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PHYLOGENETIC ANALYSIS OF THE OLENELLINA WALCOTT, 1890 (TRILOBITA, CAMBRIAN)

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ABSTRACT—Phylogenetic analysis was used to evaluate evolutionary relationships within the Cambrian suborder Olenellina Walcott, 1890; special emphasis was placed on those taxa outside of the Olenelloidea. Fifty-seven exoskeletal characters were coded for 24 taxa within the Olenellina and two outgroups referable to the "fallotaspidoid" grade. The Olenelloidea, along with the genus *Gabriellus* Fritz, 1992, are the sister group of the Judomioidea Repina, 1979. The "Nevadioidea" Hupé, 1953 are a paraphyletic grade group. Four new genera are recognized, *Plesionevadia, Cambroinyoella, Callavalonia,* and *Sdzuyomia,* and three new species are described, *Nevadia fritzi, Cirquella nelsoni,* and *Cambroinyoella wallacei.* Phylogenetic parsimony analysis is also used to make predictions about the ancestral morphology of the Olenellina. This morphology most resembles the morphology found in *Plesionevadia* and *Pseudojudomia* Egorova in Goryanskii and Egorova, 1964.

INTRODUCTION

THE ANALYSIS of evolutionary patterns during the Early Cambrian has relevance to paleontologists and evolutionary biologists for several reasons. Chief among these are expanding our knowledge of evolutionary mechanisms and topologies. Regarding evolutionary mechanisms, because the Cambrian radiation represents that key episode in earth history when the Eumetazoa diversified, and because there is a dramatic disjunction between pre- and post Early Cambrian faunas, it is of interest to determine whether evolutionary processes, specifically tempo and mode, were unique at this time (Fortey et al., 1996). This requires an understanding of evolutionary patterns (Eldredge and Cracraft, 1980; Smith, 1994). Further, regarding evolutionary topologies, evolutionary patterns from this time are of intrinsic interest because they record the initial, ramose branchings of the metazoan clade, and a key part of the history of this clade is the topology of these initial branching events. One of the major eumetazoan clades undergoing initial diversification in the fossil record at this time is the trilobite subphylum. In this study, phylogenetic patterns are evaluated within the suborder Olenellina Walcott, 1890, the basal trilobite clade [according to phylogenetic trees of the Trilobita presented by Fortey and Whittington (1989), Fortey (1990), Ramsköld and Edgecombe (1991), and Fortey and Owens (1997)]. This is done in order to study diversification of this group during the Cambrian radiation, and to assess what may have been the ancestral character states of the Olenellina. The Olenellina are a geographically widespread, diverse, and abundant group that are restricted to the Early Cambrian.

Higher-level phylogenetic patterns within the Olenellina were considered by Lieberman (1998), who divided the suborder into three superfamilies: the Olenelloidea Walcott, 1890, the Judomioidea Repina, 1979, and the Nevadioidea Hupé, 1953. Further, he re-defined the suborder so as to be monophyletic. To do this, Lieberman (1998) removed one superfamily that had traditionally been assigned to the Olenellina from that suborder, the Fallotaspidoidea Hupé, 1953, in order to avoid making the Olenellina paraphyletic. The moroccan representatives of that superfamily have been recently comprehensively treated by Geyer (1996). Based on character evidence, this superfamily shares a more recent common ancestry with the Redlichiina Richter, 1932, and thus with most if not all other trilobite orders, than it does with the other members of the Olenellina. Further, the Fallotaspidoidea as presently defined is also a paraphyletic grade (Lieberman, 1998), and will be referred to henceforth informally as the "fallotaspidoids," using the within quotes convention of Wiley (1979) for paraphyletic groups. The Olenellina is treated as sister to the group including the "fallotaspidoids" plus the Redlichiina, and potentially all other trilobites. Where the Agnostida fit within this evolutionary topology depends on whether or not one accepts the arguments of either Fortey and Whittington (1989), Fortey (1990), and Fortey and Theron (1994) or Ramsköld and Edgecombe (1991). However, topologically, the closest relatives of the Olenellina lie within the "fallotaspidoids."

Lieberman (1998) used character evidence to define the Olenellina. First, in the Olenellina the condition of the length (sag.) of the frontal lobe is greater than or equal to the length of L0 and L1 (sag.), whereas in the "fallotaspidoids" the length of the frontal lobe (sag.) is relatively much shorter, being equal to 1.0–1.1 times the length of L0 (sag.). Further, in the Olenellina the ocular lobes either merge with the lateral margins of the frontal lobe, or contact only the posterior part of the lateral margins of the frontal lobe (two separate characters). In the "fallotaspidoids" the ocular lobes always contact the entire lateral margin of the frontal lobe and they never merge with the frontal lobe. Each of these characters is discussed more fully below.

