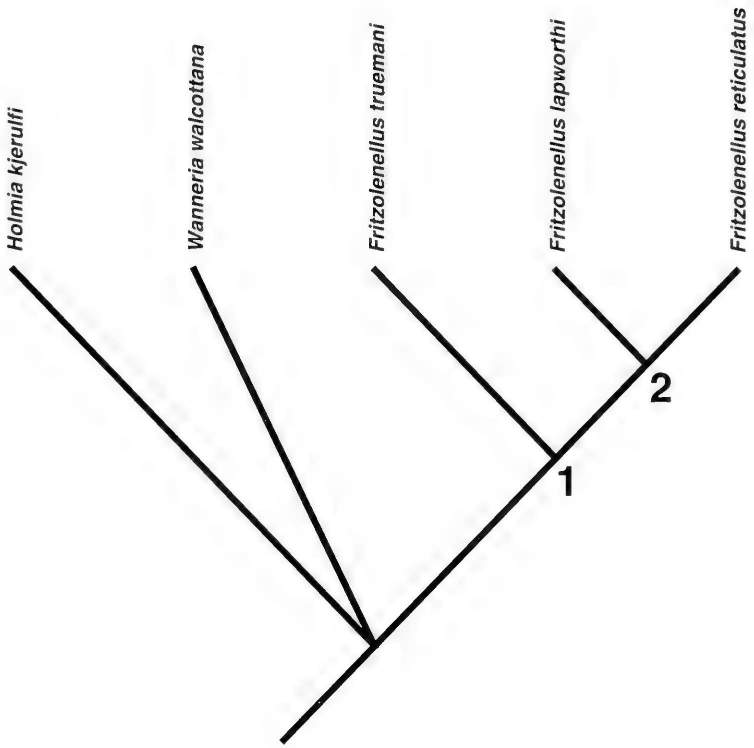


Figure 16.
The most parsimonious cladogram of length 5 steps produced from analysis of character data in Table 10 with PAUP v. 3.1.1 (Swofford 1993). The cladogram is constructed using an exhaustive search. The retention index is 0.75, and the consistency index is 0.80. The following nodes in the text were supported by the following bootstrap confidence values (see text for bootstrapping procedure used): Node *1* = 0.52; Node *2* = 0.79. Node *2* has a branch support value (Bremer 1994) of 1. Character states are placed at nodes, using MacClade v. 3.04 (Maddison and Maddison 1992), with the characters given in Table 9. The apomorphic state is given in parentheses. Node *1*, 3(1); Node *2*, 1(1), 2(1).

[1979]), modifying Laudoniinae Harrington 1956. The newly defined paraphyletic family and subfamily includes the genera *Laudonia, Mummaspis* and *Fritzolenellus*, and that supra-generic classification is followed for the purposes of this analysis.

Included Taxa

GENUS *FRITZOLENELLUS* LIEBERMAN 1998

Type species: *Olenellus truemani* Walcott 1913.
Assigned taxa: *Olenellus reticulatus* Peach 1894; *O. lapworthi* Peach 1894; *Fritzolenellus* sp. aff. *truemani*; possibly *Olenellus intermedius* Peach 1894.
Diagnosis: Anterior cephalic border developed as raised ledge; anterior border prominently separated from extraocular area by furrow; plectrum absent; anterior part of glabella prominently separated from anterior extraocular area by furrow (not anterior border furrow); prominent parafrontal band not visible in dorsal view; anterior margins of frontal lobe at each side of midline deflected posteriorly at roughly 40 degree angle rela-

tive to transverse line; length (sag.) of L4 equal to roughly 1.5 times length (sag.) of L0 and L1; L4 expands prominently dorsally; lateral margins of L4 distal to lateral margins of L0; pre-ocular furrow on frontal lobe directed inward and forward from glabellar margin; anterolateral margins of ocular lobe separated from extraocular area by prominent furrow; ocular lobe with prominent ocular furrow; line from posterior tip of ocular lobe to junction of posterior margin of lobe with glabella forms roughly 10 to 15 degree angle with sagittal line; transverse profile of ocular lobes convex dorsally; surface of interocular area arched; width (tr.) of interocular area approximately equal to maximum width of ocular lobe; anterodistal margins of L3 formed by ocular lobe; distal margins of L3 convex outward; S3 jaggedly convex, conjoined medially; line between ends of S2 transverse; L2 and L3 do not merge; S2 convex anteriorly; distal margins of L2 when proceeding anteriorly diverging; distal sector of S0 convex anteriorly, well anterior of proximal end; posterior margin of L0 roughly transverse; lateral lobes on L0 present; extraocular area flattened, width (tr.) roughly equal to 75% width of glabella at L1; length (exsag.) of genal spine roughly equal to length (sag.) of first four to five thoracic segments; genal spine angle developed opposite medial part of distal margin of L0; intergenal angle developed posterior of point half way between ocular lobes and genal spine; intergenal angle roughly parallel to transverse line; medial part of posterior border between intergenal angle and L0 roughly transverse; thorax broken up into pro- and opisthothorax; anterior margin of T3 before flexing strongly posteriorly roughly parallel to transverse line; T3 macropleural, projects posteriorly 6 to 8 thoracic segments; anterior margin of thoracic pleural furrow on T3 when proceeding from proximal to distal edge directed weakly posteriorly, before flexing strongly posteriorly; posterior margin of thoracic pleural furrow on T3 directed evenly posterolaterally; thoracic pleural spines on T5 to T8 developed as broad sweeping projections extending roughly four segments back; prothoracic axial rings without prominent lateral furrows; single nodes very faint, but present on median portion of some thoracic axial rings; thoracic pleural furrows extend width of inner pleural region; boundary between thoracic pleural furrow and anterior band sharp; thoracic pleural furrows short (exsag.), length equal to roughly half length (exsag.) of posterior band; thoracic pleural spines T5 to T8 at spine midlength with width (tr.) one half to two-thirds length (exsag.) of medial part of inner pleural region; prominent spine on 15th thoracic axial ring of length (sag.) of entire prothorax, base of spine nearly as wide (tr.) as axis of segment; segments of opisthothorax with prominent pleurae; pygidium with length (sag.) equal to width (tr.); posterior margin of pygidium weakly convex (only some of these thoracic characters, and none of the pygidial characters, could be determined in *F. lapworthi*; none of the pygidial characters could be determined in *F. reticulatus*).

Discussion: Lieberman (1998) introduced the genus *Fritzolenellus* and provided a diagnosis for it. A slightly refined diagnosis is presented here because all species within the genus could be incorporated into this analysis. One of the characters listed in the above diagnosis that merits additional discussion is the condition of L2 and L3; these do not appear to merge distally due to S2, which contacts the axial furrows. On one specimen of *F. truemani* figured by Fritz (1992, pl. 7, fig. 1) this character state is not clearly visible. In this figure, there are actually two cephala. One, GSC 99007, the inverted specimen, clearly displays the diagnostic character state. The other, GSC 99006, clearly displays the character state on the left lateral lobes, but the right lateral lobes are a different matter. Here, S2 is very weak, but appears to contact the axial furrow, faintly bisecting L2 and L3 such that they do not merge. Based on this character interpretation, this species was treated as having L2 and L3 not merging laterally.

As previously defined (Cowie and McNamara 1978; Fritz 1972, 1992; Palmer and

Table 9.
Description of characters and character states used in phylogenetic analysis of *Fritzolenellus*; (0) does not always represent the primitive state as two outgroup taxa were used in this analysis; however, for convenience, one taxon, *Holmia kjerulfi* was coded as having all (0) character states; (1) can represent the derived state.

	Primitive state	Derived states
1. Anterior cephalic border between frontal lobe and genal spine angle with length (exsag.) roughly equal to	(0) length (sag.) of L0	(1) half the length (sag.) of L0
2. Frontal lobe	(0) contacts the anterior border furrow	(1) does not contact the anterior border furrow
3. Anterolateral margins of glabella	(0) not prominently separated from extraocular area by marginal furrow	(1) prominently separated from extraocular area by marginal furrow
4. Posterior margins of ocular lobes opposite	(0) distal tip of S0	(1) medial part of distal margin of L1

Repina 1993) this taxon included a large number of phylogenetically disparate units. Some of these are more closely related to the type of the genus *Olenellus,* whereas others, including the taxa discussed below under *Fritzolenellus,* are more closely related to a clade that includes *Laudonia, Mummaspis, Bristolia, Nephrolenellus* and several other genera. A new genus was necessary for the latter species, otherwise *Olenellus* would be polyphyletic. This has implications for stratigraphic correlations in the late Early Cambrian (e.g., Palmer and Repina 1993) that rely on a genus concept (in particular the genus *Olenellus* of the eponymous *Olenellus* zone) to correlate strata. Certainly genera should be used to correlate strata only with caution, though such methods appear to predominate the stratigraphy of the Early Cambrian. If the taxonomic status of the genus *Olenellus* is changed fundamentally, it could potentially cause a concomitant change in stratigraphic patterns.

A few species formerly assigned to the genus *Olenellus* need to be reassigned to *Fritzolenellus.* In particular, what Cowie and McNamara (1978), McNamara (1978) and sources cited therein referred to as *Olenellus reticulatus* and *O. lapworthi,* two species from the middle *Olenellus* zone of northwestern Scotland, actually appear to belong to the genus *Fritzolenellus.* They bear all of the diagnostic characters of the genus given above. The thoracic material of *F. lapworthi* and *F. reticulatus* are very similar to the type of the genus, *F. truemani.* However, one difference evident between the thorax of *F. reticulatus* and that of *F. truemani* is the relatively narrower (tr.) pleural spines in the former.

This generic assignment for these two species challenges a central tenet of McNamara's (1978) paper, as he placed these species into a paedomorphic evolutionary pathway along with *Olenelloides armatus* and what is viewed here as *Mesonacis hamoculus* (discussed in

Table 10.
Character state distributions for *Fritzolenellus* and outgroups used in phylogenetic analysis. Characters and alternative states are as listed in Table 9.

	1	2	3	4
Holmia kjerulfi	0	0	0	0
Wanneria walcottana	0	0	0	1
Fritzolenellus truemani	0	0	1	1
Fritzolenellus lapworthi	1	1	1	0
Fritzolenellus reticulatus	1	1	1	1

greater detail above under the genus *Mesonacis*). *Mesonacis* and *Olenelloides* are distantly related to *Fritzolenellus,* and to one another, based on a phylogenetic analysis of the Olenelloidea by Lieberman (1998), and thus it is inconceivable that they are connected by a paedomorphic evolutionary pathway.

Character differences separating species of *Mesonacis* from species of *Fritzolenellus* include: 1. the anterior part of the glabella is prominently separated from the anterior extraocular area by a furrow in *Fritzolenellus* (not the anterior border furrow), it is not in *Mesonacis*; 2. the anterolateral margins of the ocular lobe are separated from the extraocular area by a prominent furrow in *Fritzolenellus,* they are not in *Mesonacis*; 3. the interocular area is arched dorsally in *Fritzolenellus,* it is developed as a flattened shelf in *Mesonacis*; 4. the distal sector of S0 is convex anteriorly in *Fritzolenellus,* it is straight in *Mesonacis*; 5. lateral lobes are present on L0 in *Fritzolenellus,* they are absent in *Mesonacis*; 6. the intergenal angle roughly parallels a transverse line in *Fritzolenellus,* it is directed anteriorly between 30 to 50 degrees relative to a transverse line in *Mesonacis*; 7. the anterior margin of T3 in *Fritzolenellus* parallels a transverse line medially, in *Mesonacis* medially it is directed anteriorly at least five degrees relative to a transverse line; 8. the pleural spine of T3 projects posteriorly 6 to 8 thoracic segments in *Fritzolenellus,* in *Mesonacis* it either projects posteriorly the entire length of the prothorax, or 3 to 4 segments; 9. the anterior margin of the pleural furrow on T3, when proceeding from the proximal to distal edge is directed weakly posteriorly before flexing strongly posteriorly in *Fritzolenellus,* in *Mesonacis* it parallels a transverse line, before flexing strongly posteriorly; 10. in *Fritzolenellus* the thoracic pleural furrows extend the width of the inner pleural region, in *Mesonacis* they extend onto the spines; 11. in *Fritzolenellus* the thoracic pleural furrows (excluding those of T3) are very short (exsag.), equal to half the length (exsag.) of the posterior band, in *Mesonacis* they are relatively longer (exsag.), equal to 1 to 1.5 times the length of the posterior band; 12. in *Fritzolenellus* the pygidium is relatively broader, having length (sag.) equal to the width (tr.), whereas in *Mesonacis* the pygidium has the length (sag.) equal to 1.5 times the width.

Olenellus intermedius Peach is another species from the middle *Olenellus* zone of Scotland. It is known from two poorly preserved specimens, both early ontogenetic stages. McNamara (1978) also placed this species into the paedomorphic evolutionary pathway, along with *F. reticulatus, F. lapworthi* and *M. hamoculus. Olenellus intermedius* appears to be conspecific with, or belongs to a species closely related to, either *F. reticulatus* or *F. lapworthi.* Specimens of *F. intermedius* have the following characters, found in these species and not in

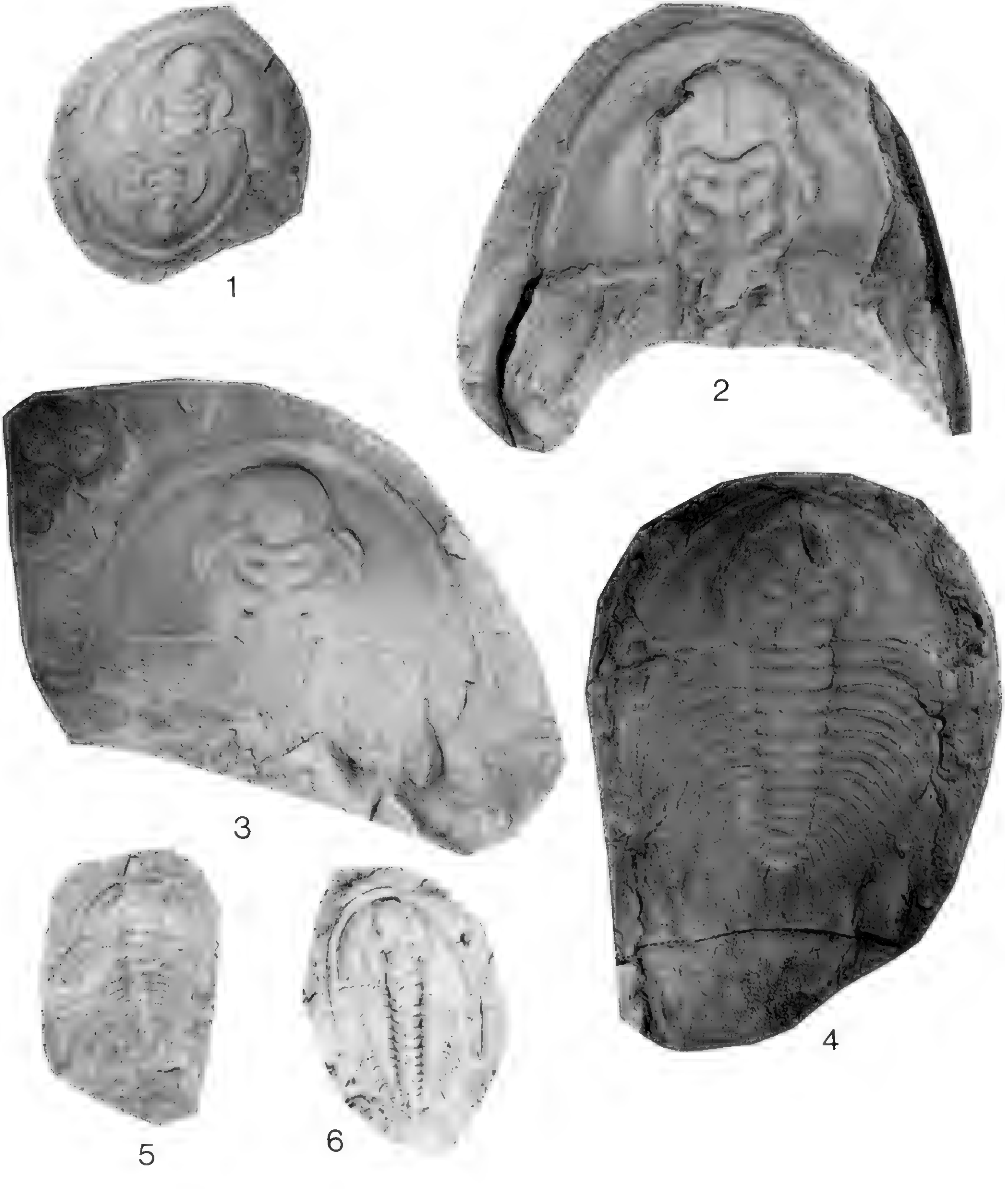


Figure 17.
1. *Fritzolenellus truemani* (Walcott), 495 ft to 575 ft above the base of the Mural Fm. (formerly Type Tah Fm.), Cinnamon Peak-Whitehorn Mountain section, just N of the Mount Robson Provincial Park boundary, western Alberta, Canada, GSC 99006 (top) and 99007, ×1.4. 2–5. ?The Mural Fm., in the talus slope immediately W of Mumm Peak, just N of the Mount Robson Provincial Park boundary, western Alberta, Canada. **2.** *Mummaspis occidens* (Walcott), MCZ 110675, ×1.5. **3.** *Mummaspis truncatooculatus* (Fritz), MCZ 110677, ×1.5. **4, 5.** *Mummaspis muralensis* (Fritz). **4.** MCZ 110676, ×1.5. **5.** MCZ 110673, ×1.5. **6.** *Mummaspis macer* (Walcott), Kinzers Shale, Fruitville, Pennsylvania, USNM 60092, ×1.7.

M. hamoculus: the lateral margins of L4 appear to be distal to, rather than anterior to, the lateral margins of L0; a prominent pre-ocular furrow directed inward and forward is visible; a furrow appears to be present in front of the anterolateral margins of the ocular lobe and the anterolateral margins of the glabella; and the lateral margins of L0 and L1 are subparallel. The chief similarities between *F. intermedius* and *M. hamoculus* are the condition of the genal spine angle, relatively advanced in both taxa (opposite S0 in the former, opposite the medial part of the distal margin of L1 in the latter) and the state of the intergenal angle, directed anteriorly at a roughly 30 to 35 degree angle relative to a transverse line. The bulk of the character evidence suggests that this species is closely related to *F. lapworthi* and *F. reticulatus,* but as it is known from poorly preserved, early ontogenetic stage material, it is only tentatively placed within the genus *Fritzolenellus.*

Fritzolenellus truemani (Walcott 1913)
Figure 17.1

Olenellus truemani; Walcott 1913:316, pl. 54, figs. 2, 6, and 8; Walcott 1916, pl. 17, figs. 2, 6, and 8; Fritz 1992:15, pl. 6, figs. 1–4, pl. 7, figs. 1–6, and text fig. 6b.
Fritzolenellus truemani (Walcott); Lieberman 1998:72.

Types: Lectotype, USNM 60084, designated in Fritz (1992).
Discussion: As discussed in Fritz (1992) and Lieberman (1998), the specimens that Lochman in Cooper et al. (1952) illustrated from the Caborca region of Mexico and assigned to *Olenellus truemani* are distinct from Walcott's (1913) original material of that species. The illustrated cephala from late ontogenetic stage individuals differ in the condition of several characters from *F. truemani*: they lack the convex (tr.) ocular lobes; have the lateral margins of the frontal lobe medial to the lateral margins of L0; have L2 and L3 merging distally; have a straight S0; and have L0 with a strongly convex posterior margin. On the basis of these and other characters the material cannot be treated as conspecific, or even congeneric, with *F. truemani.* Instead, these specimens appear to be referable to *Olenellus,* and will be discussed in a subsequent publication.

As discussed in Fritz (1992) and Lieberman (1998), the specimens Fritz (1972) illustrated and assigned to *O. truemani* are not closely related to *F. truemani* when we consider on what Walcott (1913) originally based his species truemani. The material Fritz (1972) illustrated is actually a new species, *Elliptocephala walcotti* (discussed in greater detail above under the genus *Elliptocephala*).

Fritz (1992) figured several cephala representing early ontogenetic stages that he assigned to *Mummaspis oblisooculatus* Fritz. These specimens (1992, pl. 16, figs. 4–7, and pl. 17, figs. 1, 2) are similar, if not identical, to *F. truemani.* They are referred to as *F.* sp. aff. *truemani.* The chief difference between these specimens and *F. truemani* is that in the former the frontal lobe extends relatively farther forward. Differences between these specimens of *Fritzolenellus* and those of species belonging to the genus *Mummaspis,* such as true *M. oblisooculatus,* include the following: in *Fritzolenellus* the anterior margins of the frontal lobe at each side of the midline are deflected posteriorly at a roughly 40 degree angle relative to a transverse line, whereas in *Mummaspis* the margins are deflected posteriorly at a roughly 10 degree angle relative to a transverse line; in *Fritzolenellus* S1 is not conjoined medially, at least in later ontogenetic stages, and this appears to be the case for *F.* sp. aff. *truemani,* whereas in *Mummaspis* it is conjoined medially; in *Fritzolenellus* the distal sector of S0 is straight, at least in later ontogenetic stages, and this appears to be the case for *F.* sp. aff. *truemani,* whereas in *Mummaspis* it is convex; and in *Fritzolenellus* the posterior margin of L0 is more transverse than it is in *Mummaspis.* Therefore, these specimens can no longer be assigned to the genus *Mummaspis.* Instead, they are treated as comprising a species closely related to *F. truemani* and are accordingly referred to as *F.* sp. aff. *truemani.* These specimens were not described as comprising a new species and will not be subjected to phylogenetic analysis until additional material comprising later ontogenetic stages is recovered.

As defined originally by Walcott (1913), *F. truemani* was held to be closely related to the genus *Olenellus.* However, a large number of characters separate this species from the types of *O.* (*Olenellus*) and what was formerly the type of *O.* (*Paedeumias*), and therefore *F. truemani* must be excluded from those genera. In particular: 1. in *F. truemani* the anterolateral margins of the frontal lobe are prominently separated from the anterior extraocular area by a furrow (not the anterior border furrow), whereas in *Olenellus* they are not; 2. in *F. truemani* L4 expands more prominently dorsally than it does in *Olenellus*; 3. in *F. truemani* the lateral margins of L4 are distal to L0, whereas they are proximal to or directly anterior to the lateral margins of L0 in *Olenellus*; 4. in *F. truemani* the pre-ocular furrow is directed inward and forward from the glabellar margin, whereas when visible it is transverse in *Olenellus*; 5. in *F. truemani* the anterolateral margins of the ocular lobe are prominently separated from the extraocular area by a furrow, in *Olenellus* they are not; 6. in *F. truemani* a transverse profile of the ocular lobes is convex dorsally whereas it is flattened in *Olenellus*; 7. in *F. truemani* the interocular area is arched dorsally, whereas it is developed as a flattened shelf in *Olenellus*; 8. in *F. truemani* S3 is conjoined medially whereas it is not in *Olenellus*; 9. in *F. truemani* a line between the ends of S2 is transverse, whereas it is directed inward and posteriorly at a roughly 45 degree angle relative to a transverse line in *Olenellus*; 10. in *F. truemani* L2 and L3 do not merge distally, in *Olenellus* they do; 11. in *F. truemani* S2 is convex anteriorly, in *Olenellus* it is straight; 12. in *F. truemani* the distal sector of S0 is straight whereas in *Olenellus* it is convex anteriorly; 13. in *F. truemani* lateral lobes are present on L0, they are absent in *Olenellus*; 14. in *F. truemani* the intergenal angle is developed posterior of a point half way between the ocular lobes and the genal spine angle, whereas it is developed adjacent to the genal spine angle in *Olenellus*; 15. in *F. truemani* the medial part of the posterior border between the intergenal angle and L0 is transverse, in *Olenellus* it flexes posteriorly; 16. in *F. truemani* the thoracic pleural furrows extend the width of the inner pleural region, in *Olenellus* they extend onto the spines; 17. in *F. truemani* the thoracic pleural furrows (excluding those of T3) are very short (exsag.), with length equal to half the length (exsag.) of the posterior band, in *Olenellus* they are relatively longer (exsag.), with length equal to roughly 1.5 times the length (exsag.) of the posterior band; 18. in *F. truemani* the opisthothorax has prominent pleurae whereas these are absent in *Olenellus*; 19. in *F. truemani* the pygidium is relatively broad, with the length (sag.) roughly equal to the width (tr.), whereas it is relatively narrow in *Olenellus,* with the length (sag.) roughly equal to 1.5 times the width (tr.).

Material examined: GSC 99002, 99003, 99006, 99007, 99010, 99011; USNM 60084, the lectotype, and 60085–60091.

Occurrence: Canada: Alberta, the Mural Formation, in the talus slope immediately west of Mumm Peak, and from the middle Mural Formation, 412 ft to 439 ft above the base of that formation, at the Mumm Peak section, and 495 ft to 575 ft above the base of the Mural Formation (formerly Type Tah Formation), Cinnamon Peak-Whitehorn Mountain section, in the lower *Olenellus* zone, Early Cambrian, just N of the Mount Robson Provincial Park boundary, western Alberta (see discussion in Fritz 1992).

FRITZOLENELLUS LAPWORTHI (PEACH AND HORNE 1892)

Olenellus lapworthi; Peach and Horne 1892:227, pl. 5, figs. 2–4, 6; Cowie and McNamara 1978:620, pl. 69, figs. 1–6 (see for complete synonymy); McNamara 1978:635, text figs. 3, 4i, j, 5–7.

Types: Lectotype, GSE 5364, see Cowie and McNamara (1978).
Discussion: Character evidence that this species can no longer be assigned to the genus *Olenellus* is congruent with the evidence that indicates the separation of *F. truemani* from *Olenellus,* and is discussed above under that species.
Material examined: GSE 5364, the lectotype, and GSE 13301 and 13310, both paralectotypes.
Occurrence: Scotland: The "Fucoid" Beds, middle *Olenellus* zone (according to Palmer and Repina 1993), Allt nan Righreon near the hill-track 4 mi S of Dundonnell, Ross and Cromarty, northwestern Scotland (see Cowie and McNamara 1978).

FRITZOLENELLUS RETICULATUS (PEACH 1894)

Olenellus reticulatus; Peach 1894:665, pl. 30, figs. 1–5, pl. 31, figs. 1–7; Cowie and McNamara 1978:624, pl. 69, figs. 7–15, pl. 70, figs. 1, 2, 12 (see for complete synonymy); McNamara 1978:635, text figs. 4g, h, 5–7.

Types: Lectotype, GSE 5343, see Cowie and McNamara (1978).
Discussion: One of the specimens of *F. reticulatus* illustrated in Cowie and McNamara (1978, pl. 69, fig. 10) has a slightly narrower extraocular area than that typical of the lectotype and other material of the species. As this specimen appeared to resemble typical *F. reticulatus* in the condition of all other morphological characters, at this time it was treated as conspecific with *F. reticulatus.* Character evidence that this species can no longer be assigned to the genus *Olenellus* is congruent with the evidence that indicates the separation of *F. truemani* from *Olenellus,* and is discussed above under that species.
Material examined: GSE 5343, the lectotype, and GSE 5372 and 13295.
Occurrence: Scotland: The "Fucoid" Beds, middle *Olenellus* zone (according to Palmer and Repina 1993), the northern slopes of Meall a'Ghiubhais, 3 mi WNW of Kinlochewe, and Allt nan Righreon near the hill-track 4 mi south of Dundonnell, Ross and Cromarty, northwestern Scotland (see Cowie and McNamara 1978).

· SIX ·

Phylogenetic Analysis of *Mummaspis*

Mummaspis is a small clade distributed throughout part of Laurentia (northwestern Canada and eastern Pennsylvania) in the lower middle and perhaps upper *Olenellus* zone. It includes five species, all of which were subjected to phylogenetic analysis here.

A single outgroup taxon was employed in phylogenetic analysis, *Fritzolenellus truemani* (See Chapter 5). This species is an appropriate outgroup to the genus *Mummaspis* based on the higher level phylogenetic analysis of the Olenelloidea presented in Lieberman (1998). Phylogenetic patterns were determined by parsimony analysis of five holaspid exo-skeletal characters, given in Table 11. The codings for the taxa analyzed are given in Table 12. All characters were treated as unordered (nonadditive). These data were subjected to an exhaustive search on PAUP v. 3.1.1 (Swofford 1993). One most parsimonious tree (Figure 18) was recovered of length 9 steps, consistency index = 0.78, and retention index = 0.67.

The g_1 statistic, which is used to measure tree length skewness distributions, was –0.44. However, this value does not differ from those values derived from distributions using random data at the 0.05 level of confidence (Hillis 1991) (minimum value for g_1 indicating six taxa differ significantly from random data is –0.51). The bootstrap confidence values for the nodes of the most parsimonious tree duplicated in the bootstrap analysis are given in Figure 18. Using the analysis of Bremer (1994), 9 trees of length less than or equal to 10 steps were recovered before the analysis was terminated because the consensus cladogram was a complete polytomy, implying limited total support (Bremer 1994).

All the taxa within this genus are known from the lower and middle-upper *Olenellus* zone, implying fairly good concordance between stratigraphic and phylogenetic patterns.

Systematic Paleontology

Family "Laudoniidae" Harrington 1956
Subfamily "Laudoniinae" Harrington 1956

Included Taxa

GENUS *MUMMASPIS* FRITZ 1992

Type species: *Wanneria occidens* Walcott 1913.
Assigned taxa: *Mummaspis oblisooculatus* Fritz 1992; *Olenellus truncatooculatus* Fritz 1992; *Olenellus muralensis* Fritz 1992; *Holmia*? *macer* Walcott 1913.
Diagnosis: Anterior cephalic border between frontal lobe and genal spine angle with length (exsag.) equal to length of L0; anterior border prominently separated from extraocular area by furrow; anterolateral margins of frontal lobe separated from extraocular area by furrow (not anterior border furrow); anterior margins of frontal lobe at each side of midline deflected posteriorly at roughly 10 degree angle relative to transverse line; prominent

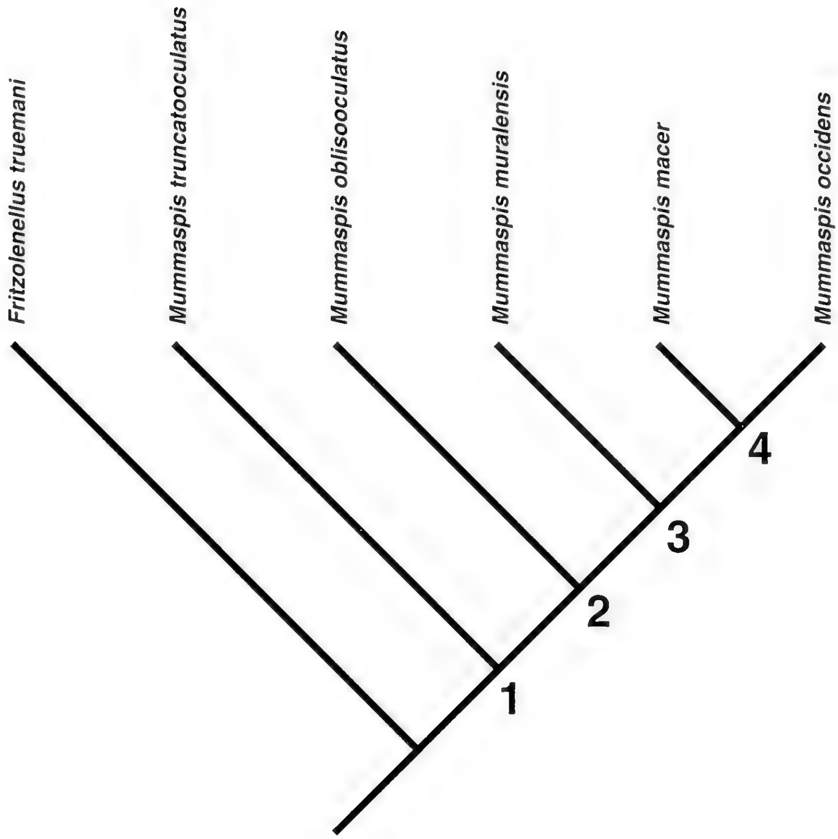


Figure 18.
The most parsimonious cladogram of length 9 steps produced from analysis of character data in Table 12 with PAUP v. 3.1.1 (Swofford 1993). The cladogram is constructed using an exhaustive search. The retention index is 0.67, and the consistency index is 0.78. The following nodes in the text were supported by the following bootstrap confidence values (see text for bootstrapping procedure used): Node *2* = 0.72; Node *3* = 0.52; Node *4* = 0.47. Character states are placed at nodes, using MacClade v. 3.04 (Maddison and Maddison 1992), with the characters given in Table 11. The apomorphic state is given in parentheses. Node *2*, 3(1); Node *3*, 2(1); Node *4*, 5(1).

parafrontal band not visible in dorsal view; L4 expands dorsally; lateral margins of L4 distal to lateral margins of L0; pre-ocular furrow on frontal lobe directed inward and forward from glabellar margin; transverse profile of ocular lobes convex dorsally; posterolateral tip of ocular lobe directly behind anterolateral tip or rotated slightly laterally; vertical shelf of ocular lobe separated from extraocular area by furrow (except in *M. truncatooculatus*); S3 jaggedly convex or carat shape, conjoined medially; line between ends of S2 transverse; S2 convex anteriorly; S1 conjoined medially; distal sector of S0 straight; lateral lobes on L0 present; posterior margin of L0 convex; extraocular area gently flattened or convex; intergenal angle developed posterior of point halfway between ocular lobes and genal spine; extraocular region opposite L1 with width (tr.) equal to roughly 75% of width of glabella at L1; intergenal ridge visible as trace; intergenal area with small pointed spine (could not be determined in *M. macer*); intergenal angle roughly parallels a transverse line; genal spine angle developed opposite medial part of distal margin of L0; T3 macropleural; boundary between thoracic pleural furrow and anterior band sharp; thoracic pleural furrows extend onto spines; length (exsag.) of thoracic pleural furrows (excluding those on T3) at medial part of segment equal to half length (exsag.) of posterior band at similar point; prominent anterolateral lobes variably present or absent on thoracic axial rings; thoracic pleural spines on segments T5 to T8 extend back approximately four segments; spine on T15 short, length (sag.) of five thoracic segments (could not be determined in *M. macer* or *M. muralensis*); and base of spine on T15 nearly as wide (tr.) as axis of segment (could not be determined in *M. macer*); pleurae present on opisthothorax (could not be determined in *M. macer* or *M. muralensis*).

Discussion: When Fritz (1992) first created this genus he assigned only two species to it, *M. occidens* and *M. obisooculatus.* As three more species are assigned to it here, and additional defining characters for the genus are recognized, an expanded diagnosis is provided. Species of the genus are known from the lower *Olenellus* zone of western Laurentia and the ?middle-upper *Olenellus* zone of eastern Laurentia (based on correlations in Fritz 1992 and Palmer and Repina 1993).

Mummaspis occidens (Walcott 1913)

Figure 17.2

Wanneria occidens; Walcott 1913:314, pl. 53, fig. 2.

Esmeraldina occidens (Walcott); Resser and Howell 1938:229.

Mummaspis occidens (Walcott); Fritz 1992:17, pl. 9, figs. 2–5, pl. 10, figs. 1–5, text fig. 6a; Palmer and Repina 1993:23, fig. 3.5; Lieberman 1998:72, fig. 4.1.

Types: Holotype, USNM 60080, see Walcott (1913).

Material examined: MCZ 110671, 110675, 110681; USNM 60080, the holotype.

Occurrence: Canada: Alberta, the Mural Formation, in the talus slope immediately W of Mumm Peak, and from the middle Mural Formation, 410.5 ft above the base of that formation, in the lower *Olenellus* zone, Early Cambrian, Mumm Peak section, just N of the Mount Robson Provincial Park boundary, western Alberta (see discussion in Fritz 1992).

Mummaspis truncatooculatus (Fritz 1992)

Figure 17.3

Olenellus truncatooculatus; Fritz 1992:16, pl. 14, figs. 3–6, pl. 15, figs. 1–9, pl. 16, figs. 1–3, text fig. 5a.

Types: Fritz (1992) failed to designate a type for this species. Accordingly, the well-preserved complete specimen Fritz (1992, pl. 15, fig. 6), USNM 443777, is designated the **lectotype.** It is from the Mural Formation, in the talus slope immediately west of Mumm Peak, in the lower *Olenellus* zone, Early Cambrian, just north of the Mount Robson Provincial Park boundary, western Alberta, Canada (see discussion in Fritz 1992). The specimens USNM 443769–443776 and 443778–443782 become paralectotypes.

Discussion: There is some variability in this species in the relative position of the ocular lobes. The posterior tip of the ocular lobes extends back to the medial part of the distal margin of L1, but one specimen Fritz figures (1992, pl. 15, fig. 4) has the posterior tip of the ocular lobes developed somewhat anterior of this, though it is still opposite the distal margin of L1. Originally, Fritz (1992) assigned this species to the genus *Olenellus*; however, there is much character evidence suggesting that it should be excluded from that genus and

Table 11.
Characters and character states used in phylogenetic analysis of *Mummaspis*; (0) represents the primitive state, and (1) and (2) represent derived states.

	Primitive state	Derived states
1. Posteriormost edge of ocular lobes	(0) deflected slightly laterally relative to anterior part of ocular lobes	(1) directly behind anterior edge of ocular lobes
2. Posterior part of ocular lobes extend back to	(0) medial part of margin of L1	(1) S0 (2) medial part of margin of L0
3. Extraocular area	(0) roughly flattened	(1) gently convex
4. S1	(0) convex	(1) transverse
5. Width (tr.) of thoracic pleural spines T5 to T8 at spine midlength	(0) more than 2/3 length (exsag.) of medial part of inner pleural region	(1) less than half length (exsag.) of medial part of inner pleural region

instead be assigned to the genus *Mummaspis. M. truncatooculatus* differs from the type species of *Olenellus,* and what was formerly referred to as the type species of *O.* (*Paedeumias*), in the condition of the following characters: 1. in *M. truncatooculatus* the anterior cephalic border between L4 and the genal spine angle has length (exsag.) equal to length (sag.) L0, in *Olenellus* it has length equal to one-half the length of L0; 2. in *M. truncatooculatus* the anterolateral margins of the frontal lobe are prominently separated from the anterior extraocular area by a furrow (not the anterior border furrow), in *Olenellus* they are not prominently separated from the anterior extraocular area; 3. in *M. truncatooculatus* the anterolateral margins of the frontal lobe at each side of the midline are deflected posteriorly at a roughly 10 degree angle relative to a transverse line, in *Olenellus* they are directed posteriorly at a roughly 40 degree angle; 4. in *M. truncatooculatus* L4 expands prominently dorsally, in *Olenellus* it does not; 5. in *M. truncatooculatus* the lateral margins of L4 are distal to the lateral margins of L0, in *Olenellus* they are proximal or directly anterior to the lateral margins of L0; 6. in *M. truncatooculatus* the pre-ocular furrow on L4 is directed inward and forward from the glabellar margin, in *Olenellus,* when visible it is transverse; 7. in *M. truncatooculatus* a transverse profile of the ocular lobes is convex dorsally, in *Olenellus* it is flattened; 8. in *M. truncatooculatus* the surface of the interocular area is arched dorsally, in *Olenellus* it is developed as a flattened shelf; 9. in *M. truncatooculatus* S3 is conjoined medially, in *Olenellus* it is not; 10. in *M. truncatooculatus* a line between the ends of S2 is transverse, in *Olenellus* such a line is directed inward and posteriorly at a roughly 45 degree angle relative to a transverse line; 11. in *M. truncatooculatus* L2 and L3 do not merge, in *Olenellus* they do; 12. in *M. truncatooculatus* S2 is convex anteriorly, in *Olenellus* it is straight; 13. in *M. truncatooculatus* the posterior margin of L0 is strongly convex posteriorly, in *Olenellus* it is roughly transverse; 14. in *M. truncatooculatus* lateral lobes on L0

are present, in *Olenellus* they are absent; 15. in *M. truncatooculatus* the intergenal angle is developed posterior of a point halfway between the ocular lobes and the genal spine angle, in *Olenellus* it is practically directly behind the genal spine angle; 16. in *M. truncatooculatus* the medial part of the cephalic posterior border between the intergenal angle and L0 flexes posteriorly, in *Olenellus* it is transverse; 17. in *M. truncatooculatus* the length (exsag.) of the thoracic pleural furrows (excluding T3) at the medial part of the segment relative to the length (exsag.) of the posterior band of the pleural segment is equal to half the length of the posterior pleural band, in *Olenellus* it is equal to 1.5 times the length of the posterior pleural band; 18. in *M. truncatooculatus* the spine on T15 is short, with length (sag.) of roughly five thoracic segments, in *Olenellus* the spine is roughly the length (sag.) of the entire prothorax; 19. in *M. truncatooculatus* the pleurae of the opisthothorax are present and continue the orientation of the prothoracic pleurae, in *Olenellus* they are absent. On the basis of these character differences *M. truncatooculatus* is placed in the genus *Mummaspis* rather than in the genus *Olenellus.* Some of these characters may be plesiomorphic for the genus *Mummaspis,* but serve to differentiate a larger clade from the genus *Olenellus.* Therefore they were included in this list.
Material examined: MCZ 110677, 110678 and many unnumbered specimens on a large slab.
Occurrence: Canada: Alberta, the Mural Formation, in the talus slope immediately W of Mumm Peak, and from the middle Mural Formation, 453 ft above the base of that formation, type section of the Mural Formation, both in the lower *Olenellus* zone, Early Cambrian, just N of the Mount Robson Provincial Park boundary, western Alberta (see discussion in Fritz 1992).

MUMMASPIS OBLISOOCULATUS FRITZ 1992

Mummaspis oblisooculatus; Fritz 1992:19, text fig. 5b, pl. 17, figs. 3–5, non 1, 2, non pl. 16, figs. 4–7.