Within the Olenellina, provisionally, Lieberman (1998) referred the following genera to the Judomioidea: *Bondonella* Hupé, 1953; *Callavia* Matthew, 1897; *Cambropallas* Geyer, 1993; *Gabriellus* Fritz, 1992; *Geraldinella* Fritz, 1993; *Judomia* Lermontova, 1951; *Judomiella* Lazarenko, 1962; *Neltneria* Hupé, 1953; *Paranevadella* Palmer and Repina, 1993; *Selindella* Repina, 1979; and *Sinskia* Suvorova, 1960. The following genera were provisionally referred by Lieberman (1998) to the Nevadioidea: *Cirquella* Fritz, 1993; *Nevadia* Walcott, 1910; and *Nevadella* Raw, 1936. Lieberman (1998, 1999) also presented an hypothesis of phylogenetic relationship, based on cladistic analysis, for the different genera and species of one of the superfamilies within the Olenellina, the Olenelloidea. However, at the scale of broader phylogenetic patterns within the Olenellina, specifically the relationships of the three superfamilies to one another, Lieberman (1998) placed the three superfamilies within the Olenellina into an unresolved trichotomy. Here, phylogenetic parsimony analysis was used to resolve the evolutionary relationships of the various lineages within this trichotomy, and to establish better constrained phylogenetic concepts for the Judomioidea and Nevadioidea. Morphological terminology used herein follows that of Palmer and Repina (1993), Whittington et al. (1997), and Lieberman (1998).

PHYLOGENETIC ANALYSIS

Taxa analyzed.—A total of 26 taxa within the Olenellina was subjected to phylogenetic analysis. This included 24 ingroup taxa.

All adequately preserved species within the Olenellina were analyzed. In order to avoid redundancy and because the Olenelloidea have already been subjected to cladistic analysis (Lieberman, 1998, 1999), a single exponent of this clade was chosen. To prevent possible biases by choosing one or a few highly derived olenelloid taxa, the taxon chosen was a consensus node, which represented the character codings for the hypothetical ancestor of all the Olenelloidea, utilizing the characters considered in this analysis. Explanation of how the character states for this node were determined is provided below. This node represents all of the olenelloids including the holmiids which are treated as ingroup Olenelloidea based on the discussions and character evidence presented in Palmer and Repina (1993, 1997) and Lieberman (1998, 1999). Three genera of the Olenellina could not be analyzed herein, and are not discussed in detail because adequately preserved material was not available. These are *Judomiella, Selindella,* and *Sinskia.* For all of the other olenellinid genera considered, when possible, all valid species were subjected to phylogenetic analysis. However, for a few species such as *Bondonella sdzuyi* Geyer and Palmer, 1995 and *Neltneria termieri* Hupé, 1953 adequately preserved material could not be obtained; other such species are discussed more fully below under the appropriate generic headings. One other taxon was analyzed that was formerly assigned to the "fallotaspidoids," *Bradyfallotaspis fusa* Fritz, 1972. This species had been assigned to the "fallotaspidoids" by Fritz (1972), Palmer and Repina (1993, 1997), Geyer (1996), and Lieberman (1998). However, it needs to be reassigned to the Olenellina because it bears the hallmark traits of that suborder. In particular, it has a relatively long (sag.) frontal lobe (character 9 state 1 in the list of characters used in phylogenetic analysis given below), and the ocular lobe contacts only the posterior part of the lateral margin of the frontal lobe (character 11 state 1 in the list of characters used in phylogenetic analysis given below) (see Fritz, 1972, pl. 3, figs. 1–7, Palmer and Repina, 1993, fig. 9.2 or Palmer and Repina, 1997, fig. 266.1 and compare with either Fritz, 1972, pl. 1, figs. 1–8, Palmer and Repina, 1993, figs. 7, 8, 9.4 or Palmer and Repina, 1997, figs. 264, 265, 266.4). Other characters that place *Bradyfallotaspis* Fritz, 1972 up the tree relative to the "fallotaspidoids" include the following character states in the list of characters used in phylogenetic analysis given below: 8(1); 17(1); 18(1); 25(1); 28(1); and 38(2).

The two outgroups chosen are the "fallotaspidoids" *Daguinaspis ambroggii* Hupé and Abadie, 1950 and *Parafallotaspis grata* Fritz, 1972. As discussed above, the "fallotaspidoids" are part of a grade. The outgroup taxa chosen belong to two different subfamilies within the "fallotaspidoids" (Palmer and Repina, 1993) in order to provide a broader constraint on ancestral morphology within the Olenellina. The specific exemplars within these subfamilies were chosen for their excellent state of preservation, which is a necessary prerequisite for determining character homologies that is unfortunately not met in many "fallotaspidoid" taxa, and also because of their relatively early appearance in the fossil record.

Characters and character states.—Phylogenetic patterns were determined by parsimony analysis of the following 57 holaspid exoskeletal characters. Characters are roughly arranged in their manner of appearance from anterior to posteriormost point on the exoskeleton. Autapomorphies are not included. (0) does not always represent the primitive state for the Olenellina as two outgroup taxa were employed in phylogenetic analysis, but for simplicity one of the outgroups, *Daguinaspis ambroggii,* was coded with all "0" character states.

1) Anterior border near but not directly anterior of frontal lobe (LA) (0) very short, length (exsag.) less than or equal to one-half length (sag.) of L0 (1) moderately long, length (exsag.) equal to length (sag.) of L0 (2) very long, length (exsag.) equal to 1.5 times length (sag.) of L0.

2) Anterior cephalic border developed as (0) flattened ledge (1) rounded ridge.

3) Anterior border (0) not prominently separated from extraocular area by furrow (1) prominently separated from extraocular area by furrow.

4) Plectrum (0) absent (1) present.

5) Frontal lobe (LA) of glabella (0) does not contact anterior border furrow (1) contacts anterior border furrow.

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

7) Parafrontal band anterior of anterolateral margins of LA (L4) (0) short (exsag.), length approximately equal to one-eighth length (sag.) of L0 (1) long (exsag.), length approximately equal to one-half length (sag.) of L0 (2) not visible.

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

9) Length (sag.) of LA (L4) (0) short, equal to 1.0–1.1 times length of L0 medially (1) long, equal to 1.5 times length of L0 and L1 medially (2) moderately long, equal to 1.0–1.1 times length of L0 and L1.

The length (sag.) of L0 and L1 in *Callavalonia callavei* (Lapworth, 1888) was difficult to measure because this species has an extremely large spine developed on the posterior margin of L0. For the purposes of calculating this length, the posterior margin of L0 was not taken as the posterior tip of the spine but rather as a point extrapolated from the continuously curving posterior margin of L0. Therefore, this species was coded as having state 0 for this character. States 1 or 2 is found in all members of the Olenellina except *Pseudojudomia egregia* Egorova *in* Goryanskii and Egorova, 1964 and *Callavalonia callavei* (Lapworth, 1888). *Pseudojudomia egregia,* based on phylogenetic analysis, is the basal member of the Olenellina, indicating that the group had not yet evolved the derived state of this character, though it had evolved the derived state of other characters. *Callavalonia callavei* is a derived member of the Olenellina, nested well within that clade on the basis of many synapomorphies discussed further below. Therefore, *P. egregia* and *C. callavei* do belong to the Olenellina, but this character does not have 100 percent consistency within the group.

10) Lateral margins of LA (L4) (0) proximal to lateral margins of L0 (1) distal to lateral margins of L0 (2) directly anterior to lateral margins of L0.

11) Ocular lobes contact frontal lobe (0) at anterior and posterior parts of frontal lobe (1) at posterior part of frontal lobe.

All members of the Olenellina possess either 11(0) and 13(1) or 11(1) and 13(0) (see discussion above) except for two caveats to this general rule. These are the genera *Cirquella* and *Paranevadella.* In all species of the genus *Cirquella,* which possess state 13(0), the ocular lobes do not merge with the lateral margins of the frontal lobe and instead contact both the anterior and posterior margins of the frontal lobe (character 11[0]). *Cirquella* is very similar to the genera *Nevadia* and *Nevadella* in many respects (Palmer and Repina, 1993; Fritz, 1995), and it is also closely related to these genera based on phylogenetic analysis, though it does not share a sister group relationship with either of them. Like *Cirquella, Nevadella* has the ocular lobes contacting but not merging with the frontal lobe (character 13[0]); however, in both *Nevadia* and *Nevadella* the ocular lobes contact only the posterior margin of the frontal lobe, i.e., character 11(1), the standard condition found throughout the Olenellina. The difference between this and what is found in *Cirquella* may be attributable to the significant telescoping of the anterior margin of the cephalon found in all species of this genus, such that the extraocular area is greatly reduced in relative size as compared to what is found in *Nevadia* and *Nevadella.* This reduction in relative size would have concomitantly influenced the geometry of the relationship between the ocular lobes and the frontal lobe. Thus, the presumed homology between the ocular lobe and the lateral margin of the frontal lobe is somewhat obscured in this genus. If this explanation is not valid then *Cirquella* would be referable to the "Fallotaspidoidea," an assignment recommended by Geyer (1996). Further, the typical homologies of the Olenellina would not exist in *Cirquella,* implying that the numerous similarities *Cirquella* shares with other representatives of the Olenellina, including the genera *Nevadia* and *Nevadella,* would have to be viewed as convergences.

Paranevadella subgroenlandicus (Repina in Khomentovskii and Repina, 1965) also is treated as a representative of the Olenellina but has 11(0) and 13(0). In this species the ocular lobes are unusually long (exsag.), relatively longer than what is seen in any other member of the Olenellina. For example, in *P. subgroenlandicus* the anteromedial margin of the ocular lobe extends as far forward as the anterior margin of LA (L4), and the posteromedial margin of the ocular lobe extends as far back as S2 in some specimens. In other members of the Olenellina and in the "fallotaspidoid" grade the posteromedial margins of the ocular lobe are never posterior of S3. This exsagittal expansion of the ocular lobe medially in *P. subgroenlandicus* would obscure the recognition of homologous points at the juncture of the ocular lobe and the frontal lobe in this species, when compared to other members of the Olenellina. Specifically, typical Olenellina with state 13(0) have state 11(1). The exsagittal expansion of the ocular lobe in *P. subgroenlandicus* would expand the area on the lateral margin of the frontal lobe that the ocular lobe contacts relative to that typical of Olenellina that have character state 13(0). It should be stated that the condition of the medial margin of the ocular lobe near the frontal lobe in *P. subgroenlandicus* is still very different from what is seen in the "fallotaspidoid" grade, and thus this special character would be properly viewed as an autapomorphy and therefore was not coded into phylogenetic analysis. In particular, it is different because in the "fallotaspidoids," although the ocular lobe contacts the entire lateral margin of the frontal lobe, it is not strongly expanded exsagittally throughout its entire length (exsag.). Instead, in the "fallotaspidoids" the anterior margin of the ocular lobe deflects sharply anteriorly near the margin of the frontal lobe, such that the entire lateral margin of the frontal lobe is circumscribed by the ocular lobes.

12) Outer band of ocular lobe near lateral margin of L4 (0) expands prominently exsagittally (1) does not expand prominently exsagittally.