Types: Fritz (1992) did not designate a type specimen for this species. Here USNM 443790 (Fritz 1992, pl. 17, fig. 4), a well-preserved, complete specimen, is designated the **lectotype,** and USNM 443789, Fritz's (1992, pl. 17, fig. 3), a well-preserved cephalon, becomes a paralectotype. The other material Fritz (1992) illustrated as *M. oblisooculatus* no longer is referable to that species, and is discussed below.
Discussion: Fritz (1992) suggested that, based on their relative stratigraphic position, *M. oblisooculatus* evolved from *M. occidens.* As these species are not sister taxa (Figure 8) this ancestor-descendant relationship is unlikely. Several of the specimens that Fritz illustrated as *M. oblisooculatus* (1992, pl. 16, figs. 4–7, and pl. 17, figs. 1, 2), all small cephala, instead appear to belong to a species closely related to *F. truemani.* These specimens share several characters in common with *F. truemani,* to the exclusion of *M. oblisooculatus.* In particular, they have the anterolateral margins of the frontal lobe at each side of the midline deflected posteriorly at a roughly 40 degree angle relative to a transverse line instead of at a roughly 10 degree angle; the posterior margins of the ocular lobes rotated laterally relative to the anterior margins; the distal sector of S0 convex anteriorly rather than straight; and the posterior margin of L0 transverse rather than convex. (In one of the specimens of *M. oblisooculatus* [Fritz 1992, pl. 17, fig. 3] the posterior margin of L0 is partly deformed as it is truncated by the anterior margin of the first thoracic segment, so its condition is difficult to discern.) These specimens do differ from typical *F. truemani* and resemble *M. oblisooculatus* in having the frontal lobe contacting the anterior border furrow, and the anterior ocular line and genal

Table 12.
Character state distributions for *Mummaspis* and outgroup used in phylogenetic parsimony analysis. Characters and alternative states are as listed in Table 11. Missing data are indicated by ?. Character states listed as X are polymorphic, where X=(1&2).

	1	2	3	4	5
Fritzolenellus truemani	0	0	0	0	0
Mummaspis occidens	1	1	1	1	1
Mummaspis truncatooculatus	0	0	0	1	0
Mummaspis oblisooculatus	1	0	1	0	0
Mummaspis macer	0	X	1	0	1
Mummaspis muralensis	0	X	1	0	0

ridge prominently developed; however, these characters are not crucial for the diagnosis of either *Fritzolenellus* or *Mummaspis.* These cephala are also discussed above under the heading of the genus *Fritzolenellus,* and are tentatively treated as *F.* sp. aff. *truemani.*
Occurrence: Canada: Alberta, the Mural Formation, in the talus slope immediately W of Mumm Peak, and from the middle Mural Formation, 490 ft and 806 ft above the base of that formation, in the lower *Olenellus* zone, Early Cambrian, Mumm Peak section, just N of the Mount Robson Provincial Park boundary, western Alberta (see discussion in Fritz 1992).

MUMMASPIS MURALENSIS (FRITZ 1992)
Figures 17.4, 17.5

Olenellus muralensis; Fritz 1992:13, pl. 8, figs. 1–7, pl. 9, fig. 1, text fig. 5c (see for additional synonymy).

Types: Fritz (1992) failed to designate a type specimen for this species. Therefore, USNM 443742, the nearly complete specimen illustrated in Fritz (1992, pl. 8, fig. 5) is designated the **lectotype.** This specimen is from the Mural Formation, in the talus slope immediately west of Mumm Peak, in the lower *Olenellus* zone, Early Cambrian, just north of the Mount Robson Provincial Park boundary, western Alberta, Canada (see discussion in Fritz 1992). The specimens USNM 443738–443741, 443743 and 443744 become paralectotypes.
Discussion: Originally this species was assigned to the genus *Olenellus.* However, analysis conducted here indicates that it should be excluded from that genus and instead be assigned to the genus *Mummaspis.* The character differences demonstrating this are identical to those listed above for *M. truncatooculatus.* However, the condition of two of these characters, the length of the thoracic axial spine on T15 and the presence or absence of the opisthothoracic pleurae, could not be determined in *M. muralensis* because the posterior region of the thorax is not adequately preserved.
Material examined: MCZ 5575 (a lot of 5 specimens), 110672–110674, 110676
Occurrence: Canada: Alberta, the Mural Formation, in the talus slope immediately W of Mumm Peak, in the lower *Olenellus* zone, Early Cambrian, just N of the Mount Robson Provincial Park boundary, western Alberta (see discussion in Fritz 1992).

MUMMASPIS MACER (WALCOTT 1913)
Figure 17.6

Holmia? *macer*; Walcott 1913:313, pl. 54, fig. 1.
Esmeraldina macer (Walcott); Resser and Howell 1938:229, pl. 8, figs. 10–12.
Wanneria macer (Walcott); Fritz 1973:13; Fritz 1995:712.
Wanneria walcottanus (Wanner); Walcott 1910:302, pl. 30, figs. 3, 4.

Types: Holotype, USNM 60092, by monotypy, see Walcott (1913).
Discussion: Walcott (1913) assigned this species to the genus *Holmia.* These taxa are not that distantly related within the Olenelloidea, based on Lieberman (1998), but they are not sister taxa. Differences between the type of *Holmia, H. kjerulfi* and *M. macer* include the following characters: 1. in *M. macer* the anterior cephalic border is prominently separated from the extraocular area by a furrow, in *H. kjerulfi* it is not; 2. in *M. macer* the anterolateral margins of the frontal lobe are prominently separated from the extraocular area by a furrow (not the anterior border furrow), in *H. kjerulfi* they are not; 3. in *M. macer* the anterolateral margins of the frontal lobe at each side of the midline are deflected posteriorly at a roughly 10 degree angle relative to a transverse line, in *H. kjerulfi* they are directed posteriorly 40 degrees; 4. in *M. macer* a line from the posterior tip of the ocular lobe to the junction of the posterior margin of the lobe with the glabella is parallel to a sagittal line, in *H. kjerulfi* it forms a 10 to 20 degree angle; 5. in *M. macer* S1 is conjoined medially, in *H. kjerulfi* it is not; 6. in *M. macer* the distal sector of S0 is straight, in *H. kjerulfi* it is convex anteriorly; 7. in *M. macer* the extraocular area is gently convex, in *H. kjerulfi* it is prominently vaulted; 8. in *M. macer* the extraocular region opposite L1 has width (tr.) equal to 75% of the width of the glabella at L1, in *H. kjerulfi* it has width equal to 40% to 50%; 9. in *M. macer* the intergenal angle roughly parallels a transverse line, in *H. kjerulfi* it is directed anteriorly at a roughly 45 degree angle relative to a transverse line; 10. in *M. macer* T3 is macropleural, in *H. kjerulfi* it is not; 11. in *M. macer* the thoracic pleural spines are relatively longer than they are in *H. kjerulfi*; 12. in *M. macer* the prothoracic axial rings lack prominent anterolateral lobes, in *H. kjerulfi* they are present; 13. in *M. macer* the thoracic pleural furrows extend onto the spines, in *H. kjerulfi* they only extend the width of the inner pleural region; 14. in *M. macer* the boundary between the thoracic pleural furrow and the anterior band is sharp, in *H. kjerulfi* it is gradational; 15. in typical *Mummaspis,* the length (exsag.) of the thoracic pleural furrows is equal to half the length of the posterior pleural band, this character is difficult to determine in *M. macer* but appears to have this state, in *H. kjerulfi* the thoracic pleural furrows are equal in length to the posterior band. On the basis of these character differences, *M. macer* must be treated as not closely related to *H. kjerulfi.*

Convergences between these taxa that may explain the misassignment of *M. macer* to the genus *Holmia* are that both have the posterior tips of the ocular lobes developed opposite the medial part of the distal margin of L0, and both have the genal spines extending back roughly 4 to 5 thoracic segments. *Mummaspis* macer also cannot be assigned to the genus *Esmeraldina,* which is closely related to *Holmia,* on the basis of character evidence similar to that discussed above.

In the past this genus has also been assigned to *Wanneria.* However, there are several character differences separating *M. macer* from *W. walcottana,* and it seems inconceivable that they could be assigned to the same genus except for the fact that they occur in rocks of the same age and from the same locality. In particular: 1. in *M. macer* the anterior cephalic border is prominently separated from the extraocular area by a furrow, in *W. walcottana* it is not prominently separated; 2. in *M. macer* the anterolateral margins of the frontal lobe are prominently separated from the extraocular area by a furrow (not the anterior border furrow), in *W. walcottana* they are not; 3. in *M. macer* L4 expands prominently dorsally, in *W. walcottana* it does not; 4. in *M. macer* a line from the posterior tip of the ocular lobe to the junction of the posterior margin of the lobe with the glabella parallels a sagittal line, in *W. walcottana* it forms a 10 to 20 degree angle with a sagittal line; 5. in *M. macer* S1 and S3 are conjoined medially, in *W. walcottana* they are not; 6. in *M. macer* the distal sector of S0 is straight, in *W. walcottana* it is convex anteriorly; 7. in *M. macer* the proximal sector of S0 is well posterior of the distal end, in *W. walcottana* the proximal and distal ends are on a transverse line; 8. in *M. macer* the posterior margin of L0 is convex posteriorly, in *W. walcottana* it is roughly transverse; 9. in *M. macer* lateral lobes are present on L0, in *W. walcottana* they are not; 10. in *M. macer* the extraocular area is gently convex, in *W. walcottana* it is flattened; 11. in *M. macer* T3 is macropleural, in *W. walcottana* it is not; 12. in *M. macer* the anterior margin of the thoracic pleural furrow on T3, when proceeding from the proximal to the distal edge, is directed weakly posteriorly before flexing strongly posteriorly, in *W. walcottana* it parallels a transverse line before flexing strongly posteriorly; 13. in *M. macer* the thoracic pleural furrows extend onto the spines, in *W. walcottana* they extend only half of the width of the inner pleural region; 14. in *M. macer* the boundary between the thoracic pleural furrow and the anterior band is sharp, in *W. walcottana* it is gradational; 15. in *M. macer* the length (exsag.) of the thoracic pleural furrows (excluding those of T3) at the medial part of the segment are short, equal to roughly half the length (exsag.) of the posterior pleural band, in *W. walcottana* they are equal to 1.5 times the length of the posterior band; 16. in *M. macer* the width (tr.) of the thoracic pleural spines T5 to T8 at the spine midlength is less than half the length (exsag.) of the medial part of the inner pleural region, whereas they are roughly thicker in *W. walcottana*, more than two-thirds the length of the medial part of the inner pleural region.

The bulk of the character evidence suggests that this species belongs with *Mummaspis*. It matches the diagnostic characters of that genus and shares many more characters with the type of this genus than it does with any other genus.

Material examined: USNM 60092, the holotype.

Occurrence: Pennsylvania: the Kinzers Formation, in the middle upper *Olenellus* zone, according to Palmer and Repina (1993), from 2 mi N of York, from Fruitville, 3 mi N of Lancaster, and 0.5 mi S of East Petersburg.

• SEVEN •

Phylogenetic Analysis of the Bristoliinae

The subfamily Bristoliinae is a moderately diverse clade nested within the Olenelloidea that contains the genera *Bristolia, Fremontella* and *Lochmanolenellus.* All of the component taxa bear prominent genal spines and advanced genal spine angles. *Bristolia* consists of seven described species and one fragmentary cranidium of an undescribed species, and is restricted to the Lower Cambrian *Olenellus* zone of western Laurentia. All but one species occurs in the Great Basin of eastern California and western Nevada. One species is known from the Mackenzie Mountains, Northwest Territories, Canada. One new species of *Bristolia* is described here. *Lochmanolenellus* consists of a single species known from southwestern Laurentia, and *Fremontella* consists of a single species known from eastern Laurentia.

A total of 11 taxa was subjected to phylogenetic analysis, including nine ingroup taxa. All species within the genus were analyzed, including what was termed *Laudonia*? sp. by Fritz (1972; later reassigned to *Bristolia* by Fritz 1992), here *Bristolia* sp., an extremely poorly preserved taxon, known from an external mold of about one-half of a cephalon. It is certainly a species of *Bristolia,* bearing the hallmark characteristics of the genus. On the basis of phylogenetic analysis, it is most closely related to *B. anteros* Palmer and Halley and is discussed in greater detail under that species. Because of its poor state of preservation, it was not described as a new species.

The two known species of the genus *Laudonia, L. bispinata* and *L. amputata,* were used as outgroups in phylogenetic analysis. *Laudonia* is the sister taxon of a clade that includes *Fremontella, Lochmanolenellus* and *Bristolia,* based on higher level phylogenetic patterns within the Olenelloidea (Lieberman 1998). For the purposes of rooting the phylogeny of *Fremontella, Lochmanolenellus* and *Bristolia,* the two outgroup species of *Laudonia* were treated as monophyletic. Evolutionary relationships within *Bristolia* were determined by parsimony analysis of 17 exo-skeletal characters (only cephalic characters could be used because of the dearth of thoracopygidia known for members of *Fremontella, Lochmanolenellus* and *Bristolia*), given in Table 13. The codings for the taxa analyzed are given in Table 14. These data were subjected to an exhaustive search using PAUP v. 3.1.1 (Swofford 1993). Four most parsimonious trees of length 35 steps were recovered. A strict consensus of these trees is shown in Figure 19. The retention index of the tree is 0.80, and the consistency index is 0.67 when uninformative characters are excluded. Uncertainty in resolution in this consensus cladogram concerns the relationships of some of the species of *Bristolia,* which essentially only differ in the relative position of the genal spine angle and also in the angle the intergenal angle forms with a transverse line. The g_1 statistic, used to measure tree length skewness distributions, was –0.70, and this value differs from those values derived from distributions using random data at the 0.01 level of confidence (Hillis 1991). This suggests that there is a strong and robust phylogenetic signal to the character data given in Table 14. The confidence values for the nodes of the consensus tree duplicated in the bootstrap analysis are given in Figure 19.

Using the analysis presented in Bremer (1994), 30 trees of length less than or equal to 36

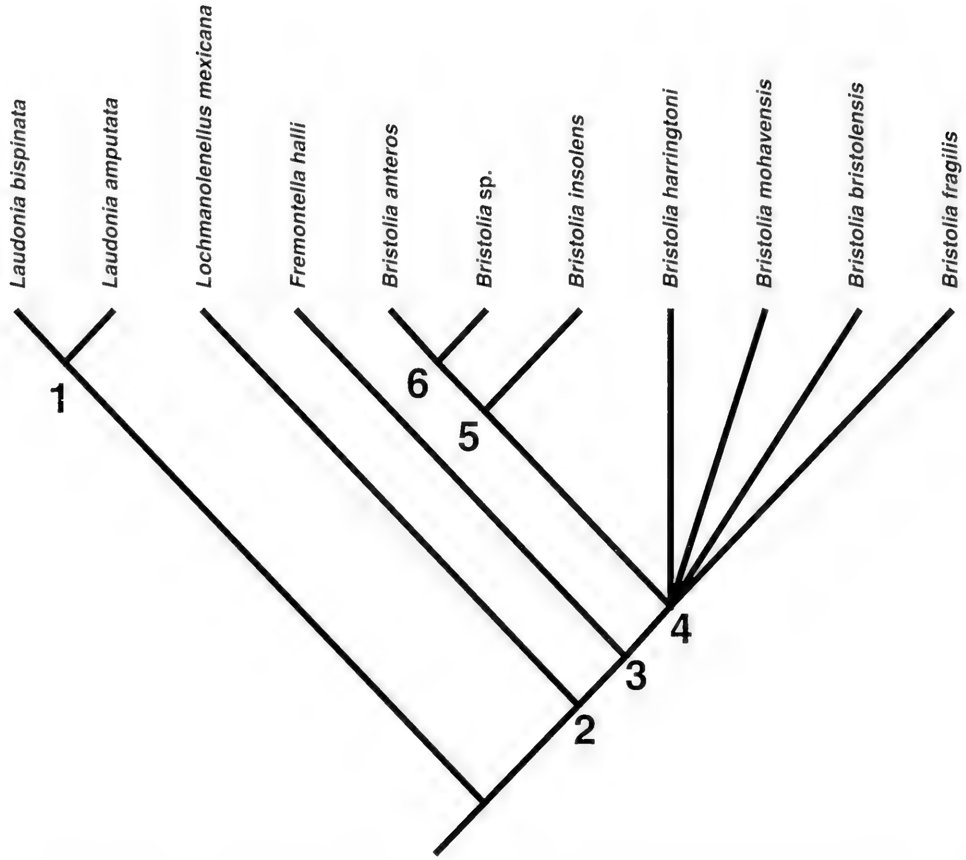


Figure 19.
A strict consensus of the four most parsimonious cladograms of length 35 steps produced from analysis of character data in Table 14 with PAUP v. 3.1.1 (Swofford 1993). The cladogram is constructed using an exhaustive search. The retention index is 0.80, and when uninformative characters are excluded the consistency index is 0.67. The following nodes in the text were supported by the following bootstrap confidence values (see text for bootstrapping procedure used): Node *2* = 0.94; Node *3* = 0.76; Node *4* = 0.64; Node *5* = 0.66; Node *6* = 0.96. The following branch support values (Bremer 1994) were recovered for the following nodes: Node *2* = 1; Node *3* = 1; Node 6 = 1. Character states are placed at nodes, using MacClade v. 3.04 (Maddison and Maddison 1992), with the characters given in Table 13. The apomorphic state is given in parentheses. Square parentheses indicate equivocal character states that are ambiguous because of missing data, polymorphisms or multiple equally parsimonious resolutions. Equivocal characters are placed only at their basal phylogenetic position, and only unambiguous reversals are shown. Node *1*, 1(4), 3(1), 5(1), 9[0, 2], 14[0, 1]; Node *2*, 10(1), 11(1); Node *3*, 7(1), 8(1), 12(1), 15[0, 1]; Node *4*, 1[1, 2, 3, 4], 9[0, 1, 2], 13[0, 1]; Node *5*, 1(3), 4[0, 1], 6(1), 9(2), 14(0), 15(0), 17(1); Node *6*, 4(0), 5(0), 7(0), 16(1).

steps, and 117 trees of length less than or equal to 37 steps were recovered before the analysis was terminated because the consensus cladogram was a complete polytomy. The amount of branch support for the various nodes is given in Figure 19. The total support index (Bremer 1994) for the tree is 0.09, towards the low end of the examples given in Bremer (1994).

If the stratigraphic correlations of Fritz (1972) are correct for the Canadian sections, then *Bristolia* sp. (*Laudonia* sp. of Fritz 1972), nested within the *Bristolia* clade, predates the other members of the genus in the fossil record (lower versus upper *Olenellus* zone). Its phylogenetic position indicates that the lineages leading to *B. insolens* and the other species of

Bristolia (and also to *B. anteros*, if *Bristolia* sp. is not ancestral to that species) must have differentiated by the lower *Olenellus* zone. This would imply at least a moderate gap in the history of the lineages leading to the different species of *Bristolia*, equivalent in duration to the difference in ages of the early *Olenellus* zone and *Bristolia* zonule of the upper *Olenellus* zone. However, it is also conceivable that either the Canadian sections may have been incorrectly correlated with older strata, or the Great Basin sections may have been incorrectly correlated with younger strata.

As mentioned above, phylogenetic analysis conducted here retrieved relatively little phylogenetic structure within the genus *Bristolia*. The evolution of the genus is depicted (Figure 19) as containing a basal polytomy due to lack of phylogenetically informative character differences between most species of *Bristolia*. The bulk of differentiating criteria between species center around the relative position of the genal spine angle and the angle the intergenal angle forms with a transverse line. These allow for easy discrimination between individual species of *Bristolia*, but basically do not provide phylogenetic resolution within the genus, unless they were to be ordered using some additional criterion. As no reasonable criterion could be found to order these characters, they were treated as unordered in phylogenetic analysis. The only taxa that group together within the genus are *B. insolens*, *B. anteros* and *B.* sp. These all possess distinctive genal spines, which loop anterolaterally before deflecting posteriorly, and short (exsag.) anterior cephalic borders. Additional morphometric data were gathered to settle the relative relationships of taxa within the genus *Bristolia*. Unfortunately, suitable sample sizes of measurable specimens exist for only four species: *B. harringtoni* n. sp. (43 specimens measured), *B. bristolensis* (Resser) (34 specimens measured), *B. insolens* (6 specimens measured) and *B. mohavensis* (Hazzard and Crickmay) (30 specimens measured). All available specimens in the collections of the UCR and the LACMIP were measured from each of these species. The following 10 measurements were taken on cephala of each of these species: cephalic length (sag.); cephalic width (tr.) (excluding the genal spines); length (sag.) from posterior margin of L0 to genal spine angle; width (tr.) of L0; width (tr.) of L1; maximum width of L4 (tr.); maximum width (tr.) between the distalmost edges of the ocular lobes; length (sag.) of L0 and L1; length (sag.) of L4; and width (tr.) of the extraocular area measured from distal most edge of ocular lobe to the genal spine angle. (All data are available from the author on request.) A series of univariate and multivariate statistical analyses were conducted on these data, corresponding to those conducted in Lieberman et al. (1994, 1995), to determine whether or not differences in individual morphological variables between species were statistically significant, and also to determine how these species would be grouped based on multivariate morphometric data. None of the procedures for eliminating size-based differences seemed to be efficacious in the case of these morphometric data, so the data were not corrected for differences in size. Therefore, morphometric differences between species represent some combination of both size and shape.