13) Ocular lobes (0) gradually decrease dorso-ventral elevation between mid-point of ocular lobes and axial furrows (1) of constant dorso-ventral elevation between mid-point of ocular lobes and axial furrows.

14) Region of anterior part of ocular lobe between putative visual surfaces and L4 (0) broad (tr.), 25–33 percent width of glabella at L1 (1) narrow (tr.), nearly in contact.

15) Line from posterior tip of ocular lobe to junction of posterior margin of lobe with glabella (0) forms 45 degree angle with sagittal line (1) parallel to sagittal line (2) forms 10–25 degree angle with sagittal line.

16) Posterior tips of ocular lobes developed opposite (0) medial part of distal margin of L0 (1) S0 (2) medial part of distal margin of L1

17) width (tr.) of interocular area (0) equal to two to three times width of ocular lobe at its midlength (1) about half to two thirds width of ocular lobe at its midlength (2) approximately equal to 1.0–1.4 times width of ocular lobe at its midlength.

18) Anterodistal margins of L3 formed by (0) axial furrows (1) ocular lobes.

19) Distal margins of L3 (0) straight (1) convex outward.

Based on a re-evaluation of homologies the character coding for *Neltneria jacqueti* was changed relative to the coding of the equivalent character 26 in Lieberman (1998). However, using the initial character coding from Lieberman (1998) for this species does not perturb the results retrieved herein. Moreover, recoding this character for the matrix used in Lieberman (1998) also leaves the phylogenetic patterns that analysis retrieved unchanged.

20) Course of S3 (0) straight (1) gently convex (2) jaggedly convex or carat shape (3) not prominently incised.

21) S3 (0) not conjoined medially (1) conjoined medially.

22) Lateral margins of glabella between L0–L2 (0) convergent (1) sub-parallel.

23) Line between ends of S2 (0) directed inward and posteriorly at roughly 35–45 degree angle to transverse line (1) transverse.

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

25) S2 (0) not conjoined medially (1) conjoined medially.

26) S2 (0) straight (1) convex anteriorly.

27) Distal margins of L2 when proceeding anteriorly (0) converging (1) diverging (2) sub-parallel.

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

29) Distal sector of S0 (0) straight to concave anteriorly (1) convex anteriorly (2) sinuous.

30) S0 (0) conjoined medially (1) not conjoined medially.

31) Distal sector of S0 with (0) proximal end well posterior of distal end (1) proximal and distal ends on transverse line.

32) Axial part of L0 (0) smooth (1) with node present (2) with spine present.

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

34) Medial of eye, intergenal ridge (0) prominently developed (1) not visible.

This is equivalent to the mid-interocular ridge of Geyer (1996).

35) Extraocular region opposite L1 (0) very narrow, width (tr.) less than or equal to 15 to 20 percent of the width of the glabella at L1 (1) narrow, width (tr.) 35–50 percent of the width of the glabella at L1 (2) broad, width (tr.) greater than or equal to 65–75 percent of the width of the glabella at L1.

36) Length (exsag.) of genal spine (0) genal spine not well developed or absent (1) equal to length (sag.) of first three to five thoracic segments (2) equal to length (sag.) of at least eight thoracic segments (3) equal to length (sag.) of first two thoracic segments.

37) Genal spine angle developed opposite medial part of (0) distal margin of L0 (1) distal margin of L1 (2) first thoracic segment (3) distal margin of L2.

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

39) Intergenal spine (0) weakly or not at all developed (1) prominent.

40) Intergenal angle relative to a transverse line (0) directed anteriorly at roughly 60–70 degree angle (1) deflected at roughly −10 to 10 degree angle (2) directed anteriorly at roughly 30 degree angle (3) deflected at roughly −30 to −40 degree angle.

41) Medial part of posterior border between L0 and intergenal angle (0) flexes posteriorly (1) transverse (2) flexes anteriorly.

42) Thorax (0) not prominently divided up into pro- and opisthothorax (1) broken up into pro- and opisthothorax.

43) Number of thoracic segments (0) 16–19 (1) 23–27.

44) Anterior margin of third thoracic pleural segment, before

flexing strongly posteriorly (0) parallel to a transverse line or very weakly directed posteriorly (1) directed anteriorly.

45) Third thoracic segment (0) normal (1) macropleural.

46) Anterior margin of thoracic pleural furrow on third segment when proceeding from proximal to distal edge (0) directed weakly posteriorly, before flexing strongly posteriorly (1) parallels a transverse line, before flexing strongly posteriorly.

47) Posterior margin of thoracic pleural furrow on third thoracic segment (0) directed evenly posterolaterally (1) medial part parallel to a transverse line, distal part deflected weakly anterolaterally (2) medial part parallel to a transverse line, lateral part deflected weakly posteriorly.

48) Thoracic pleural spines on segments 5–8 (0) do not sweep significantly back (1) developed as short projections extending two to four thoracic segments back (2) developed as broad sweeping projections extending back six to eight thoracic segments.

49) Lateral margins of prothoracic axial rings 1–5 (0) sub-parallel (1) converging when proceeding from anterior to posterior.

50) Single nodes on median part of thoracic axial rings (0) absent (1) present.

51) Thoracic pleural furrows (0) extend onto spines (1) extend 85–100 percent width of inner pleural region (2) extend only half to 65 percent width of inner pleural region.

52) Boundary between thoracic pleural furrow and anterior band (0) sharp (1) gradational.

53) Length (exsag.) of thoracic pleural furrows at medial part of thoracic segment relative to length at distal part of segment (0) equal to twice length of pleural furrows on distal part of segment (1) equal to one to 1.3 times length of pleural furrows on distal part of segment.

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

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

56) Last segments of thorax (0) do not merge with pygidium (1) merge with pygidium.

57) Pygidium (0) relatively narrow, length (sag.) 1.5 times width (tr.) (1) relatively broad, length (sag.) equal to width (tr.) (2) very broad, 2–2.1 times as wide (tr.) as long (sag.).

The codings for the taxa analyzed are given in Table 1. The Olenelloidea, as mentioned above, was treated as a single consensus node, representing the hypothesized ancestral morphology of that superfamily. To code this node, all taxa considered by Lieberman (1998) and where applicable by Lieberman (1999) were coded for all of the characters utilized in the phylogenetic analysis presented above. There are other characters which vary within the Olenelloidea, but which are absent or invariant in the other exponents of the Olenellina. Therefore, these autapomorphic characters were not considered in this study. Then, using the cladograms of the Olenelloidea from Lieberman (1998, 1999), these character codings were assigned to the terminal taxa. These characters were then optimized to the basal node of the Olenelloidea using the trace changes option of MacClade v. 3.04 (Maddison and Maddison, 1992). The character states representing the codings of the basal node are given in the data matrix in Table 1 under the heading "Olenelloidea."

TABLE 1—Character state distributions for taxa used in phylogenetic analysis. Characters and character states are as listed in text. Missing data are indicated by "?". Character numbers are listed at top of table. Character states listed as "X", "Y", "W", and "Z" are polymorphic, where "X" = (0&1), "Y" = (1&2), "Z" = (0&2), and "W" = (0&1&2).

	000000000111111111122222222223333333333444444444455555555 123456789012345678901234567890123456789012345678901234567
Daguinaspis ambroggii	000000000000000000000000000000000000000000000000000000000
Parafallotaspis grata	10110010000100200001100001001101012?00010???????????????1
Pseudojudomia egregia	100?0??1001100Z0Z0???000100100011?Y120030????????????????
Plesionevadia burri	100?0011101100210010000011001X01001?02010????????????????
Nevadia weeksi	001100012011012120001000100101000023010111100002011010100
Nevadella cartlandi	101????1101101202????0000?011001001?22010??1100?1??0?2???
Nevadella eucharis	101?00011011012220000000010011010 12?22010111100211101210?
Nevadella mountjoyi	101010011011012Y2X00100011011X01012122010001100211100210?
Nevadella perfecta	101100011011012Y2X0010001X011X0101210201X001100211211210?
Cirquella espinata	011101212001012Y200010001101100111200102 0????????????????
Cirquella nummularia	01110120200101222000100011011001112011001????????????????
Cirquella nelsoni	01110??12001012Y20???0000?01?0011110000??????????????????
Bradyfallotaspis fusa	110?0001121101101100110010210001011?02010????????????????
Paranevadella subgroenlandicus	01110001200101101 11??11010?1?01?012?22030????????????????
Cambroinyoella wallacei	1111001?200010102112100011110?01012?00020?0010010010101??
Geraldinella corneiliana	10100011200111222111100011110001012?02010???????????????2
Cambropallas telesto	210010101000112201111100111111010112220100011010111000112
Andalusiana cornuta	11011000100010YX21121110011010110012000 10???10001110X10??
Gabriellus sp.	011010112001112X110210100110110001113210210101221100011 00
Olenelloidea	001011011W11112W211200XX0X10X10101210Y110100X101110X1010W
Callavia broeggeri	11101011200111200111001001111?02001121110?0000011110020?2
Callavalonia callavei	20101011000111200111001001101102001?21110??????1??2012?02
Sdzuyomia lotzei	111100?1220111210001?010?1?0?1??10132?010?000000?021?201?
Judomia tera	100010012201111011020110012021101 12?2301000000110021 00?10
Bondonella typica	11101000120111111113?10001Y01X111111000111000011112100000
Neltneria jacqueti	100010002201111211120101001011101111010111000010112100100

Parsimony analysis.—These data were then subjected to a heuristic search on PAUP 4.0 beta version (Swofford, 1998) using a stepwise addition sequence with 100 random replications. All multistate characters were treated as unordered (nonadditive) because there were no clear criteria for ordering them. Three most parsimonious trees were recovered of length 287 steps. A strict consensus of these trees is shown in Figure 1. These trees occupied a single island (Maddison, 1991). The retention index of the most parsimonious trees is 0.53, and the consistency index (when uninformative characters are excluded) is 0.40. The value of the consistency index is near the mean value of data sets of this size based on the compilations of Archie (1989) and Sanderson and Donoghue (1989), and is also within the range of consistency indices for phylogenies of this size (in terms of numbers of taxa) generated using molecular sequence data (Klassen et al., 1991). Further, the value for the consistency index exceeds values derived from similarly sized data matrices constructed from random data (consistency index of 0.14) at the 0.05 level of significance, based on Klassen et al. (1991). Thus, we can have some confidence that there is reasonable phylogenetic structure replicated in these character data. This provides additional evidence, beyond