A principal components analysis using Minitab v. 10Xtra (1995) was conducted on the data to determine which variables or combinations of variables contributed the greatest amount of variance to the data set. The covariance matrix was used to emphasize potential differences in variance. The first principal component explained 92.9% of the variance in the data and the second principal component explained 5.5%. All subsequent principal components contributed less than 0.7% of the variance and shall not be discussed further.

The loadings of the variables for principle components 1 and 2 are given in Table 15. The first has higher negative loadings on variables B and J, indicating that these con-

Table 13.
Description of characters and character states used in phylogenetic analysis of Bristoliinae; (0) does not always represent the primitive state as two outgroup taxa were employed in phylogenetic analysis, but for simplicity one of the outgroups, *Laudonia bispinata,* was coded with all "0" character states.

1. In adult genal spine angle opposite	(0) medial tip of S4	(1) distal tip of S0 (2) distal tip of S2 (3) medial part of margin of L4 (4) distal tip of S3 (5) medial part of margin of L1
2. Angle formed between transverse line and intergenal area	(0) 85° to 95°	(1) 35° to 55° (2) 115° to 120°
3. Posterior edge of ocular lobe opposite	(0) medial part of margin of L2	(1) medial part of margin of L1
4. Lateral and medial tips of S2	(0) roughly as far forward	(1) medial edge declined posteriorly
5. Line from posterior tip of ocular lobe to junction of posterior margin of lobe with glabella forms following angle relative to sagittal line	(0) approximately 40°	(1) approximately 10°
6. Medial margins of genal spine	(0) deflect posteriorly	(1) loop anteriorly before deflecting posteriorly
7. Faint ventral depression across entire region where ocular lobe hits frontal lobe	(0) absent	(1) present
8. Prominent intergenal spine in adult	(0) present	(1) absent
9. Length (exsag.) of anterior cephalic border at point midway between anterior tip of L4 and genal spine angle	(0) long, length (sag.) of L1 and L2	(1) very short, length less than or equal to half the length of L1 (sag.) (2) short, length equal to the length of L1 (sag.)

Continued

Table 13 continued.

	Primitive state	Derived states
10. S3	(0) deepest medially	(1) same depth laterally as medially
11. Anterior cephalic border developed as	(0) flattened ledge	(1) elevated ridge
12. Intergenal ridge	(0) developed as prominently expanded lineament	(1) visible as faint trace
13. Approximate length (exsag.) of genal spine	(0) 4 to 5 thoracic segments (sag.)	(1) 8 thoracic segments (sag.)
14. Lateral margins of glabella between posterior margin of L0 and L1	(0) constricting anteriorly	(1) roughly parallel
15. Width (tr.) of genal field	(0) short, equal to one-third width between distal most tips of ocular lobes	(1) moderate, equal to one-half width between distal most tips of ocular lobes (2) broad, equal to two-thirds width between distal most tips of ocular lobes (3) very broad, equal to three-quarters width between distal most tips of ocular lobes
16. Lateral and medial tips of S3	(0) at same position	(1) medial tip deflected further anteriorly
17. S2	(0) convex	(1) transverse

Figure 20.
1. *Laudonia bispinata* Harrington, locality is the same as Figure 17.2, MCZ 110679, ×1.5. 2–4. Locality is the same as Figure 3.4. 2. *Bristolia insolens* (Resser), UCR 10/2003, ×1.7. 3. *Bristolia harringtoni,* new species, plaster cast of UCR 10/7, the holotype, ×1.4. 4. *Bristolia mohavensis* (Hazzard and Crickmay), UCR 10/1185, ×1.5. 5. *Bristolia mohavensis* (Hazzard and Crickmay), locality is the same as Figure 3.2, UCR 7002/6, ×1.3. 6. *Nephrolenellus jasperensis,* new species, 10 m above the top of the Gog Group, about 2 mi SW of Mount Simla, Jasper Park, Western Alberta, Canada, GSC 16858, plaster cast of the holotype, ×1.5. 7. *Bolbolenellus groenlandicus* (Poulsen), Cape Kent Fm., Cape Kent, NE end of Inglefield Land, NW Greenland, latex cast of MGUH 2235, ×1.7.

tribute a disproportionate amount of the variance explained by this component. The second has a high negative loading on variable J, and somewhat elevated, positive loadings on variables B and C. From this we can conclude that the bulk of the variance in the data set is associated with differences in variables B, C and J, essentially involving the overall width of the extraocular area and the cephalon, and the relative position of the genal spine angle.

A discriminant analysis was also conducted using Minitab (1995) to calculate Mahalanobis differences between the centroids of each of the four species of *Bristolia.* To perform a discriminant analysis, the number of specimens for each group should be equal and the data should be multivariate normal with a homogeneous variance-covariance structure. All available specimens of the four species were measured. For three of these species roughly equivalent amounts of specimens were available; however, for one, *B. insolens,* far fewer specimens were available. Assessing multivariate normality can be difficult. If samples are not univariate normal, then they will not be multivariate normal. Using the Anderson-Darling test for normality on Minitab (1995), the following variables for the following groups were found to not be normal at the 0.05 level of confidence: *Bristolia insolens* for variable E; *B. mohavensis* for variable A; and *B. harringtoni* for variable C. Thus most, but not all, variables for all of the species were normal, indicating that the assumption of multivariate normality may not strictly hold.

The results of a discriminant analysis are presented as a classification matrix (Table 16) and as a matrix displaying the squared Mahalanobis distance between groups (Table 17). The classification matrix gives the proportion of specimens that can be assigned correctly to the group they are presumed to belong to, in this case the different species of *Bristolia.* Specimens of *B. insolens* could always be classified correctly, indicating that it is a well-constrained group morphologically. Very high percentages of the other species were also classified correctly, indicating that they too are very well-constrained groups morphologically. Specimens of *B. mohavensis* were occasionally confused with *B. harringtoni,* as were specimens of *B. bristolensis.* A single specimen of *B. bristolensis* was incorrectly classified with *B. insolens,* specimens of *B. harringtoni* were occasionally confused with *B. mohavensis,* and one specimen of *B. harringtoni* was incorrectly classified with *B. bristolensis.*

These results, along with the Mahalanobis distance values in Table 17, suggest several patterns. First, *B. insolens* is clearly distinct from the other species of *Bristolia* for which morphometric data exist. The phylogenetic analysis conducted here and the cladogram given in Figure 19 confirm this, as *B. insolens* is more closely related to *B. anteros* and *B.* sp., whereas the other species considered in morphometric analysis are part of a basal polytomy within the genus *Bristolia.* Second, these results suggest that in terms of their overall morphology, *B. mohavensis* and *B. harringtoni* are more closely similar to one another than either is to *B. bristolensis.* Finally, specimens of *B. bristolensis* are more similar to specimens of *B. harringtoni* than they are to specimens of *B. mohavensis.* These results are intuitively appealing and generally match the overall patterns of morphological similarity.

Since phylogenetic analysis failed to provide resolution for the evolutionary relationships of *B. mohavensis, B. bristolensis* and *B. harringtoni* due to a paucity of informative characters, these morphometric data will be used as a proxy for relationship. Therefore, within the clade of unresolved *Bristolia,* on the basis of morphometric data *B. mohavensis* and *B. harringtoni* are sister species, and *B. bristolensis* is sister to the clade they form. This hypothesis of course leaves the relationships of the unsampled taxon *Bristolia fragilis* Palmer in Palmer and Halley still unresolved.

Systematic Paleontology

FAMILY "Laudoniidae" Harrington 1956
SUBFAMILY "Laudoniinae" Harrington 1956

Included Taxa

GENUS *LAUDONIA* HARRINGTON 1956

Type species: *Laudonia bispinata*; Harrington 1956.
Assigned taxa: *L. amputata*; Fritz 1992.
Discussion: This genus is treated as monophyletic and restricted to the lower *Olenellus* zone of western Alberta. Its two component taxa are united by their shared possession of the following characters: anterior cephalic border between L4 and genal spine angle with length (exsag.) of L1 and L2 (sag.), developed as flattened ledge, not prominently separated from extraocular area by furrow; plectrum absent; anterolateral margins of glabella prominently separated from extraocular area by furrow; frontal lobe intersects anterior border furrow, expands dorsally, anterolateral margins relative to transverse line deflected at about a 10 degree angle; intergenal angle developed posterior of genal spine angle; intergenal angle deflected at 85 to 95 degrees relative to transverse line; lateral margins of L4 distal to lateral margins of L0; distal tip of pre-ocular furrow directed inward and backward from glabellar margin; S3 convex, line between ends transverse, conjoined medially; S2 convex, contacts axial furrows; line between ends of S2 transverse; S1 conjoined medially; ocular lobe with prominent furrow, not dorsally flattened; interocular area arched dorsally; axial tubercle on L0; extraocular area flattened; prominent anastomosing ridges absent from extraocular area; genal spine length (exsag.) of four to five thoracic segments (sag.), deflected at roughly 45 degree angle relative to sagittal line; intergenal ridge developed as prominently expanded lineament; prominent intergenal spine present; T3 macropleural, spine projecting posteriorly six to eight thoracic segments; anterior margin of T3 transverse before flexing posteriorly; nodes present on medial part of thoracic axial rings; anterior and posterior margins of thoracic pleural furrow on T3 directed weakly posterior laterally.

LAUDONIA BISPINATA HARRINGTON 1956
Figure 20.1

Laudonia bispinata; Fritz 1992:26, pl. 12, figs. 4–8, pl. 13, figs. 1–8, pl. 14, figs. 1, 2, text fig. 6c (see for more complete synonymy); Palmer and Repina 1993:24; Lieberman 1998:73, fig. 4.2.

Types: Holotype, KUMIP 32400, designated in Harrington (1956).
Material examined: KUMIP 32400, the holotype; MCZ 110679, 110680.
Occurrence: Canada: Alberta, the Mural Formation, in the talus slope immediately west of Mumm Peak, from the middle Mural Formation, 453 ft and 555 ft above the base of that formation, in the lower *Olenellus* zone, Early Cambrian, immediately W of Mumm Peak, just N of the Mount Robson Provincial Park boundary, and between Cinnamon Peak-Whitehorn Mountain, at the western end of Mount Robson Provincial Park (Fritz 1992).

Table 14.
Character state distributions for Bristoliinae and outgroups used in phylogenetic parsimony analysis. Characters and alternative states are as listed in Table 13. Missing data are indicated by ?. Character states listed as W, X, Y and Z are polymorphic, where W=(0&1), X=(2&4), Y=(1&5) and Z=(2&5).

										1	1	1	1	1	1	1	1
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7
Laudonia bispinata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Laudonia amputata	4	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Lochmanolenellus mexicana	4	0	1	0	1	0	0	0	2	1	1	0	0	1	0	0	0
Fremontella halli	4	0	1	0	1	0	1	1	0	1	1	1	0	1	1	1	0
Bristolia bristolensis	X	0	1	1	1	0	1	1	1	1	1	1	1	0	1	0	1
Bristolia insolens	3	2	1	1	1	1	1	1	2	1	1	1	1	0	0	0	1
Bristolia anteros	3	0	1	0	0	1	0	1	2	1	1	1	1	0	0	1	1
Bristolia sp.	3	0	1	0	0	1	0	?	2	1	1	1	1	0	0	1	1
Bristolia mohavensis	Y	1	1	0	1	0	1	1	1	1	1	1	1	0	1	0	0
Bristolia harringtoni	Z	1	1	W	1	0	1	1	1	1	1	1	1	0	1	0	W
Bristolia fragilis	1	1	1	1	1	0	1	1	1	1	1	1	1	0	1	0	1

LAUDONIA AMPUTATA FRITZ 1992

Laudonia amputata; Fritz 1992:26, pl. 11, figs. 1–5, pl. 12, figs. 1–3, text fig. 6d; Palmer and Repina 1993, fig. 4.4; Palmer and Repina 1997:412, fig. 259.2.

Types: Fritz (1992) figured and described this species, but never designated types. All his figured material (USNM 443752–443756) thus become syntypes. Here the most well-preserved of his syntype specimens, USNM 443754, is designated the **lectotype.** The specimens USNM 443752, 443753, 443755 and 443756 become paralectotypes.
Occurrence: Canada: Alberta, the Mural Formation, in the lower *Olenellus* zone, Early Cambrian, immediately west of Mumm Peak, just north of the Mount Robson Provincial Park boundary (Fritz 1992).

FAMILY Biceratopsidae Pack and Gayle 1971
SUBFAMILY Bristoliinae Harrington 1956

Discussion: Lieberman (1998) presented results of a phylogenetic analysis of the Olenelloidea that recognized a clade of olenelloids including the genera *Fremontella, Lochmanolenellus* and *Bristolia,* which he assigned to the family Biceratopsidae Pack and Gayle. A paraphyletic family within the Biceratopsidae, the "Bristoliinae," was recognized that included the genera *Bristolia, Fremontella, Lochmanolenellus, Nephrolenellus, Bolbolenellus* and *Olenelloides.* Lieberman (1998) treated the "Bristoliinae" as paraphyletic. Now that detailed phylogenetic patterns are better understood within this part of the olenelloid tree and detailed species level analyses have been conducted including the genera *Laudonia, Fremontella, Lochmanolenellus* and *Bristolia,* the Bristoliinae is redefined as a monophyletic subfamily that includes only the genera *Fremontella, Lochmanolenellus* and *Bristolia.* This subfamily can be defined by the possession of the following diagnostic characters (thoracic characters only found in a few species of *Bristolia,* the only members of the subfamily for which thoracic remains exist): 1. anterior cephalic border developed as an elevated ridge, and prominently separated from extraocular area by furrow; 2. anterolateral margins of frontal lobe not prominently separated from anterior extraocular area by furrow (not anterior border furrow); 3. prominent parafrontal band not visible in dorsal view; 4. anterolateral margins of frontal lobe at each side of midline deflected posteriorly at roughly 10 degree angle relative to transverse line; 5. S3 same depth laterally as medially; 6. anterodistal margins of L3 formed by ocular lobes; 7. surface of interocular area slopes evenly from tip of ocular lobe to glabella; 8. genal spine angle developed opposite S0 or position anterior of S0; 9. posterior edge of ocular lobe developed anterior of or opposite medial part of distal margin of L1; 10. lateral lobes absent from L0; 11. distal sector of S0 transverse; 12. intergenal angle relative to transverse line directed anteriorly at least 35 degrees; 13. T3 macropleural, pleural spine of T3 projects further posteriorly than length of entire prothorax; 14. anterior margin of thoracic pleural furrow on T3, when proceeding from proximal to distal edge, parallels a transverse line before flexing strongly posteriorly; 15. posterior margin of thoracic pleural furrow on T3 with medial part directed strongly posteriorly, distal part parallel to a transverse line or weakly flexing anterolaterally; 16. thoracic pleural spines on segments 5 to 8 developed as short projections extending two thoracic segments back; 17. sharp boundary between thoracic pleural furrow and anterior band; 18. prominent spine present on 15th thoracic axial ring.

GENUS *LOCHMANOLENELLUS* LIEBERMAN 1998

Type species: *Wanneria mexicana prima* Lochman in Cooper at al. 1952.
Assigned taxa: Monotypic.
Diagnosis: See Lieberman (1998).

LOCHMANOLENELLUS MEXICANA (LOCHMAN IN COOPER ET AL. 1952)

Wanneria mexicana prima; Lochman in Cooper et al. 1952:96, pl. 18, figs. 1–3.
Laudonia mexicana (Lochman in Cooper et al.); Fritz 1992:12.
Laudonia sp.; Nelson 1976:31, pl. 5 (upper right hand corner).
Lochmanolenellus mexicana (Lochman in Cooper et al.); Lieberman 1998:74, fig. 4.4.

Types: Holotype, USNM 115681, paratypes USNM 115682, 115683, designated by Lochman in Cooper et al. (1952).
Discussion: Lochman (Cooper et al. 1952) assigned this species to the genus *Wanneria.* However, based on phylogenetic topology within the Olenelloidea, this species belongs to *Lochmanolenellus,* a genus distantly related to the type of the genus *Wanneria, W. walcottana.* Character differences separating *Lochmanolenellus* from *Wanneria* include: 1. in *Lochmanolenellus* the anterior cephalic border is developed as a raised ridge, in *Wanneria* it is a flattened ledge; 2. in *Lochmanolenellus* the anterior cephalic border is prominently separated from the extraocular area by a furrow, in *Wanneria* it is not; 3. in *Lochmanolenellus* a plectrum is developed, in *Wanneria* it is absent; 4. in *Lochmanolenellus* the length (sag.) of L4 is approximately equal to the length of L0 and L1 (sag.), in *Wanneria* it is approximately equal to 1.5 times the length of L0 and L1 (sag.); 5. in *Lochmanolenellus,* L4

expands prominently dorsally, in *Wanneria* it does not; 6. in *Lochmanolenellus* the surfaces of the interocular area slope evenly from the tip of the ocular lobe to the glabella, in *Wanneria* it is developed as a flattened shelf; 7. in *Lochmanolenellus* the posterior margins of the ocular lobes are developed opposite the distal tips of S1, in *Wanneria* they are developed opposite the medial part of the distal margin of L1; 8. in *Lochmanolenellus* the width (tr.) of the interocular area is approximately equal to about half the width of the ocular lobe at its midlength, in *Wanneria* it is equal to at least the width of the ocular lobe; 9. in *Lochmanolenellus* S0, S1, S2 and S3 are conjoined medially, in *Wanneria* they are not; 10. in *Lochmanolenellus* L1, L2 and L3 are all strongly transversely convex, in *Wanneria* they are only gently convex; 11. in *Lochmanolenellus* the distal sector of S0 is straight, in *Wanneria* it is convex anteriorly; 12. in *Lochmanolenellus* the proximal end of S0 is well posterior of the distal end, in *Wanneria* the proximal and distal ends of S0 lie on a transverse line; 13. in *Lochmanolenellus* the posterior margin of L0 is convex posteriorly, in *Wanneria* it is roughly transverse; 14. in *Lochmanolenellus* the extraocular area is prominently vaulted, in *Wanneria* it is flattened; 15. in *Lochmanolenellus* the intergenal ridge is prominently expanded, in *Wanneria* it is only visible as a trace; 16. in *Lochmanolenellus* the extraocular region is about 40% to 50% of the width (tr.) of the glabella at L1, in *Wanneria* it is greater than 75% of the width of the glabella at L1; 17. in *Lochmanolenellus* the genal spine near where it hits the cephalic border is directed posterolaterally at a roughly 65 to 80 degree angle relative to a sagittal line, in *Wanneria* it is directed posterolaterally at roughly a 10 to 20 degree angle; 18. in *Lochmanolenellus* the genal spine angle is developed opposite the medial part of the distal margin of L3, in *Wanneria* it is developed opposite the medial part of the distal margin of L0; 19. in *Lochmanolenellus* the intergenal angle is developed directly behind the genal spine angle, in *Wanneria* it is developed posterior of a point halfway between the ocular lobes and the genal spine angle; 20. in *Lochmanolenellus* the intergenal spine is prominently developed, in *Wanneria* it is represented only by a slight dorsally directed swelling; 21. in *Lochmanolenellus* the intergenal angle is directed anteriorly at a roughly 80 to 90 degree angle relative to a transverse line, in *Wanneria* it roughly parallels a transverse line.

On the basis of this large number of character differences it is clear that *Lochmanolenellus* is distantly related to *Wanneria*, and the assignment of this species to the genus by Lochman (Cooper et al. 1952) appears to be untenable. More recently, Nelson (1976) and Fritz (1992) suggested that this species belonged in the genus *Laudonia*. Although *Lochmanolenellus* is much more closely related to *Laudonia* than it is to *Wanneria*, there are a fair number of character differences, and a few key characters, that separate the species of these genera. Conceivably *Lochmanolenellus* could be lumped with the genus *Laudonia*; however, because of phylogenetic topology within the Olenelloidea (Lieberman 1998), this would necessitate either lumping the genera *Nephrolenellus, Bolbolenellus, Olenelloides, Peachella, Biceratops, Fremontella* and *Bristolia* within *Laudonia*, or making *Laudonia* paraphyletic. Because *Bristolia, Laudonia* and the other aforementioned genera as they are currently construed represent good monophyletic genera, some of them containing several species, it seems preferable to treat *Lochmanolenellus* as a monotypic genus rather than to significantly alter the taxonomic status of *Laudonia, Bristolia* and the rest of the Biceratopsidae.

Differences separating *Lochmanolenellus* and *Laudonia* include: 1. in *Lochmanolenellus* the anterior cephalic border between L4 and the genal spine angle has length (exsag.) equal to length (sag.) of L0, in *Laudonia* the length equals approximately 1.5 times the length of L0; 2. in *Lochmanolenellus* the anterior cephalic border is developed as a raised ledge that is prominently separated from the extraocular area by a furrow, in *Laudonia* the anterior cephalic border is flattened and is not prominently separated from the extraocular area by a furrow; 3. in *Lochmanolenellus* a plectrum is present, in *Laudonia* it is absent; 4. in *Lochmanolenellus* the anterolateral margins of the glabella are not prominently separated from the extraocular area by a furrow (not the anterior border furrow), in *Laudonia* it is; 5. in *Lochmanolenellus* L4 is of length (sag.) equal to the length (sag.) of L0 and L1, in *Laudonia* it is approximately equal to 1.5 times the length of L0 and L1; 6. in *Lochmanolenellus* the pre-ocular furrow on L4 is directed inward and forward from the glabellar margin, in *Laudonia* it is directed inward and backward; 7. in *Lochmanolenellus* S3 is of equal depth medially and laterally, in *Laudonia* it is deeper medially; 8. in *Lochmanolenellus* the ocular lobe smoothly merges into the extraocular area, in *Laudonia* it is separated from the extraocular area by a furrow; 9. in *Lochmanolenellus* the surface of the interocular area slopes evenly from the tip of the ocular lobe to the glabella, in *Laudonia* the interocular area is arched; 10. in *Lochmanolenellus* the width (tr.) of the interocular area is approximately equal to the width of the ocular lobe, in *Laudonia* it is equal to about half the width of the ocular lobe; 11. in *Lochmanolenellus* L1, L2 and L3 are strongly transversely convex, in *Laudonia* they are gently convex; 12. in *Lochmanolenellus* the lateral margins of the glabella are roughly parallel between the posterior margin of L0 and L1, in *Laudonia* the glabella constricts anteriorly in this region; 13. in *Lochmanolenellus* S0 is conjoined medially, in *Laudonia* it is not; 14. in *Lochmanolenellus* the extraocular area is prominently vaulted, in *Laudonia* it is flattened; 15. in *Lochmanolenellus* the width of the extraocular area is equal to the width (tr.) of 40% to 50% of the glabella at L1, in *Laudonia* it is approximately equal to 75% of the width of the glabella at L1; 16. in *Lochmanolenellus* the genal spine near where it hits the cephalic border is directed posterolaterally at a roughly 65 to 80 degree angle relative to a sagittal line, in *Laudonia* it is directed posterolaterally at a roughly 45 degree angle; 17. in *Lochmanolenellus* the medial part of the posterior border between L0 and the intergenal angle flexes posterolaterally, in *Laudonia* it is transverse. Thus, on the basis of these character differences, *Lochmanolenellus* is treated as distinct from *Laudonia*, though the two are held to be closely related.

Phylogenetic analysis of the Olenelloidea in Lieberman (1998) suggested that *Lochmanolenellus* was more closely related to the genus *Bristolia* than *Fremontella*. However, when all the species of *Laudonia* and *Bristolia* are considered it actually appears that *Fremontella* is sister to *Bristolia* to the exclusion of *Lochmanolenellus*. This is only a slight change in phylogenetic topology, but the basic premise of Lieberman (1998) that *Laudonia* is sister to a clade including *Fremontella*, *Lochmanolenellus* and *Bristolia* is upheld by this analysis.

Material examined: USNM 115683 and 115681, the holotype.

Occurrence: Mexico: 590 ft above the base of the Puerto Blanco Formation section at the W side of the Proveedora Hills on the N side of Puerto Blanco, 6 to 7 mi W of Caborca. California: the upper part of the Poleta Formation, White-Inyo Mountains/Death Valley region, both treated as in the lower *Olenellus* zone, following Nelson (1976) and Fritz (1992).

GENUS *FREMONTELLA* HARRINGTON 1956

Type species: *Wanneria halli* Walcott 1910.

Assigned taxa: Monotypic.

Diagnosis: Length (exsag.) anterior cephalic border near but not directly anterior to frontal lobe very long, equal to length (sag.) of L1 and L2; length (sag.) L4 equal to 1.5 times length (sag.) of L0 and L1; distal margins of L2 subparallel; S0, S1 not conjoined medially; L0 smooth, convex posteriorly; genal spine near cephalic border directed posterolaterally at 35 to 45 degree angle relative to sagittal line, length (exsag.) equal to four times length (sag.) L0; genal spine angle opposite medial part of distal margin of L3; cephalic posterior border transverse between intergenal angle and L0.

FREMONTELLA HALLI (WALCOTT 1910)

Wanneria halli; Walcott 1910:301, pl. 31, figs. 1–11.
Olenellus halli (Walcott); Resser 1938:52, pl. 5, figs. 7, 8, 18.
Olenellus alabamensis; Resser 1938:53, pl. 5, figs. 16, 17.
Fremontella halli (Walcott); Harrington 1956:58, pl. 15, figs. 1–3, 8–9, text fig. 1c; Harrington et al. 1959:O192, fig. 133.1; Palmer and Repina 1993:23, fig. 3.4; Palmer and Repina 1997:408, fig. 256.2; Lieberman 1998:74.

Types: Lectotype, USNM 56806b, designated by Resser (1938), not USNM 56806c, which was erroneously designated as the lectotype in Harrington (1956) and subsequently reported as such in Palmer and Repina (1993, 1997). Paralectotypes USNM 56808c–k were designated in Resser (1938) (he called them paratypes). The specimen USNM 56806a was part of Walcott's (1910) original type series for his *Wanneria halli*. Resser (1938) assigned this to his new species, *Olenellus alabamensis*, which is identical to *F. halli* and a junior subjective synonym. Thus USNM 56806a is also a paralectotype of *F. halli*.
Discussion: This species is the type and only known species of the genus. Harrington (1956) suggested that this genus belonged to the Olenellinae Walcott 1890 and was closely related to the genus *Olenellus*. He also added that it was easily distinguishable from the genus *Wanneria*, to which it was originally assigned by Walcott (1910). However, clear differences exist between *Fremontella* and the genus *Olenellus* (including what was formerly referred to as the subgenus *O.* [*Paedeumias*]), and phylogenetic patterns within the Olenelloidea (Lieberman 1998) suggested that these taxa are distantly related.

These taxa differ in the condition of several characters, including: 1. in *Fremontella* the anterior cephalic border between L4 and the genal spine angle has length (exsag.) roughly equal to 1.5 times length (sag.) of L0, in *Olenellus* it is roughly equal to half the length of L0; 2. in *Fremontella* the anterolateral margins of L4 at each side of the midline are deflected posteriorly at a roughly 10 to 15 degree angle relative to a transverse line, in *Olenellus* they are directed posteriorly at a roughly 40 degree angle; 3. in *Fremontella* the pre-ocular furrow on L4 is directed inward and forward from the glabellar margin, when visible in *Olenellus,* it is transverse; 4. in *Fremontella* the surface of the interocular area slopes evenly from the tip of the ocular lobe to the glabella, in *Olenellus* it is developed as a flattened shelf; 5. in *Fremontella* the posterior tips of the ocular lobes are developed opposite the medial part of the distal margin of L1, in *Olenellus* they extend further posteriorly; 6. in *Fremontella* the interocular area is relatively much narrower than it is in *Olenellus*; 7. in *Fremontella* S0, S2, and S3 are conjoined medially, in *Olenellus* they are not; 8. in *Fremontella* a line between the ends of S2 is transverse, in *Olenellus* it is directed inward and posteriorly at a roughly 45 degree angle relative to a transverse line; 9. in *Fremontella* S2 is convex anteriorly, in *Olenellus* it is straight; 10. in *Fremontella* L2 and L3 do not merge, in *Olenellus* they do; 11. in *Fremontella* the lateral margins of L2 are subparallel, in *Olenellus* they diverge anteriorly; 12. in *Fremontella* the posterior margin of L0 is convex posteriorly whereas in *Olenellus* it is more transverse; 13. in *Fremontella* the genal spine near where it hits the cephalic border is directed posterolaterally at a roughly 35 to 45 degree angle relative to a sagittal line, in *Olenellus* it is directed posterolaterally at a roughly 10 to 20 degree angle; 14. in *Fremontella* the genal spine angle is developed opposite the medial part of the distal margin of L3, in *Olenellus* it is developed opposite the medial part of the distal margin of L0; 15. in *Fremontella* the intergenal spine is not developed, whereas in *Olenellus* it is; 16. in *Fremontella* the medial part of the posterior border between L0 and the intergenal angle is transverse, in *Olenellus* it flexes posteriorly. Based on these and other character differences it is clear that *Fremontella* is distantly related to *Olenellus,* contra Harrington's (1956) and Palmer and Repina's (1993) contention and Resser's (1938) generic assignment of halli to the genus *Olenellus.* Whatever characters these taxa share are either primitive retentions or convergences based on phylogenetic topology within the Olenelloidea (Lieberman 1998).

Occurrence: Alabama: the Rome Formation, NE of Helena (Resser 1938), treated as in the upper part of the *Olenellus* zone, following Barnaby and Read (1990).

GENUS *BRISTOLIA* HARRINGTON 1956

Type species: *Mesonacis bristolensis* Resser 1928.

Assigned taxa: *Mesonacis bristolensis* Resser 1928; *Mesonacis insolens* Resser 1928; *Bristolia harringtoni* n. sp.; *Bristolia anteros* Palmer in Palmer and Halley 1979; *Paedeumias mohavensis* Hazzard and Crickmay 1933; *Bristolia fragilis* Palmer in Palmer and Halley 1979; *Bristolia* sp.

Diagnosis: Anterior cephalic border between L4 and genal spine angle relatively short, length (exsag.) less than or equal to length (sag.) of L1; anterior cephalic border developed as elevated, flattened ridge, prominently separated from extraocular area; frontal lobe contacts anterior border furrow; anterolateral margins of frontal lobe deflected posteriorly at roughly 10 degree angle relative to transverse line; frontal lobe moderately long (sag.), length equal to length of L0 and L1 medially; glabellar furrows prominently incised; S3 same depth laterally as medially; lateral margins of L2 when proceeding anteriorly bulging laterally relative to L0; lateral margins of glabella between posterior margin of L0 and L1 constrict; distal tips of S0 straight; extraocular region flattened; intergenal ridge visible as faint trace; intergenal spine absent in adult; genal spine length (exsag.) of approximately first eight thoracic segments; thorax divided into pro- and opisthothorax; nodes present on medial part of thoracic axial rings; T3 macropleural, spine length (exsag.) greater than length of thoracopygidium; anterior margin of T3 deflects anteriorly before flexing posteriorly; anterior margin of pleural furrow on T3 parallels transverse line before flexing posteriorly; anterior margin of thoracic pleural furrow separated from body of segment by prominent ridge; thoracic pleural spines, behind T4, developed as short sweeping projections extending two to three thoracic segments back, lying in roughly same dorso-ventral plane as pleural segments; prominent spine on axial ring of T15 (see Harrington 1956 and Lieberman 1998 for additional characters).

Discussion: This genus comprises a moderately diverse radiation. Described species are restricted to roughly coeval deposits of the Carrara Formation, in the Great Basin of the United States. All of the Great Basin species occur in the *Bristolia* zonule, which lies in the upper part of the *Olenellus* zone (Nelson 1976; Palmer and Halley 1979). A single fragmentary cranidium, referable to *Bristolia,* Fritz's (1972) *Laudonia*? sp., is known from the Sekwi Formation, lower *Olenellus* zone, the Mackenzie Mountains, Northwest Territories, Canada. This species is too poorly preserved to be described as a new species. However, it is placed within the genus *Bristolia* and subjected to phylogenetic analysis. The first occurrence of this species, if the stratigraphic correlations for the Canadian sections are correct, extends the range of *Bristolia* throughout the *Olenellus* zone.

Poulsen (1927) figured two new taxa from the Lower Cambrian Cape Kent Formation, upper *Olenellus* zone (Poulsen 1964), Cape Kent, NW Greenland, that he referred to as *Olenellus groenlandicus* and *O. kentensis.* These were later reassigned to *Bristolia* by Poulsen (1964). However, as discussed in detail below under the genus *Bolbolenellus,* these taxa must be removed from the genus *Bristolia* and reassigned to the genus *Bolbolenellus.*

BRISTOLIA BRISTOLENSIS (RESSER 1928)

Mesonacis bristolensis; Resser 1928:7, pl. 2, figs. 5–8.
Bristolia bristolensis (Resser); Harrington 1956:59, text fig. 1d; Riccio 1952:30, pl. 7, figs. 1, 2, 5, non pl. 8; Harrington et al. 1959:O192, fig. 133.3; Mount 1976:175, fig. 12; Palmer in Palmer and Halley 1979:64, pl. 1, figs. 14, 16, 17 non 18, 19; Mount 1980:27, fig. 12; Palmer and Repina 1993:24, non figs. 4.5, 13; Palmer and Repina 1997:409, non fig. 258.1; Lieberman 1998:73, fig. 4.3.
Olenellus gilberti (Meek); Walcott 1910, pl. 37, figs. 16, 18, 19.
?*Fremontella* sp.; Nelson 1976:31, pl. 8 (center).

Types: USNM 78390, the lectotype (defined in Palmer and Repina 1993); paralectotypes USNM 78391 and 78392.

Discussion: *Bristolia bristolensis* had originally been recognized (e.g., Riccio 1952; Palmer and Halley 1979; Palmer and Repina 1993) as a highly variable species, particularly in the condition of the intergenal and genal spine angles. However, Lieberman (1998) used univariate measurements and statistical analyses to define a well-constrained *B. bristolensis* based on Resser's (1928) lectotype, and demonstrated that what had traditionally been treated as a broadly variable *B. bristolensis* was actually two different species. The species referred to as *Bristolia* n. sp. in Lieberman (1998) is described here as *B. harringtoni* n. sp. *Bristolia bristolensis* has the intergenal angle deflected at an 80 to 95 degree angle relative to a transverse line and the genal spine angle is variably developed opposite and/or between the distal tips of S2 and S3. In *B. harringtoni* the intergenal angle is deflected at a 50 to 65 degree angle relative to a transverse line and the genal spine angle is developed variably opposite the distal tip of S2 or the medial part of L1.

Originally, Resser (1928) assigned this species to the genus *Mesonacis.* However, species of *Bristolia* differ from species of *Mesonacis* in the condition of several characters, including: 1. in *Bristolia* the anterolateral margins of the frontal lobe at each side of the midline are deflected posteriorly at roughly a 10 degree angle relative to a transverse line, whereas in *Mesonacis* the margins are deflected posteriorly at a roughly 40 degree angle; 2. in *Bristolia* the length (sag.) of L4 is roughly equal to the length (sag.) of L0 and L1, in *Mesonacis* it is roughly equal to 1.5 times the length of L0 and L1, except in *M. hamoculus* (Cowie and McNamara 1978), a derived member of the genus *Mesonacis,* where the length of L4 is similar to that found in *Bristolia*; 3. in *Bristolia* the lateral margins of L2, when proceeding anteriorly, bulge laterally relative to L0, in *Mesonacis* they do not bulge laterally relative to L0; 4. in *Bristolia* the surface of the interocular area slopes evenly from the tip of the ocular lobe to the glabella, whereas in *Mesonacis* it is arched or developed as a flattened shelf; 5. in *Bristolia* the width (tr.) of the interocular area is about half the width of the ocular lobe at its midlength, whereas in *Mesonacis* it is as wide as the width

Table 15.
The first two principal components generated from analysis of morphometric data from species of the genus *Bristolia* using Minitab v. 10Xtra. The covariance matrix was used. Character variables are abbreviated, and explained in the text.

Variable	PC1	PC2
A	– 0.335	0.066
B	– 0.608	0.463
C	– 0.158	0.483
D	– 0.167	0.088
E	– 0.135	0.045
F	– 0.176	0.068
G	– 0.251	– 0.052
H	– 0.096	0.037
I	– 0.148	0.056
J	– 0.567	– 0.725

of the ocular lobe; 6. in *Bristolia* the posterior margin of L0 is convex posteriorly, whereas in *Mesonacis* it is roughly transverse; 7. in *Bristolia* the genal spine near where it hits the cephalic border is directed posterolaterally at a roughly 35 to 45 degree angle relative to a sagittal line, or loops prominently anteriorly before deflecting posteriorly, whereas in *Mesonacis* it is directed posterolaterally at a roughly 10 to 20 degree angle relative to such a line, except in *M. cylindricus* (Palmer in Palmer and Halley 1979), a highly derived member of the genus *Mesonacis*; 8. in *Bristolia* an intergenal spine is not developed in the adult, whereas in *Mesonacis* it is; 9. in *Bristolia* the posterior margin of the thoracic pleural furrow on the third segment medially deflects strongly posteriorly before distally flexing anteriorly to parallel a transverse line, whereas in *Mesonacis* the posterior margin of this furrow is directed evenly posterolaterally (this thoracic character not preserved in all species of *Mesonacis* and/or *Bristolia*). On the basis of these and other characters, *B. bristolensis,* and all other species of *Bristolia,* must be excluded from the genus *Mesonacis.* These two genera are distantly related based on phylogenetic topology within the Olenelloidea (Lieberman 1998).

Material examined: LACMIP 4908/8, 4917/5 and several unnumbered specimens in the general stratigraphic collections; SDSNH 16785, 16829, 16832, 16834, 16835, 16840, 16843 (2 specimens), 16899, 17014, 17017; UCR 10 (2 specimens), 10/8 (3 specimens), 10/10, 10/81 (3 specimens), 10/87, 10/127 (3 specimens), 10/128, 10/509, 10/531, 10/1100, 7270, 7967, 7968 (2 specimens), 7969; USNM 78390, the lectotype.

Occurrence: California: the Carrara Formation, in the lower *Bristolia* zonule, upper part of the *Olenellus* zone, Early Cambrian, following Nelson (1976) and Palmer and Halley (1979), in the Grapevine, Funeral and Resting Spring ranges, the White-Inyo/Death Valley region, and in the Latham Shale, Marble Mountains, 190 m W of the limestone quarry, 0.5 mi E of Cadiz, in the Mojave Desert portion of San Bernardino County, possibly equivalent to Hazzard's (1933) locality M-5, treated as in the *Bristolia* zonule.

BRISTOLIA INSOLENS (RESSER 1928)
Figure 20.2

Mesonacis insolens; Resser 1928:8, pl. 2, figs. 1–4.
Olenellus insolens (Resser); Riccio 1952:30, pl. 5, figs. 1–13, pl. 6, figs. 1–3.
Bristolia insolens (Resser); Mount 1976:175, fig. 14; Mount 1980:27, fig. 14.

Types: **Lectotype,** designated here, USNM 78387 (Resser 1928, pl. 2, fig. 2), from "Bristol Mountain, near Cadiz, California, on the Santa Fe Railroad, about 100 mi east of Barstow" (Resser 1928:1). Possibly equivalent to Hazzard and Crickmay's (1933) locality M-5. Paralectotypes USNM 78386, 78388, 78389, from the same horizon as the lectotype.

Discussion: Mount (1976, 1980) correctly recognized that this species should be assigned to the genus *Bristolia* rather than to the genera *Olenellus* or *Mesonacis.* All species of *Bristolia,* including *B. insolens,* differ from species of *Mesonacis* in the condition of characters discussed above under *B. bristolensis.* Species of *Bristolia* differ from species of *Olenellus* (including what was formerly referred to as the subgenus *O.* [*Paedeumias*]) in the condition of the following characters: 1. in *Bristolia,* the length (sag.) of L4 is approximately equal to the length of L0 and L1, in *Olenellus* it is typically equal to approximately 1.5 times the length of L0 and L1; 2. in *Bristolia* the lateral margins of L4 are distal to the lateral margins of L0, in *Olenellus* they are either proximal or directly anterior of the lateral margins of L0; 3. in *Bristolia* the pre-ocular furrow on L4 is directed inward and forward from the glabellar margin, in *Olenellus,* when visible, the furrow is transverse; 4. in *Bristolia,* the ocular lobes are convex dorsally in transverse profile, in *Olenellus* they are flattened; 5. in *Bristolia* the surface of the interocular area slopes evenly from the tip of the ocular lobe to the glabella, in *Olenellus* it is developed as a flattened shelf; 6. in *Bristolia* the posterior tips of the ocular lobes are developed opposite the medial part of the distal margin of L1, in *Olenellus* they are developed opposite the medial part of the distal margin of L0; 7. in *Bristolia,* the width (tr.) of the interocular area is equal to about half the width of the ocular lobe at its midlength, in *Olenellus* the width of the interocular area is greater than or equal to the width of the ocular lobe; 8. in *Bristolia,* S2 and S3 are conjoined medially, in *Olenellus* they are not conjoined; 9. in *Bristolia* the genal spine near where it hits the cephalic border is either directed posterolaterally at a roughly 35 to 45 degree angle relative to a sagittal line, or loops strongly anteriorly before deflecting posteriorly, in *Olenellus* the genal spine is directed posterolaterally at a roughly 10 to 20 degree angle relative to such a line; 10. in *Bristolia* an intergenal spine is absent, whereas in *Olenellus* it is present; 11. in *Bristolia,* the intergenal angle is directed anteriorly at a 30 to 120 degree angle relative to a transverse line, in *Olenellus* it is deflected at a roughly 0 to 10 degree angle relative to a transverse line; 12. in *Bristolia* the genal spine angle is always further forward than in *Olenellus*; 13. in *Bristolia* the posterior margin of the thoracic pleural furrow on T3 medially deflects strongly posteriorly before distally flexing anteriorly to parallel a transverse line, whereas in *Olenellus* the posterior margin of this furrow is directed evenly posterolaterally. On the basis of these and other characters, *B. insolens,* and all other species of *Bristolia,* must be excluded from the genus *Olenellus.* These two genera are distantly related based on phylogenetic topology within the Olenelloidea (Lieberman 1998).