FIGURE *1*—The strict consensus of three most parsimonious trees of length 287 steps produced from analysis of character data in Table 1 with PAUP 4.0 (Swofford, 1998). Cladogram constructed using a heuristic search with a stepwise addition sequence and 100 random replications. All characters were treated as unordered. The retention index is 0.53 and the consistency index excluding uninformative characters is 0.40. The following nodes of the tree were supported by the following jackknife confidence values (see text for jackknife procedure utilized): Node *2* = 0.54; Node *3* = 0.39; Node *6* = 0.59; Node *7* = 0.57; Node *8* = 0.60; Node *9* = 0.51; Node *10* = 0.97; Node *11* = 0.41; Node *12* = 0.89; Node *13* = 0.55; Node *14* = 0.50; Node *15* = 0.77; Node *16* = 0.90; Node *17* = 0.59; Node *18* = 0.87; Node *19* = 0.57; Node 20 = 0.42; Node *21* = 0.46; Node *22* = 0.97; Node *23* = 0.85. The following nodes of the tree were supported by the following bootstrap confidence values (see text for bootstrapping procedure utilized): Node *2* = 0.31; Node *3* = 0.16; Node *6* = 0.16; Node *7* = 0.14; Node *8* = 0.14; Node *9* = 0.14; Node *10* = 0.70; Node *11* = 0.15; Node *12* = 0.43; Node *13* = 0.16; Node *15* = 0.18; Node *16* = 0.29; Node *17* = 0.18; Node *18* = 0.44; Node *19* = 0.14; Node *21* = 0.28; Node *22* = 0.59; Node *23* = 0.63. The following branch support values (Bremer, 1994) were recovered for the following nodes: Node *1* = 2+; Node *16* = 1; Node *22* = 1. Total tree support (Bremer, 1994) is at least 0.02. Character states are placed at nodes (using MacClade v. 3.0.4 [Maddison and Maddison, 1992]), with the characters given in the text. The apomorphic state is given in parentheses. Brackets indicate equivocal character states which 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, except for multistate characters.

that presented in Lieberman (1998), that morphological variation in trilobites, if evident as homoplasy, was not unduly extreme in the Early Cambrian, and there is no reason to believe that Cambrian trilobites are any more or less recalcitrant to phylogenetic analysis than any other type of organism [see discussion in McNamara (1986), Hughes (1991), and Lieberman (1998)].

To assess overall phylogenetic signal within the database, 1,000 random trees were generated from the character data in Table 1 ten separate times using PAUP 4.0. For each iteration, the distribution of these tree lengths was evaluated and the g_1 statistic, a measure of tree-length skewness, was obtained. The mean value from these 10 iterations was -0.36. This value differs at the 0.05 level of significance from g_1 values obtained from cladograms generated using random character data. This implies strong phylogenetic signal in these data (Hillis, 1991).

To further assess the quality of, and overall phylogenetic signal within, the character data of Table 1, PTP tests (Faith, 1991; Faith and Trueman, 1996) were performed using PAUP. PTP compares the length of trees generated using randomized data (character states are assigned randomly to taxa) with the length of the most parsimonious tree(s). The proportion of the randomized data trees having a most parsimonious cladogram length equal to or less than that of the original most parsimonious cladogram is tabulated. This is referred to as the cladistic permutation tail probability or PTP and treated as equivalent to a *P*-value at which the character data differ from random data. This method is described in detail in Faith (1991), Swofford et al. (1996), and Faith and Trueman (1996). Two separate PTP tests were implemented. In the first, the character data for all taxa were randomized 1,000 times, and in each of these replications a heuristic stepwise search with a random addition sequence and five replications was used to find the most parsimonious cladogram based on the random data. For each replication, the difference between the tree length of the random data set and the original set were calculated. In this test the PTP value was <0.001, a highly significant value, implying good cladistic structure and phylogenetic signal in the database. Following the recommendation of Swofford et al. (1996), a PTP test was also employed that only randomized the ingroup taxa. Again, the PTP was <0.001, implying good phylogenetic signal in the character data of Table 1.

A bootstrap analysis was also conducted using PAUP 4.0 (Swofford, 1998) to determine the support for each of the nodes that appear in the most parsimonious consensus cladogram. One hundred bootstrap replications were employed in a stepwise search that used five random replications per bootstrap replication, and groups were retained that were compatible with the 50 percent majority rule consensus tree. The confidence values for the nodes of the tree duplicated in the bootstrap analysis are given in the caption for Figure 1. Many, but not all of the nodes appear in both the bootstrap and most parsimonious consensus trees. In a similar test of cladogram support and phylogenetic structure the jackknife analysis of PAUP 4.0 (Swofford, 1998) was implemented. In this technique, a percentage of characters chosen by the user are randomly deleted in several iterations and the effect of this on cladogram structure is determined. In effect, the test asks what part of the pattern would be replicated if a certain number of characters had never been found. The percentage value chosen was five percent, which is equivalent to three characters in this database. As with the bootstrap analysis, groups were retained that were compatible with the 50 percent majority rule consensus tree (Fig. 1). Again, many but not all of the nodes appear in both the jackknife and most parsimonious consensus trees. The implication is that even if not all of the morphological characters uncovered in this analysis were found by another worker, the phylogenetic topology would be replicated fairly faithfully if these character data were analyzed using a parsimony based computer algorithm.