Material examined: LACMIP 200-E and 22 unnumbered specimens in the general stratigraphic collections; UCR 10 5/22, 10/2003, 10/2011, 10/2014, 10/2016, 10/2024, 2836/2, 7002, 7271 (1b), 7271 (8c), 7313/6.

Occurrence: If the type locality is equivalent to Hazzard and Crickmay's (1933) locality M-

Table 16.
A summary of classification produced from a linear discriminant analysis using Minitab (1995). Rows represent the species a specimen was assigned to, and columns represent the true species it belongs to based on qualitative character analysis. The proportion correctly assigned is shown underneath each species.

	1	2	3	4
Bristolia insolens (1)	6	0	1	0
Bristolia mohavensis (2)	0	24	0	3
Bristolia bristolensis (3)	0	0	27	1
Bristolia harringtoni (4)	0	6	6	39
Proportion correct	1.0	0.8	0.8	0.9

5, then the species would occur in California: the Latham Shale, Marble Mountains, 190 m W of the limestone quarry, 0.5 mi E of Cadiz, in the Mojave Desert portion of San Bernardino County, treated as in the *Bristolia* zonule, upper *Olenellus* zone, Early Cambrian.

BRISTOLIA ANTEROS PALMER IN PALMER AND HALLEY 1979

Bristolia anteros; Palmer in Palmer and Halley 1979:63, pl. 1, figs. 1–13; Mount 1980:27, fig. 15.
Bristolia new species A; Mount 1976:175, fig. 15.
?*Callavia* ? *nevadensis*; Walcott 1910:285, pl. 38, fig. 13.

Types: Holotype, USNM 177181, see Palmer and Halley (1979).
Discussion: This species is closely related to a fragmentary cranidium from the Sekwi Formation, lower *Olenellus* zone, of the Mackenzie Mountains, Northwest Territories, Canada, figured as *Laudonia*? sp. by Fritz (1972:27, pl. 9, fig. 21), later reassigned to *Bristolia* by Fritz (1992), and referred to here as *Bristolia* sp. This cranidium, GSC 27303, examined by the author for this study, bears all of the diagnostic characteristics of the genus *Bristolia* listed above, and also shares many character states with *B. anteros*, including: 1. genal spine angle opposite medial part of distal margin of L4; intergenal angle forms roughly 95 degree angle with transverse line; 2. posterior edge of ocular lobe opposite medial part of distal margin of L1; 3. medial tip of S3 further anterior than lateral tip; 4. S2 transverse, contacts axial furrow; 5. line from anterior to posterior edge of ocular lobe forms roughly 40 degree angle relative to sagittal line; 6. medial margins of genal spines loop anteriorly before deflecting posteriorly; 7. prominent furrow does not extend across entire margin of point where eye hits frontal lobe. These characters, and the possession of characters diagnostic of *Bristolia*, group this partial cephalon with the genus *Bristolia* rather than with the genus *Laudonia*. Because *Bristolia* sp. is so poorly preserved it is not described as a new species here; however, it was coded for the characters given in Table 13 and was subjected to phylogenetic analysis. Complete character state codings for *Bristolia* sp. are given in Table 14. According

to the phylogeny presented in Figure 10, *B. anteros,* from the Great Basin, is sister to *Bristolia* sp. from the Mackenzie Mountains, rather than to other Great Basin taxa.

Walcott's (1910, pl. 38, fig. 13) *Callavia ? nevadensis* is poorly preserved, but appears to represent a specimen closely related to, if not conspecific with, *B. anteros.* In particular, it has the advanced genal spines that loop prominently forward. Because of the poor state of preservation of this specimen, it is only questionably assigned to *B. anteros* at this time.
Material examined: LACMIP 4908-6 (6 specimens); UCR 10-3/1, 7271/8, 7271/14, 7271/16 (2 specimens).
Occurrence: Nevada: the upper *Bristolia* zonule, uppermost *Olenellus* zone, Early Cambrian, in the Grapevine Mountains and Last Chance Range, the Funeral Mountains, Desert Range, and Nevada Test Site (Palmer and Halley 1979); California: the upper *Bristolia* zonule, White-Inyo Mountains/Death Valley region.

BRISTOLIA MOHAVENSIS (HAZZARD AND CRICKMAY 1933)
Figures 20.4, 20.5

Paedeumias mohavensis; Hazzard and Crickmay 1933:74, pl. 1, figs. c–e, non f; Riccio 1952:33, pl. 9, figs. 7, 8.
Paedeumias sp.; Riccio 1952, pl. 9, fig. 9.
Olenellus mohavensis (Hazzard and Crickmay); Mount 1976:175, fig.9; Mount 1980:27, fig. 9.
Bristolia new species B; Mount 1976:175, fig. 16.
Bristolia new species; Mount 1980:27, fig. 16.

Types: Holotype, see Hazzard and Crickmay (1933).
Discussion: Hazzard and Crickmay's (1933, pl. 1, fig. f), one of their paratypes for *B. mohavensis,* appears to represent a specimen of *Mesonacis fremonti,* but their holotype and other paratypes are still valid. However, the holotype could not be located and may be missing. At this time a neotype is not erected as it is not essential for the purposes of taxonomic stability. Originally this species was assigned to the genus *Paedeumias* (here treated as equivalent to *Olenellus*); however, on the basis of its possession of certain characters diagnostic for the genus *Bristolia* and the absence of characters diagnostic of *Olenellus,* it is assigned to the genus *Bristolia.* A large number of character differences between *Bristolia* and *Olenellus* are listed above under the species *B. insolens.*
Material examined: LACMIP 4917-15 (3 specimens) and 4 unnumbered specimens in the general stratigraphic collections; UCR 10 (10 specimens), 10/110, 10/316, 10/320, 10/709, 10/1185, 10/2025 (2 specimens), 2847/1, 4079/19, 4079/23, 4081/70, 7002 (2 specimens), 7002/2 (2 specimens), 7002/4, 7002/6, 7313/3, 7313/7.
Occurrence: California: the Latham Shale, treated as in the *Bristolia* zonule, upper *Olenellus* zone, at the southern end of the Marble Mountains, near Chambless in the Mojave Desert portion of San Bernardino County, at the end of the dirt road on the opposite side of the hill from the limestone quarry (Chambless Limestone), about 1.25 mi N, 28 degrees E of Cadiz railroad station, Hazzard and Crickmay's (1933) locality M-5. Locality lies just above the crossbedded Zabriskie Quartzite at the end of the dirt road. Fossils in gray-brown shale, equal to the upper Latham Shale, which is 6 to 10 m thick. It is 416 ft W, 216 ft S of NE corner sec 11, T 5 N, R 14 E, San Bernardino baseline and meridian, on the USGS 15 ft Danby Quadrangle. Riccio (1952) also reports the species from the Latham Shale, Marble Mountains, 190 m W of the limestone quarry, 0.5 mi E of Cadiz, in the Mojave Desert portion of San Bernardino County, possibly equivalent to Hazzard and Crickmay's (1933) locality M-5.

Table 17.
The results of a linear discriminant analysis using Minitab (1995). Shown are the squared Mahalanobis distances between species.

	1	2	3	4
Bristolia insolens (1)	0	40.7	15.2	29.0
Bristolia mohavensis (2)	40.7	0	13.8	2.9
Bristolia bristolensis (3)	15.2	13.8	0	6.2
Bristolia harringtoni (4)	29.0	2.9	6.2	0

BRISTOLIA HARRINGTONI LIEBERMAN NEW SPECIES
Figure 20.3

Olenellus bristolensis (Resser); Riccio 1952:30, pl. 8, figs. 1–11 non pl. 7, figs. 1, 2, 5.
Bristolia bristolensis (Resser); Mount 1976:175, fig. 13; Palmer in Palmer and Halley 1979:64, pl. 1, figs. 18, 19, non 14–17; Mount 1980:27, fig. 13; Palmer and Repina 1993:24, figs. 4.5, 13; Palmer and Repina 1993:409, fig. 258.1.
Bristolia sp.; Harrington 1956:59, pl. 15, fig. 7.
Bristolia n. sp.; Lieberman 1998:73.

Types: The holotype is UCR 10/7 (Figure 20.3) from UCR locality 10, the Latham Shale, *Bristolia* zonule, at the southern end of the Marble Mountains, near Chambless in the Mojave Desert portion of San Bernardino County, California, at the end of the dirt road on the opposite side of the hill from the limestone quarry (Chambless Limestone), about 1.25 mi N, 28 degrees E of Cadiz railroad station, equivalent to horizon of Hazzard and Crickmay's (1933) locality M-5. Locality lies just above the crossbedded Zabriskie Quartzite at the end of the dirt road. Fossils in gray-brown shale, equal to the upper Latham Shale, which is 6 to 10 m thick. It is 416 ft W, 216 ft S of NE corner sec 11, T 5 N, R 14 E, San Bernardino baseline and meridian, on the USGS 15 ft Danby Quadrangle.
Diagnosis: Anterior cephalic border between L4 and genal spine angle very short (exsag.), length equal one-half length (sag.) L0; genal spine angle opposite medial part of distal margin of L1 or S2; intergenal angle forms roughly 50 to 60 degree angle with transverse line; slight ventral depression across entire margin of frontal lobe at point where ocular lobe intersects frontal lobe; lateral and distal tips of S3 as far forward; S2 convex or transverse, medial edge declined posteriorly relative to lateral edge, lateral edge generally not contacting axial furrows; line from posterior tip of ocular lobe to junction of posterior margin of lobe with glabella forms 10 degree angle relative to sagittal line; posterior edge of ocular lobe opposite medial part of distal margin of L1; width (tr.) of extraocular area roughly equal to two-thirds width between distal most tips of ocular lobes; spine on T15 developed as long needle shaped projection.
Description: Anterior cephalic border narrow, raised ridge, length (exsag.) at point halfway between lateral margin of L4 and genal spine angle equal to one-half length (sag.) L0; frontal lobe contacts anterior border furrow; anterolateral margins of frontal lobe deflected posteriorly at roughly 10 degree angle relative to transverse line; lateral margins of frontal lobe distal to lateral margins of L0; where ocular lobes contact frontal lobe slight depression

visible; lateral margins of glabella expand from posterior margin of L2 to midpoint of margin of L3; lateral margins of glabella contract between midpoint of L3 and S3; S3 convex or transverse, medial edge declined posteriorly, conjoined medially; S2 convex or transverse, medial edge declined posteriorly; L2 and L3 typically merge distally; line from posterior edge of ocular lobe to junction of posterior margin of lobe with glabella roughly forms 10 degree angle relative to sagittal line; S0, S1 transverse, contact axial furrows, medial edges declined posteriorly; lateral margins of glabella constrict between L0 and L1 when proceeding anteriorly; posterior edge of ocular lobe opposite medial part of distal margin of L1; S1 conjoined medially; posterior margin of L0 weakly convex posteriorly, with faint axial node; genal spines developed as long projections, length (exsag.) of 8 to 10 thoracic segments (sag.), sweeping backward at roughly 45 degree angle relative to sagittal line for first two-thirds of length; posterior third of genal spines roughly parallel sagittal line; genal spine angle opposite medial part of distal margin of L1 or S2; intergenal angle prominently developed, without spine, inclined at 50 to 60 degree angle relative to transverse line; extraocular region broad, width (tr.) approximately two-thirds width between distal most tips of ocular lobes; faint anastomosing ridges visible on extraocular region; faint intergenal and genal ridges visible; posterior margin of cephalic posterior border roughly transverse.

Thorax divided into pro- and opisthothorax; faint nodes present on medial part of thoracic axial rings; axial rings at T4 30% width of pleural field, excluding spines; T3 macropleural, spines length (exsag.) greater than length of thoracopygidium; medially, anterior margin of T3 deflects anteriorly before flexing posterolaterally; medially, pleural field of T3 length (exsag.) equal to length of segments four to seven; spines of T3 deflected posteriorly at roughly 30 degree angle relative to sagittal line; anterior margin of thoracic pleural furrow of T3 transverse before flexing posterolaterally; posterior margin of pleural furrow of T3 deflects strongly posteriorly medially, distally it is transverse; anterior margins of thoracic pleural furrows prominently separated from anterior band; thoracic pleural furrows extend onto spines; thoracic pleural spines behind T4 developed as short sweeping projections extending two to three thoracic segments back, lie in roughly same dorso-ventral plane as pleural segments; prominent spine on axial ring of T15 developed as long needle shaped projection.

Pygidium not known.

Discussion: Specimens of this species have been confused with *B. bristolensis*; however, statistical analyses given in Lieberman (1998) and above indicate that *B. harringtoni* must be viewed as distinct from *B. bristolensis*. Phylogenetic analysis indicates that these species are closely related and map as part of a basal polytomy within the genus *Bristolia*. However, morphometric data suggest that in terms of overall similarity, *B. harringtoni* more closely resembles *B. mohavensis*.

Etymology: Named for H. J. Harrington, who did some of the important early research on Cambrian trilobites with advanced genal spines.

Material examined: LACMIP 4875-0 and many unnumbered specimens in the general stratigraphic collections; MCZ 7371 (4 specimens); SDSNH 16949, 17004, 17007, 20711 (10 specimens), 20803 (5 specimens); UCR 10 (4 specimens), 10/3, 10/4, 10/5, 10/7, 10/8–28, 10/22 (2 specimens), 10/113 (4 specimens), 10/330, 10/855, 10/1104, 10/1173, 10/2013, 10/2014, 2836/1, 7002 (5 specimens), 7002/11, 7271, 7272, 7272/2.

Occurrence: California: in addition to the type locality known from Riccio's (1952) locality in the Latham Shale of the Marble Mountains (these horizons are possibly equivalent), also from the Carrara Formation, lower *Bristolia* zonule, Salt Spring Hills and Grapevine Mountains, White-Inyo/Death Valley region (Palmer and Halley 1979).

BRISTOLIA FRAGILIS PALMER IN PALMER AND HALLEY 1979

Olenellus fremonti; Walcott 1910:320, pl. 37, fig. 18.
Fremontia fremonti (Walcott); Harrington 1956:57, pl. 15, fig. 6.
Bristolia fragilis; Palmer in Palmer and Halley 1979:65, pl. 2, figs. 1–6.

Types: Holotype, USNM 177190, see Palmer and Halley (1979).
Material examined: UCR 2847/1.
Occurrence: Nevada: the Carrara Formation, Grapevine and Funeral Mountains, California, and Nevada Test Site and Desert Range; California: White-Inyo/Death Valley region, upper *Bristolia* zonule (Palmer and Halley 1979).

Phylogenetic Analysis of *Bolbolenellus*

The genus *Bolbolenellus* is a small clade comprised of five species nested among several of the derived genera of the Olenelloidea. Its members occur throughout Laurentia in strata assigned to the middle-upper *Olenellus* zone of the Early Cambrian. The results of a phylogenetic analysis of the five species within the genus are presented here.

A total of seven taxa was subjected to phylogenetic analysis. This includes all species of the genus *Bolbolenellus* and two outgroup taxa: *Nephrolenellus multinodus* and *N. jasperensis* n. sp. These taxa are appropriate outgroups to the genus *Bolbolenellus* based on the higher level phylogenetic analysis of the Olenelloidea presented in Lieberman (1998). The outgroups were treated as forming part of a basal polytomy. Species were assigned to the genus *Bolbolenellus* based on diagnostic characters elucidated below, recognized in part from a phylogenetic analysis of the Olenelloidea. Phylogenetic patterns were determined by parsimony analysis of seven holaspid exo-skeletal characters (Table 18). The codings for the taxa analyzed are given in Table 19. All characters were treated as unordered (nonadditive). These data were subjected to an exhaustive search on PAUP v. 3.1.1 (Swofford 1993). One most parsimonious tree (Figure 21) was recovered of length 12 steps, consistency index = 0.67, and retention index = 0.60. The distribution of all tree lengths was left-skewed relative to the distribution of tree lengths produced by random data, but the g_1 statistic, used to measure tree length skewness distributions, was –0.16. This value does not differ significantly fr1om those obtained from distributions constructed using random character data. Thus, these data do not have a strong phylogenetic signal, probably due to the limited number of character differences among these different species. The bootstrap confidence values for the nodes of the consensus tree duplicated in the bootstrap analysis are given in Figure 21. There is limited bootstrap support for all of the nodes in the phylogeny.

When the analysis presented in Bremer (1994) was conducted, 29 trees of length less than or equal to 13 steps were recovered before the analysis was terminated because the consensus cladogram was a complete polytomy, and no branch support exists for the cladogram in Figure 21. This is probably because these various taxa are separated by relatively few character differences and are presumed to be very closely related. This is attributed to the verisimilitude of the taxa within the genus *Bolbolenellus* and the fact that thoracic material for different species within the genus is not preserved, eliminating a potential line of exploration for character differences. All taxa within the genus *Bolbolenellus* are known from the middle lower *Olenellus* zone, implying good congruence between stratigraphic and phylogenetic information.

Systematic Paleontology

FAMILY Biceratopsidae Pack and Gayle 1971
SUBFAMILY Biceratopsinae Pack and Gayle 1971

Lieberman (1998) assigned the genera *Bristolia, Fremontella, Lochmanolenellus, Nephrolenellus, Bolbolenellus, Olenelloides, Peachella* and *Biceratops* to the family Biceratopsidae. Within

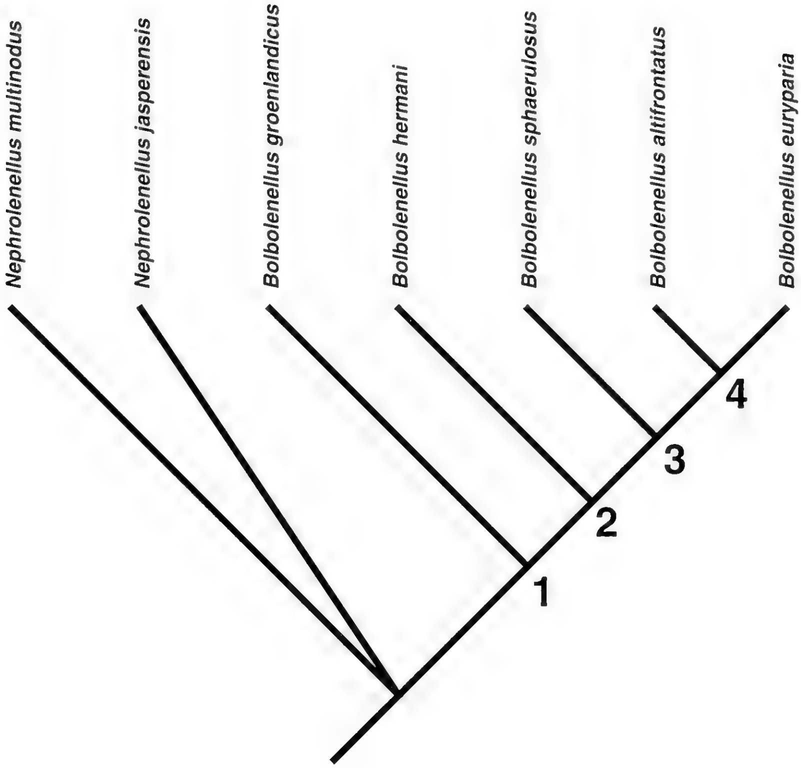


Figure 21.
The most parsimonious tree of length 14 steps produced from analysis of character data in Table 19 with PAUP v. 3.1.1 (Swofford 1993). The cladogram is constructed using an exhaustive search. The retention index is 0.60, and the consistency index is 0.67. The value of the g_1 statistic is –0.16. The following nodes in the text were supported by the following bootstrap confidence values (see text for bootstrapping procedure used): Node *1* = 0.58; Node *2* = 0.44; Node *3* = 0.31; Node *4* = 0.25. Character states are placed at nodes, using MacClade v. 3.04 (Maddison and Maddison 1992), with the characters given in Table 18. The apomorphic state is given in parentheses. Square parentheses indicate equivocal character states that are ambiguous because of missing data or multiple equally parsimonious resolutions. Equivocal characters are placed only at their basal phylogenetic position, and only unambiguous reversals are shown. Node *1*, 4(1); Node *2*, 5(1), 6(1); Node *3*, 7(1); Node *4*, 3(1).

that family, Lieberman (1998) placed two subfamilies, the Biceratopsinae, comprised of *Peachella* and *Biceratops*, and the paraphyletic "Bristoliinae," which included the rest of the aforementioned genera. In Lieberman (1998), "Bristoliinae" contained basically the same genera as in Palmer and Repina (1993) since some of the supra-generic categories had been tentatively defined until all available species within these genera could be considered. This study presents data from all available species for several different olenelloid genera, and is thus an appropriate place to reconsider supra-generic classification within the Olenelloidea.