A Bremer branch support analysis (Bremer, 1994) was also conducted to examine the support of the different individual nodes of the cladogram. One hundred fifty-eight trees of length less than or equal to 288 steps, and 3,621 trees of length less than or equal to 289 steps were found before the analysis was terminated when a completely polytomous ingroup was recovered. Thus, branch support values represent minimums, and may actually be slightly higher for one of the nodes. Individual branch support values are given in the caption of Figure 1. The total support index (Bremer, 1994) for the tree is at least 0.02.

Finally, to further assess the general support for the tree presented in Figure 1 a series of experiments were conducted involving substituting different taxa within the Olenelloidea for the reconstructed ancestral node of the Olenelloidea that was used in the initial parsimony analysis. The taxa substituted for the consensus node singly or in combination were *Olenellus thompsoni* (Hall), *O. transitans* (Walcott), *Mesonacis vermontanus* (Hall), *Mesolenellus hyperborea* (Poulsen), *Elliptocephala asaphoides* Emmons, *E. logani* (Walcott), and *Wanneria walcottana* (Wanner)because these are among the basal representatives of the Olenelloidea according to Lieberman (1998, 1999). Irrespective of the taxa used, the basic tree structure presented in Figure 1 was still recovered. However, in some cases there were subtle topological shifts or resolution was lost. For example, in the case of the "Nevadioidea," depending on which of the olenelloid taxa were included, the positions of *Plesionevadia* and *Cirquella* did sometimes move on the tree. In addition, depending on which olenelloid taxa were included, the positions of the *Cambropallas* and *Andalusiana* clade and the genus *Gabriellus* did sometimes move slightly relative to the Judomioidea and the Olenelloidea. Because none of the olenelloid taxa listed above, when chosen singly or in combination, provides the complete morphological information known about the ancestral state of the Olenelloidea, because there are an astronomical number of groupings of olenelloid taxa that could be chosen, and because the decision to exclude or include those olenelloids listed above, or indeed other individual olenelloid taxa is arbitrary except in the case when all information can be encoded, the phylogenetic hypothesis that considered information from all the Olenelloidea is to be preferred. However, it is reassuring that the basic phylogenetic pattern described herein continues to emerge even when a more limited

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←

Node *1,* 1[0, 1], 4[0, 1], 12[0, 1], 15[0, 2], 21[0, 1], 26[0, 1], 28[0, 1], 29[0, 1], 32[0, 1], 35[0, 2], 40[0, 1]; Node *2,* 1(1), 4(1), 8(1), 11(1), 12(1), 15(2), 25(1), 32(1), 35(2), 36(1), 40(1); Node *3,* 9[0, 1, 2], 16(1), 38(2); Node *4,* 3(1), 9[1, 2], 14(1), 17(2), 21(1), 28(1), 48(2), 50(1), 51(1), 53(1), 55(1); Node *5,* 16(2), 26(1), 34(1), 45(1), 49[0, 1]; Node *6,* 9(1), 29(1), 44(1), 49(1), 54(2); Node *7,* 37(2); Node *8,* 21[0, 1], 25(0); Node *9,* 2(1), 9(2); Node *10,* 1(0), 33(1), 36(0), 38[0, 1, 2], 40[0, 1, 2]; Node *11,* 15[1, 2], 18(1), 19[0, 1], 27[0, 1, 2], 29(0); Node *12,* 15(1), 17(1), 22(1), 26(0); Node *13,* 7(1), 13(1), 19(1), 20[0, 1, 2], 27(1), 48(1); Node *14,* 4(0), 15(2), 20[1, 2], 57(2); Node *15,* 5(1), 23[0, 1], 25[0, 1], 28[0, 1], 29(1), 30[0, 1], 35(0), 49(1); Node *16,* 3(0), 8(0), 9(1), 12(0), 22(1), 36(2), 48(0); Node *17,* 21[0, 1], 23(1), 25(0), 30(1), 39(1), 42[0, 1], 45(0); Node *18,* 1(0), 20(2), 28(0), 42(1), 46(1), 51(0); Node *19,* 17(0), 20(1), 21(0), 32(2), 34(0), 37(2), 54(2), 55(0); Node *20,* 2[0, 1], 28(0), 51(2); Node *21,* 10(2), 16[0, 1], 19[0, 1], 33(1), 39(0), 52(1); Node *22,* 3[0, 1], 15(1), 17(1), 20(2), 22(1), 31(1), 32(0), 34(1), 47(1), 54(0), 57(0); Node *23,* 8(0), 16[0, 1, 2], 19(1), 23(0), 37(0), 41(1), 42(1).

sampling of olenelloid morphology was used in parsimony analysis.

SUPRA-FAMILIAL CLASSIFICATION WITHIN THE OLENELLINA

Phylogenetic analysis of the Olenellina suggests several broad scale evolutionary patterns that are relevant to the classification of that suborder. First (see Fig. 1), the genus *Gabriellus* is sister to the Olenelloidea. Second, the Judomioidea is the sister group of the Olenelloidea and *Gabriellus*. Third, the "Nevadioidea" is paraphyletic, and the Olenelloidea, *Gabriellus*, and the Judomioidea are closely related to the derived "nevadioids" *Cambropallas* and *Andalusiana*. Each of these broad scale patterns is summarized in greater detail below.