Above, under the genus *Bristolia*, Bristoliinae was redefined to be monophyletic and restricted to the genera *Bristolia*, *Fremontella* and *Lochmanolenellus*. Consequently, all other taxa within the Biceratopsidae were reassigned to a monophyletic, expanded Biceratopsinae, including those assigned to that subfamily in Lieberman (1998) and to the genera *Bolbolenellus*, *Nephrolenellus* and *Olenelloides*. These taxa were placed within the Biceratopsinae rather than either erecting a series of monotypic subfamilies for each of these three genera or creating a new paraphyletic subfamily. The subfamily Biceratopsinae is defined here by the possession of the following characters (thoracic characters not verifiable for all species as thoracic remains do not always exist): 1. length (exsag.) of anterior cephalic border between the lateral margins of L4 and the genal spine angle roughly equal to half length (sag.) of L0; 2. anterior cephalic border developed as a raised ridge; 3. prominent parafrontal band not visible; 4. pre-ocular furrow not visible on L4; 5. ocular lobe smoothly merges with extraocular area (except in *B. sphaerulosus* [Fritz]); 6. line from posterior tip of ocular lobe to junction of posterior margin of lobe with glabella forms roughly 10 to 20 degree angle relative to sagittal line; 7. distal margins of L3 convex outward; 8. line between ends of S2 transverse; 9. S1 conjoined medially; 10. distal sector of S0 straight or convex anteriorly; 11. lateral lobes on L0 absent (except in *Olenelloides armatus* Peach); 12. extraocular area prominently vaulted; 13. thorax broken up into pro- and opisthothorax; 14. T3 macropleural, pleural spine projects further posteriorly than length of entire prothorax; 15. anterior margin of thoracic pleural furrow on T3 when proceeding from proximal to distal edge parallels a transverse line before flexing strongly posteriorly; 16. thoracic pleural furrows extend onto spines (except in *Nephrolenellus*); 17. boundary between thoracic pleural furrow and anterior band sharp; 18. pleurae of opisthothoracic segments present, with orientation distinct from that of prothoracic segments, flexing less strongly posterolaterally.

Included Taxa

GENUS *NEPHROLENELLUS* PALMER AND REPINA 1993

Type species: *Olenellus multinodus* Palmer in Palmer and Halley 1979.
Included species: *Nephrolenellus jasperensis* new species.
Diagnosis: Anterior cephalic border prominently separated from extraocular area by furrow; plectrum absent; L4 contacts anterior border furrow; anterior margins of L4 at each side of midline deflected posteriorly at roughly 10 to 20 degree angle relative to transverse line; length (sag.) of L4 equal to 1.5 times length of L0 (sag.); L4 expands prominently dorsally; lateral margins of L4 distal to lateral margins of L0; region of anterior part of ocular lobe between visual surfaces and L4 broad (tr.), one-third width of glabella at L1; ocular lobe without prominent ocular furrow; line from posterior tip of ocular lobe to junction of posterior margin of lobe with glabella forms roughly 45 degree angle with sagittal line; transverse profile of ocular lobes convex dorsally; posterior tips of ocular lobes developed opposite medial part of distal margin of L1; width (tr.) of interocular area greater than width of ocular lobe; S3 jaggedly convex, not conjoined medially; L2 and L3 do not merge; S2 convex anteriorly, conjoined medially; distal margins of L2 when proceeding anteriorly diverging; S1 conjoined medially; S0 convex anteriorly, not conjoined medially, proximal and distal ends on transverse line; L0, L1, L2 and L3 with axial spine; posterior margin of L0 convex posteriorly; prominent anastomosing ridges absent on extraocular area; width (tr.) of extraocular region opposite L1 equal to 75% of width of glabella at L1; genal spine near cephalic border directed posterolaterally at roughly 35 to 45 degree angle relative to sagittal line; genal spine short (exsag.), length approximately equal to length of first 2 to 3 thoracic segments; genal spine angle developed opposite medial part of distal margin of L0; intergenal angle deflected anteriorly at least 30 degrees relative to transverse line; medial part of posterior border between intergenal angle and L0 flexes posteriorly.

Discussion: This genus is known from the western part of Laurentia in strata equivalent to the upper *Olenellus* zone, late Early Cambrian.

NEPHROLENELLUS MULTINODUS (PALMER IN PALMER AND HALLEY 1979)

Olenellus multinodus; Palmer and Halley 1979:72, pl. 4, figs. 1–5, 7–9.
Nephrolenellus multinodus (Palmer and Halley); Palmer and Repina 1993:24, fig. 4.6; Palmer and Repina 1997:411, fig. 258.4a.

Types: Holotype, USNM 177225, see Palmer and Halley (1979).

Discussion: This species is the type of the genus. It has a small intergenal spine at the intergenal angle. The intergenal angle of *N. jasperensis* n. sp. is too poorly preserved to determine whether this character state is also present in this species, potentially making it an additional diagnostic character of the genus.

Occurrence: California: upper Carrara Formation and Pioche Shale, *Nephrolenellus multinodus* zonule, uppermost *Olenellus* zone following Palmer and Halley (1979), southern Great Basin in the Funeral Mountains, Resting Springs Range, Eagle Mountains, Grapevine Range; Nevada: same formation, Desert and Delamar Ranges.

NEPHROLENELLUS JASPERENSIS LIEBERMAN NEW SPECIES
Figure 20.6

Olenellus multinodus; Palmer in Palmer and Halley 1979:72, pl. 4, fig. 6.

Types: Holotype, GSC 16858, designated here (Figure 20.6), from 10 m above the top of the Gog Group, upper or ?uppermost *Olenellus* zone, following Fritz (1972), about 2 mi SW of Mount Simla, Jasper Park, western Alberta, Canada (locality described in detail in Mountjoy 1962).

Diagnosis: Posteromedial part of L4 at same elevation as glabella at L3; entire margin of S3 arched furthest anteriorly at point midway between midline of glabella and axial furrows; medial and distal tips of S2 deflected as far forward anteriorly; S2 arching first anteriorly then posteriorly when going from medial to lateral tip; posterior margin of ocular lobes developed opposite medial part of distal margin of L1; medial part of intergenal angle developed at point about two-thirds of way between distal tip of ocular lobes and genal spine angle; intergenal angle forms 30 to 35 degree angle with transverse line; genal spine angle opposite distal edge of medial margin of L0.

Description: Anterior cephalic border narrow, raised, rounded ridge, length (exsag.) between L4 and genal spine angle equal to one-half length L1, prominently separated from extraocular area by furrow; frontal lobe contacts anterior border furrow; plectrum absent; anterior margins of L4 at each side of midline deflected posteriorly at roughly 10 to 20 degree angle relative to transverse line; lateral margins of frontal lobe distal to L0; frontal lobe expanded dorsally, long, length (sag.) equal to roughly 1.5 times length of L0 (sag.); lateral margins of glabella expand from posterior margin of L2 to midpoint of margin of L3; lateral margins of glabella contract between midpoint of L3 and S3; S3 jaggedly convex, conjoined medially; S2 convex, conjoined medially; L2 and L3 do not merge distally; line from posterior tip of ocular lobe to junction of posterior margin of lobe with glabella forms roughly 45 degree angle relative to sagittal line; L0, L1, L2 and L3 with axial node; S0, S1 straight, contact axial furrows, medial edges declined posteriorly; lateral margins of glabella

Table 18.
Description of characters and character states used in phylogenetic analysis of *Bolbolenellus*; (0) does not always represent the primitive state as two outgroup taxa were employed in phylogenetic analysis, but for simplicity one of the outgroups, *Nephrolenellus multinodus*, was coded with all 0 character states.

1. Genal spine angle developed opposite	(0) medial part of margin of L0	(1) medial part of margin of L1 (2) anteriormost tip of S3
2. Medial and distal tips of S2	(0) on transverse line	(1) medial tip deflected further anteriorly
3. Medial most part of intergenal angle developed	(0) directly behind genal spine	(1) point two-thirds of the way between distal tip of ocular lobes and genal spine angle
4. Entire margin of S3 arched furthest anteriorly	(0) at point midway between midline of glabella and axial furrows	(1) at point three-quarters of way between midline of glabella and axial furrows
5. Postero-medial part of L4	(0) at same level as posterior part of glabella between lobes L1 to L3	(1) significantly elevated above posterior part of glabella between lobes L1 to L3
6. S2	(0) arching first anteriorly, then posteriorly, when going from medial to lateral tip (jaggedly convex)	(1) roughly transverse
7. Posterior margin of ocular lobes developed opposite	(0) medial part of margin of L1	(1) distal tips of S0

contract between L0 and L1; line from posterior tip of ocular lobe to junction of posterior margin of lobe with glabella forms roughly 45 degree angle with sagittal line; region of anterior part of ocular lobe between visual surfaces and L4 broad (tr.), one-third width of glabella at L1; ocular lobes without prominent ocular furrow; transverse profile of ocular lobes convex dorsally; posterior edges of ocular lobes opposite medial part of distal margin of L1; S0 and S1 conjoined medially; posterior margin of L0 convex posteriorly; genal spines developed as short projections, length (exsag.) approximately equal to length (sag.) of two to three thoracic segments, sweeping posterolaterally at roughly 35 to 45 degree angle relative to sagittal line; genal spine angle opposite medial part of distal margin of L0; intergenal angle inclined at 30 to 35 degree angle relative to transverse line; extraocular region broad, width (tr.) approximately 75% of width of glabella at L1; faint anastomosing ridges not visible on extraocular region; medial part of intergenal angle developed at point about two-thirds of way between distal tip of ocular lobes and genal spine angle; posterior margin of cephalic posterior border between L0 and intergenal angle deflected posterolaterally.

Thorax and pygidium unknown.

Discussion: This species is unfortunately known from very limited material. Originally Palmer in Palmer and Halley (1979) suggested that material from western Alberta was conspecific with *N. multinodus* from the Great Basin. However, there are subtle differences between the holotype specimen of *N. jasperensis* and all material from the Great Basin assigned to *N. multinodus* that indicate these species are subtly distinct, and therefore a new species was described.

Etymology: Species name derived from Jasper Park, in Canada, where the species is found.

Material examined: GSC 16858, the holotype.

Occurrence: Canada: Alberta, 10 m above the top of the Gog Group, upper or ?uppermost *Olenellus* zone, following Fritz (1972), about 2 mi SW of Mount Simla, Jasper Park.

GENUS *BOLBOLENELLUS* PALMER AND REPINA 1993

Type species: *Olenellus euryparia* Palmer in Palmer and Halley 1979.

Assigned taxa: *Olenellus altifrontatus* Fritz 1972; *O. cylindricus* Palmer in Palmer and Halley 1979; *O. groenlandicus* Poulsen 1927; *O. sphaerulosus* Fritz 1991; *O. hermani* Kindle and Tasch 1948.

Diagnosis: Anterior cephalic border prominently separated from extraocular area by furrow, developed as raised, rounded ridge; plectrum absent; L4 contacts anterior border furrow; anterior margins of L4 at each side of midline deflected posteriorly at roughly 40 degree angle relative to transverse line; length (sag.) of L4 equal to 1.5 times length of L0 and L1 (sag.); L4 expands prominently dorsally; lateral margins of L4 distal to lateral margins of L0; region of anterior part of ocular lobe between visual surfaces and L4 narrow (tr.); ocular lobe with ocular furrow; line from posterior tip of ocular lobe to junction of posterior margin of lobe with glabella forms roughly 10 degree angle relative to sagittal line; transverse profile of ocular lobes convex dorsally; interocular area arched; posterior tips of ocular lobes developed opposite S0 or medial part of distal margin of L1; width (tr.) of interocular area roughly equal to width of ocular lobe; S3 jaggedly convex, conjoined medially; entire margin of S3 arched furthest anteriorly at point three-quarters of way between midline of glabella and axial furrows; L1, L2, and L3 of strong transverse convexity; L2 and L3 do not merge; S2 conjoined medially; distal margins of L2 when proceeding anteriorly subparallel; S1 conjoined medially; distal sector of S0 straight, conjoined medially, proximal end well posterior of distal end; axial part of L0 with axial node; posterior margin of L0 convex posteriorly; lateral lobes on L0 absent; posterior cephalic border between L0 and intergenal angle deflected posterolaterally; prominent anastomosing ridges present on extraocular area; width (tr.) of extraocular region opposite L1 equal to roughly 75% of width of glabella at L1; genal spine near cephalic border directed posterolaterally at angle greater than or equal to 25 degrees relative to sagittal line; genal spine length (exsag.) greater than or equal to length of first 4 to 5 thoracic segments; intergenal angle developed two-thirds of way between distal tips of ocular lobes and genal spine angle, or directly behind genal spine angle.

Discussion: Originally, all species assigned to this genus had been assigned to the genus *Olenellus*. However, Palmer and Repina (1993) recognized that the type of the genus, *B.*

Table 19.
Character state distributions for *Bolbolenellus* and outgroups used in phylogenetic parsimony analysis. Characters and alternative states are as listed in Table 18. Missing data are indicated by "?."

	1	2	3	4	5	6	7
Nephrolenellus multinodus	0	0	0	0	0	0	0
Nephrolenellus jasperensis	0	0	1	0	0	0	0
Bolbolenellus euryparia	1	1	1	1	1	0	1
Bolbolenellus groenlandicus	2	1	0	1	0	0	0
Bolbolenellus hermani	?	0	?	1	1	1	0
Bolbolenellus sphaerulosus	0	0	0	1	1	1	1
Bolbolenellus altifrontatus	0	0	1	1	0	1	1

euryparia, was distinct from members of the genus *Olenellus* and belonged in a new genus, *Bolbolenellus.* Based on phylogenetic topology within the Olenelloidea (Lieberman 1998), species of the genera *Olenellus* and *Bolbolenellus* are distantly related. Species of *Bolbolenellus* can always be distinguished from species of *Olenellus* (including what was formerly referred to as *O.* [*Paedeumias*]) by the condition of the following characters: 1. in *Bolbolenellus* the anterior cephalic border is developed as a rounded ridge, in *Olenellus* it is a flattened ledge; 2. in *Bolbolenellus* the anterolateral part of L4 is more prominently separated from the extraocular area than it is in *Olenellus*; 3. in *Bolbolenellus* L4 expands prominently dorsally, in *Olenellus* it does not; 4. in *Bolbolenellus* the lateral margins of L4 are distal to the lateral margins of L0, in *Olenellus* the lateral margins of L4 are directly anterior to or proximal to the lateral margins of L0; 5. in *Bolbolenellus* the ocular lobes are convex dorsally in transverse profile, in *Olenellus* the ocular lobes are flattened dorsally; 6. in *Bolbolenellus* the interocular area is arched dorsally, in *Olenellus* it is developed as a flattened shelf; 7. in *Bolbolenellus* the posterior tips of the ocular lobes are developed opposite the medial part of the distal margin of L1 or opposite S0, in *Olenellus* they are developed opposite the medial part of the distal margin of L0; 8. in *Bolbolenellus* S3, S2 and S0 are conjoined medially, in *Olenellus* they are not; 9. in *Bolbolenellus* the middle sector of S3 is linear, in *Olenellus* it is convex anteriorly; 10. in *Bolbolenellus* a line between the ends of S2 is transverse, in *Olenellus* it is directed inward and posteriorly at a roughly 45 degree angle relative to a transverse line; 11. in *Bolbolenellus* L2 and L3 do not merge laterally, in *Olenellus* they do; 12. in *Bolbolenellus* the distal margins of L2 when proceeding anteriorly are roughly subparallel, whereas in *Olenellus* they expand; 13. in *Bolbolenellus* the posterior margin of L0 is more convex than it is in *Olenellus*; 14. in *Bolbolenellus* the extraocular area is more prominently vaulted than it is in *Olenellus*; 15. in *Bolbolenellus* prominent anastamosing ridges are present on the extraocular area, in *Olenellus* they are not; 16. in *Bolbolenellus* the genal spine near where it hits the cephalic border is directed posterolaterally at an angle greater than or equal to 35 degrees relative to a transverse line (except for *B. sphaerulosus*), in *Olenellus* it is directed posterolaterally at a roughly 10 to 15 degree angle. On the basis of these and other characters, species of *Bolbolenellus* are easily distinguished from species of *Olenellus.*

BOLBOLENELLUS EURYPARIA (PALMER IN PALMER AND HALLEY 1979)

Olenellus fremonti; Walcott 1910:320, pl. 37, figs. 1, 4, 5.
Olenellus euryparia; Palmer in Palmer and Halley 1979:69, pl. 2, figs. 15–18; Fritz 1991:15.
Bolbolenellus euryparia (Palmer in Palmer and Halley); Palmer and Repina 1993:24, fig. 4.10; Palmer and Repina 1997:409, fig. 258.3.
Olenellus sp.; Nelson 1976:31, pl. 8 (upper right hand corner of plate).

Types: Holotype, USNM 177204, see Palmer and Halley (1979).
Discussion: Palmer in Palmer and Halley (1979) was correct in recognizing the close affinity between this species and *B. altifrontatus* (Fritz). On the basis of phylogenetic analysis of the genus *Bolbolenellus* (Figure 10), these species appear to be sister taxa.
Material examined: UCR 7271A.
Occurrence: California: upper Carrara Formation, *Bristolia* zonule, upper *Olenellus* zone, following Nelson (1976) and Palmer and Halley (1979), Eagle Mountain, White/Inyo Mountain region; and the middle part of the Latham Shale, the *Bristolia* zonule, E slope of hill 1440 in southern end of the Marble Mountains, 834 ft E and 1,999 ft N of the SW corner sec 12, T 5 N, R 14 E, San Bernardino County.

BOLBOLENELLUS GROENLANDICUS (POULSEN 1927)
Figures 20.7, 22.1

Olenellus groenlandicus; Poulsen 1927:254, pl. 24, figs. 28–31.
Bristolia groenlandica (Poulsen); Poulsen 1964:10.
?*Olenellus kentensis*; Poulsen 1927:255, pl. 24, fig. 32.
?*Bristolia kentensis* (Poulsen); Poulsen 1964:11.

Types: Poulsen (1927) did not designate a particular specimen as the type of his *O. groenlandicus*. Poulsen (1964) designated MGUH 2233, the most well-preserved specimen of Poulsen's (1927) suite of specimens, as the holotype. However, since several specimens were figured by Poulsen (1927), this actually qualifies as a lectotype designation. Poulsen's specimen (1927, pl. 24, figs. 29, 30), MGUH 2233, is the lectotype of the species (Figure 22.1) and MGUH 2232 and 2234 (Poulsen 1927, pl. 24, figs. 28 and 31, respectively) become paralectotypes. MGUH 2235 was designated the holotype of *O. kentensis* by monotypy in Poulsen (1964). This remains the holotype of the species, but *O. kentensis* is treated here as a junior subjective synonym of *Bolbolenellus groenlandicus* (Figure 20.7; see discussion below for explanation).
Discussion: Poulsen (1927) figured and described two new taxa from the Lower Cambrian Cape Kent Formation, upper *Olenellus* zone (Poulsen 1964), Cape Kent, NE end of Inglefield Land, NW Greenland, which he referred to as *Olenellus groenlandicus* and *O. kentensis*. These were later reassigned to *Bristolia* by Poulsen (1964) primarily on the basis of the possession of an advanced genal spine (sensu Harrington 1956) in *Bolbolenellus groenlandicus* (presumably what he referred to as *Bristolia kentensis*). However, there are several other genera within the Olenelloidea that bear advanced genal spines, including *Fremontella, Lochmanolenellus, Laudonia, Elliptocephala* and *Mesonacis* (for these genera see discussions above under the appropriate generic headings), and the condition of this character thus should not be the sole arbiter of the taxonomic status of a species. Indeed, Poulsen (1964) actually considered this and was cautious in his generic assignment, sug-

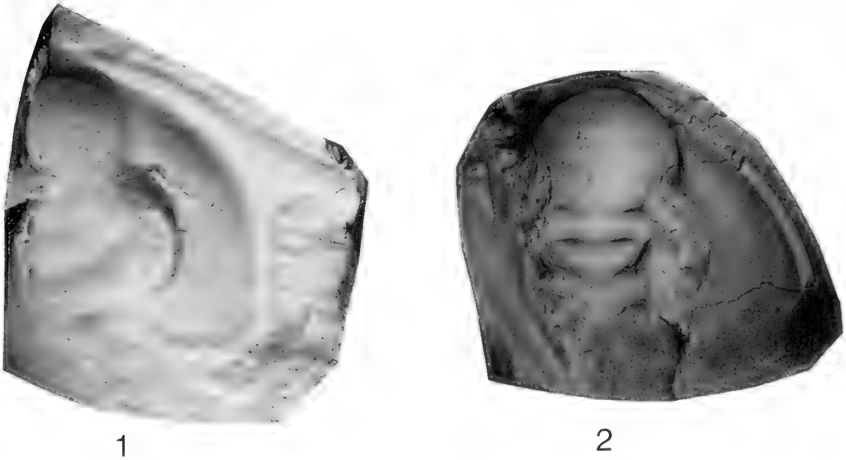


Figure 22.
1. *Bolbolenellus groenlandicus* (Poulsen), locality is the same as Figure 20.7, latex cast of the holotype, MGUH 2233, ×1.5. 2. *Bolbolenellus altifrontatus* (Fritz), locality is the same as Figure 12.2, GSC 27435, the holotype, ×1.6.

gesting that what he called *Bristolia groenlandica* might be related either to *Fremontella* or to some other new genus. Poulsen (1964) marshaled additional character evidence to suggest a close relationship between *Bristolia bristolensis* (Resser) and *Bolbolenellus groenlandicus.* In particular, he argued that these species have a similar general outline of the cephalon, convexity of the border and position of the genal spines, though he admitted that they did differ in other respects. What Poulsen (1927) referred to as *Olenellus kentensis* is very poorly preserved, lacking the anterior and lateral cephalic borders, and is thus difficult to comment on. However, it appears very similar to, if not identical with, *Bolbolenellus groenlandicus.* Poulsen (1964) claimed that *Olenellus kentensis* and *B. groenlandicus* differed in the condition of L4, which he claimed attained its maximum width at the midline of L4, whereas *B. groenlandicus* attained its maximal width at the anterior margin of L4; and what he called the transglabellar furrow (S3), which he claimed was shallower in *O. kentensis* than in *B. groenlandicus.* Since the anterior margin of L4 and the cephalon in *O. kentensis* are not preserved, it is very difficult to ascertain whether it truly differs from *B. groenlandicus* in the condition of L4 described above. S3 appears to be equally incised in both taxa. Because *O. kentensis* is so poorly preserved and known from such limited material, and because it seems to show no significant differences from *B. groenlandicus,* at this time it is treated as conspecific with *B. groenlandicus* until additional material can be recovered.

When considered in detail, *Bolbolenellus groenlandicus* has the following characters: 1. the intergenal angle forms a 90 degree angle with a transverse line; 2. there is a long (exsag.) genal spine, with the genal spine angle opposite the medial tip of S3; 3. there is a thin anterior cephalic border developed as a raised, rounded ridge; there is a prominently incised anterior border furrow; 4. the lateral margins of L0 and L1 when proceeding anteriorly constrict; 5. the extraocular area is prominently arched and very narrow; 6. S0 to S3 are all conjoined medially; 7. S2 is convex, contacts the axial furrow, and the medial tip is further anterior than the distal tip; 8. there is a prominent node on L0; 9. the posterior edge of the ocular lobe is nearly directly behind the anterior edge of the ocular lobe, rather than being rotated laterally; 10. the posterior cephalic border, when proceeding laterally, first deflects posterolaterally and then anterolaterally.

Bolbolenellus groenlandicus does bear a superficial resemblance to *Bristolia bristolensis* and other species of the genus *Bristolia*, as Poulsen (1964) implied by his assignment of this species to the genus *Bristolia*. In particular, it does have a prominent genal spine deflected far forward anteriorly, and the intergenal angle forms a roughly 90 degree angle with a transverse line. However, based on the possession of the diagnostic characters of the genus *Bolbolenellus* presented above, this species appears to be referable to that genus rather than to the genus *Bristolia*. In particular, *B. groenlandicus* has the following characters, which suggest it lies with the genus *Bolbolenellus* rather than with *Bristolia*: 1. the anterior cephalic border is developed as a narrow, raised, and rounded ridge (rather than raised and flattened as in *Bristolia*); 2. the anterolateral margins of L4 at each side of the midline are deflected posteriorly at a roughly 40 degree angle relative to a transverse line rather than at a roughly 10 degree angle as in *Bristolia*; 3. L4 is relatively longer (sag.) than it is in *Bristolia*; L4 expands prominently dorsally, it does not in *Bristolia*; 4. a pre-ocular furrow is not visible, it is in *Bristolia*; 5. the interocular area is arched rather than sloping gently from the ocular lobe to the glabella as it does in *Bristolia*; 6. the interocular area is relatively broader than it is in *Bristolia*; 7. the extraocular regions are far more vaulted and narrow (tr.) than they are in *Bristolia*; 8. S0 is conjoined medially, it is not typically in *Bristolia*; 9. S2 is jaggedly convex, rather than transverse or gently convex (as in *Bristolia*); 10. S2 has the medial end further anterior than the distal end, and this is never found in *Bristolia*. On the basis of this character evidence *Bolbolenellus groenlandicus* is excluded from the genus *Bristolia* and thus *Olenellus gronelandicus*, and by default *O. kentensis*, are referred to the genus *Bolbolenellus*. This expands the number of genera with highly advanced (sensu Harrington 1956) genal spines in the superfamily Olenelloidea.

Poulsen (1927) figured a hypostome that he assigned to his *O. groenlandicus*. This hypostome is treated as within that species until additional evidence can either confirm or deny this contention.

Material examined: MGUH 2232, a paralectotype, 2233, the lectotype, and 2235 (formerly referred to *O. kentensis*).

Occurrence: Denmark: Greenland, Cape Kent Limestone, upper *Olenellus* zone, NE end of Inglefield Land, NW Greenland, following Poulsen (1927, 1964).

BOLBOLENELLUS HERMANI (KINDLE AND TASCH 1948)

Olenellus hermani; Kindle and Tasch 1948:136, pl. 1, figs. 1–3; Tasch 1949:210; Shaw 1955:792; Tasch 1952:486, fig. 1-l; Fritz 1972:13; Fritz 1991:15.

Esmeraldina hermani (Kindle and Tasch); Shaw 1962:333, pl. 50, figs. 30–33.

Types: The holotype appears to be a specimen illustrated in Kindle and Tasch (1948, pl. 1, figs. 1, 2) and reported as in the private collection of C. H. Kindle. At present the whereabouts of this material has unfortunately not been ascertained, despite numerous attempts.

Discussion: Shaw (1962) assigned this species to the genus *Esmeraldina*; however, that generic assignment appears untenable as *Esmeraldina rowei* is distantly related to *B. euryparia* (Lieberman 1998). A fragmentary cephalon apparently identical to *B. hermani* was recently recovered from the upper *Olenellus* zone of the White/Inyo Mountain region in California (Palmer, pers. comm. 1996). Although poorly preserved, as is the type of the species and other available material for *B. hermani*, this specimen appears to be almost identical to

B. hermani from Vermont, and thus these taxa at this point in time are treated as conspecific. They both possess the spinose projection on the expanded posterior part of L4.
Material examined: MCZ 5029.
Occurrence: Vermont: 30 m above the base of the Monkton Quartzite, middle upper *Olenellus* zone, following Rankin et al. (1989), 0.5 mi W of the junction of interstate highways 2 and 7, near Clay and Red Rock Points on Lake Champlain (Kindle and Tasch 1948), lower 10 ft of the Parker Slate, 2 mi W of Georgia Center; California: the upper *Olenellus* zone, White/Inyo Mountain region. Thus, this species was presumed to be distributed throughout much of Laurentia during the upper *Olenellus* zone.

Bolbolenellus Altifrontatus (Fritz 1972)
Figure 22.2

Olenellus altifrontatus; Fritz 1972:12, pl. 18, figs. 14–17; Palmer in Palmer and Halley 1979:70; Fritz 1991:15.

Types: Holotype, GSC 27435, see Fritz (1972).
Discussion: Fritz (1972) suggested that this species was closely related to *Olenellus hermani* Kindle and Tasch, a conclusion supported by the current analysis. Both species are reassigned to the genus *Bolbolenellus*, and in the phylogenetic analysis conducted here (Figure 21) they appear to be closely related but not sister taxa. Both uniquely share the transverse condition of S2, treated as a convergent similarity in this analysis.
Material examined: GSC 27435, the holotype.
Occurrence: Canada: Northwest Territories, the type section of the Sekwi Formation (Handfield 1968), 0.2 mi SE of June Lake, uppermost Sekwi Formation, 2367 ft above the base of the formation, upper *Olenellus* zone, following Fritz (1972), south end of the Sekwi Range, Mackenzie Mountains, District of Mackenzie.

Bolbolenellus sphaerulosus (Fritz 1991)

Olenellus sphaerulosus; Fritz 1991:15, pl. 10, figs. 1–13.
?*Olenellus bufrontis*; Fritz 1991:12 , pl. 12, figs. 6–8.

Types: Holotype, GSC 91835, see Fritz (1991).
Discussion: Early ontogenetic stages of this species in some cases have the posterior tips of the ocular lobes developed opposite the medial part of the distal margin of L0. However, in typical adult material the ocular lobes only extend back to S0, and the species was coded as having this character state in this analysis. *Olenellus bufrontis* Fritz appears almost identical to *B. sphaerulosus*, differing solely from that taxon in coming from a much earlier ontogenetic stage. As the only known locality of *O. bufrontis* is identical to one of the localities of *B. sphaerulosus*, they are provisionally treated as conspecific. Fritz (1991) noted that *B. sphaerulosus* was closely related to *B. altifrontatus* and *B. euryparia*, and also to *B. hermani*, and this conclusion is supported by this analysis. *Bolbolenellus sphaerulosus* is the only species within the Biceratopsinae that has a prominent furrow or depression separating the ocular lobe from the extraocular area, and the ocular lobe also sits on a raised ledge so that it does not smoothly merge into the extraocular area. An ocular lobe smoothly merging with the extraocular area is a feature considered diagnostic of the Biceratopsinae. However, because *B. sphaerulosus* matches all other species of *Bolbolenellus* and the Biceratopsinae in

the condition of so many other characters, it is treated as belonging to the genus *Bolbolenellus,* and the condition of this character is treated as a convergence in a relatively derived species within the genus. Other taxa that typically bear such a feature include *Fritzolenellus truemani* and *Laudonia bispinata,* taxa not closely related to the genus *Bolbolenellus* (Lieberman 1998).

Occurrence: Canada: Yukon Territory, the upper part of the Illtyd Formation, Fritz's (1991) Unit 6, ?upper *Olenellus* zone, Early Cambrian, Wernecke Mountains.

· NINE ·

Integrating Phylogenetic and Stratigraphic Data

These phylogenetic data from separate clades can be integrated along with the results from Lieberman (1998) to give a detailed picture of patterns of evolution and speciation in the Olenelloidea during the Early Cambrian. Such a phylogenetic tree for the Olenelloidea is shown in Figure 23. Phylogenetic topology is taken directly from this study and Lieberman (1998), except for the addition to the tree of *Peachella brevispina* Palmer in Palmer and Halley. This species is assumed to be the sister taxon of *P. iddingsi* (Walcott). It includes information about the relative appearance of species in the fossil record based on the correlation schemes of Ahlberg et al. (1986), Ahlberg (1991), Kirschvink et al. (1991), Rozanov (1992), Bowring et al. (1993), Palmer and Repina (1993), Isachsen et al. (1994), Geyer and Palmer (1995), Brasier et al. (1996), Kaufman et al. (1996), Knoll (1996), Vidal and Moczydlowska-Vidal (1997) and Landing et al. (1998). The ghost lineage method elaborated in Edgecombe (1992) is used to determine the latest time that a lineage must have diversified by, with dashed lines representing that part of a species' range not preserved in the fossil record. This tree can be used to elaborate biogeographic patterns during the Early Cambrian using the method of Lieberman and Eldredge (1996), as was done in Lieberman (1997), and also to look at how speciation rates during the Early Cambrian may have differed from those at subsequent time periods in the fossil record (Lieberman 1999). Based on patterns of speciation and the stratigraphic distribution of taxa, it appears that all the major groups within the Olenelloidea must have diversified prior to the Cambrian Radiation, though speciation events are also distributed throughout the interval traditionally consigned to the Radiation. This implies either that there is a gap in the fossil record of indeterminate duration that cloaks the history of the Olenelloidea, or that the group diversified with startling rapidity and in a single pulse, right at the base of the *S. mickwitzi* zone. Even assuming that a gap is present in the history of the Olenelloidea, levels of speciation appear to be quite intense. For instance, when compared with levels of speciation in trilobites from other time periods that have been well-studied in the fossil record using phylogenetic methods, such as the Middle Devonian (see Lieberman 1994), it is apparent that speciation may have been occurring at a much higher rate in the Early Cambrian.

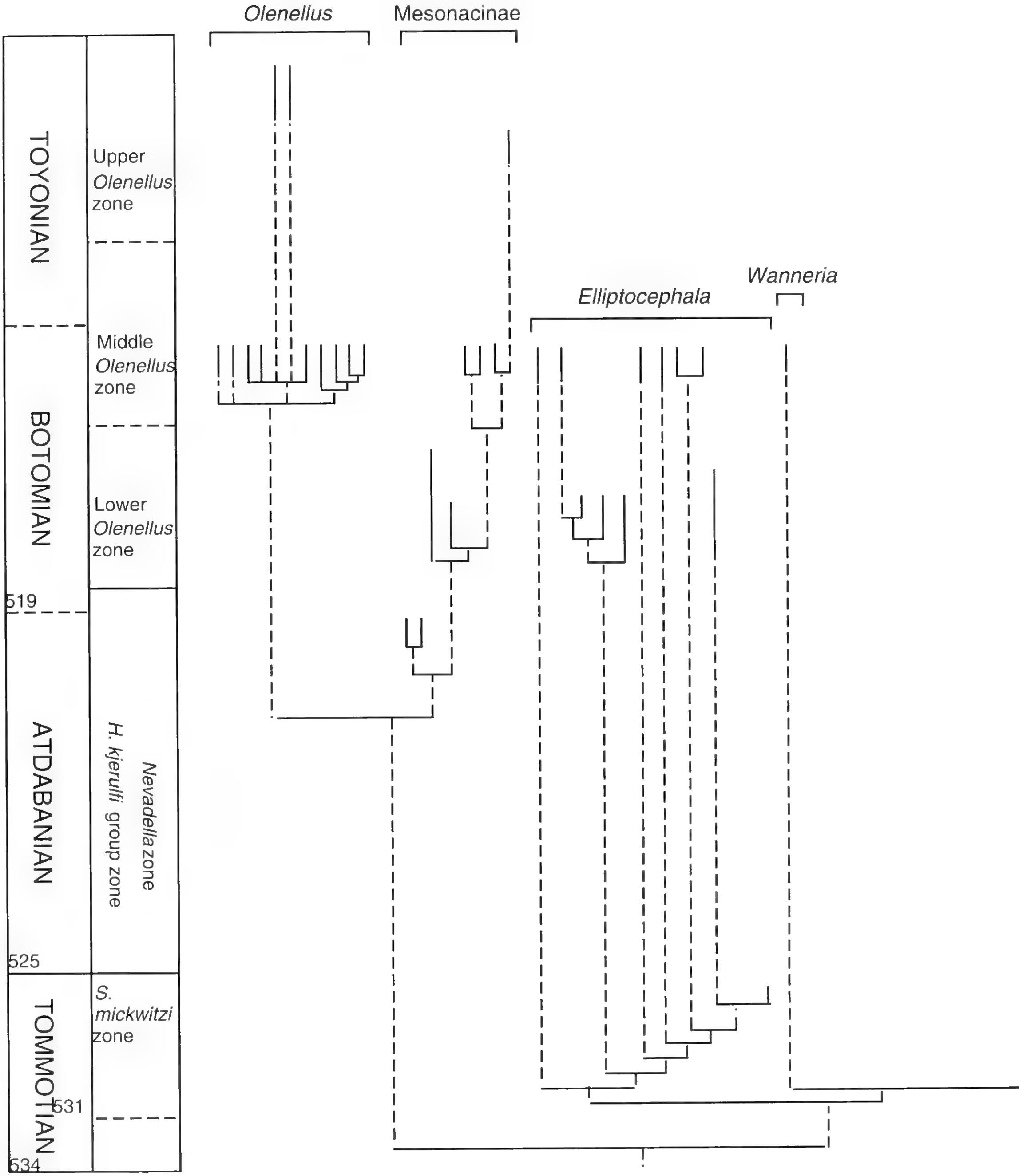
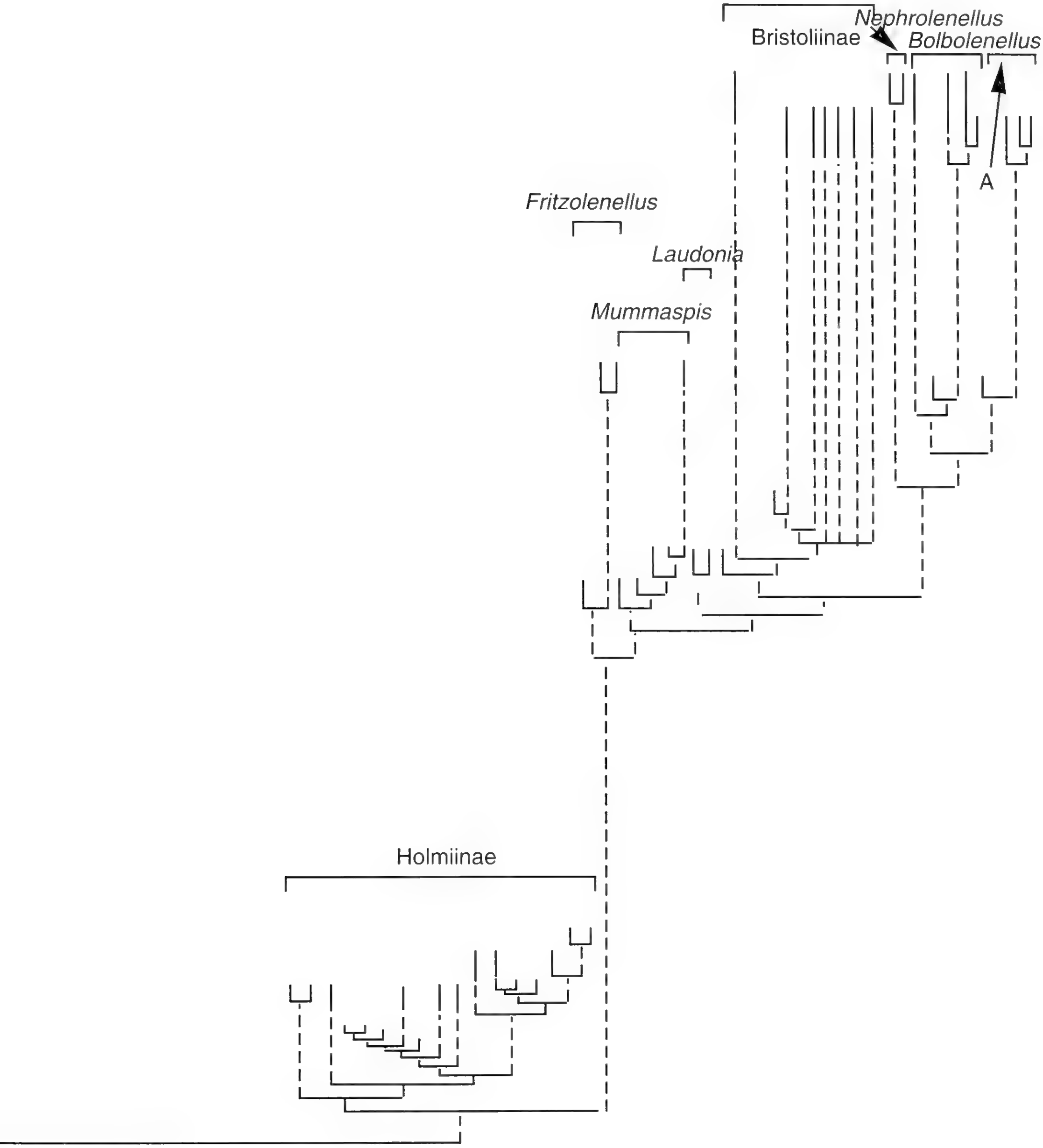


Figure 23.
A phylogenetic tree depicting topology and timing of patterns of speciation in the Olenelloidea. Tree built using information from phylogenetic analyses presented herein and in Lieberman (1998). Stratigraphic correlations and provisional radiometric dates from Ahlberg et al. (1986), Ahlberg (1991), Kirschvink et al. (1991), Rozanov (1992), Bowring et al. (1993), Palmer and Repina (1993), Isachsen et al. (1994), Geyer and Palmer (1995), Brasier et al. (1996), Kaufman et al. (1996), Knoll (1996), Vidal and Moczydlowska-Vidal (1997) and Landing et al. (1998). Solid lines represent approximate stratigraphic ranges of species. However, in many instances, based on



phylogenetic information, the ancestral lineages leading to these species must have appeared earlier. The ranges of these species were extended to make them square with information based on phylogenetic topology. Extended lineages are depicted as dashed lines that represent ghost lineages sensu Edgecombe (1992). The generic or subfamilial name is placed above each of the clades within the Olenelloidea. The Clade A refers to the following nested set of taxa: *Olenelloides armatus* Peach, *Biceratops nevadensis* Pack and Gayle, *Peachella iddingsi* (Walcott) and *P. brevispina* Palmer in Palmer and Halley.

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