Palmer and Repina (1993, 1997) assigned *Gabriellus* to the Olenelloidea. Lieberman (1998) subsequently removed it from the Olenelloidea because it lacked some of the defining characters of that superfamily; however, based on the phylogenetic topology given in Figure 1, it is clear that *Gabriellus* is closely related to the Olenelloidea. This genus could either be elevated to the rank of superfamily, be subsumed within the Olenelloidea, or treated as an unranked taxon sister to the Olenelloidea. The latter taxonomic decision is followed at this time to avoid changing the definition of the Olenelloidea. However, the degree of support for the close relationship between *Gabriellus* and the Olenelloidea can be quantified by implementing the topology-dependent permutation test (T-PTP test) of Faith (1991) on PAUP (Swofford, 1998). This test was conducted using a search that randomized all taxa, and employed a stepwise, random addition sequence with five random iterations per replication with a total of 1,000 replications. If it is assumed a-priori that these taxa are closely related then the P-value for the T-PTP test is 0.002, a highly significant value. This implies that there is strong support for a close relationship between the Olenelloidea and *Gabriellus* based on the character data presented in Table 1.

In Figure 1, sister to the monophyletic clade including the Olenelloidea and *Gabriellus* there is a clade comprising the genera *Callavia, Callavalonia* n. gen., *Sdzuyomia* n. gen., *Judomia, Neltneria,* and *Bondonella.* This clade is treated as equal to a monophyletic Judomioidea, and it is close to the concept of that superfamily used by Lieberman (1998). However, Lieberman (1998) defined the Judomioidea as those members of the Olenellina having the ocular lobes merging with the entire lateral margin of the frontal lobe, and on that basis he also assigned *Paranevadella, Gabriellus, Cambropallas, Andalusiana* Sdzuy, 1961, and *Geraldinella* to that superfamily. As redefined herein, all members of the Judomioidea do have the ocular lobes merging with the entire lateral margin of the frontal lobe. However, if other taxa that possess this character, such as *Gabriellus, Geraldinella, Andalusiana, Cambropallas,* and *Paranevadella,* were to be included within the Judomioidea it would necessitate sinking the Olenelloidea and *Gabriellus* within that superfamily. Since the Olenelloidea is a superfamily that is already well established, this taxonomic decision was not followed. The Judomioidea is instead treated as sister to the clade Olenelloidea plus *Gabriellus* and can be defined by the shared possession of the following character states from the character list given above: 5(1) (this character is lost in *Sdzuyomia lotzei* (Richter and Richter, 1941) and is also found in *Nevadella mountjoyi* Fritz, 1992); 11(0); 13(1); 21(0); 29(1 or 2); 35(1) (35[2] in *Judomia tera* Lazarenko, 1960); 36(1 or 3); 37(0 or 2); 40(1); 43(0); 44(0); 45(0); 46(0); 47(0 or 2); 48(0 or 1); 51(2) (51[1] in *Callavia broeggeri* [Walcott, 1890]); 54 (0 or 2); 55(0) (this character state is lost in *Neltneria jacqueti* [Neltner and Poctey, 1949]); 57(0 or 2). Now, *Paranevadella, Gabriellus, Cambropallas, Andalusiana,* and *Geraldinella* form part of a paraphyletic grade sister to the clade containing the Olenelloidea, *Gabriellus,* and the Judomioidea.

Based on character evidence discussed above, *Bradyfallotaspis* is nested within the Olenellina. The degree of support for this hypothesis was also quantified by the T-PTP test of PAUP. Using the same protocol described above, if we were to have predicted a-priori that *Bradyfallotaspis* was nested up the tree, which is valid given the character evidence grouping it with the Olenellina discussed above, then the P-value for the T-PTP test is 0.02, a significant value, suggesting that this hypothesis of evolutionary relationship is well supported. However, if this relationship were to be postulated a posteriori a Bonferroni (or some other) correction would be necessary in order to avoid Type I error and the result would no longer be significant because of the large number of possible comparisons.

According to the phylogenetic analysis conducted herein, the genus *Callavia* is nested within the Judomioidea, matching the suggestions of Lieberman (1998). The relatively close relationship this implies between *Callavia* and *Judomia* was also predicted by Hupé (1953) and Harrington et al. (1959), and the relatively close relationship this implies between *Callavia* and *Bondonella* was also predicted by Bergström (1973), though the classification presented herein does differ in respects from the classifications presented in each of these publications.

Palmer and Repina (1993, 1997) suggested that *Callavia* was nested within the Olenelloidea; however, Lieberman (1998) argued that *Callavia* lacked the defining characters of the Olenelloidea and must be excluded from that superfamily. Based on the phylogenetic analysis conducted herein the contention of Lieberman (1998) is supported as *Callavia* is not the sister group of the Olenelloidea. However, *Callavia* is relatively closely related to the Olenelloidea because it, along with *Gabriellus* and the Olenelloidea, do form a paraphyletic grade.

This study also suggests that *Neltneria* and *Bondonella,* the Neltneriidae Hupé, 1953 as discussed by Palmer and Repina (1993, 1997), are nested within the Judomioidea, matching the predictions of Lieberman (1998). Ahlberg et al. (1986) also suggested that the genera *Judomia* and *Neltneria* shared some evolutionary affinity, and their contention is supported by this study, though again their classification differs somewhat from the classification presented herein. Specifically, Ahlberg et al.'s (1986) classification differs from the one presented herein because they posited a closer relationship between *Judomia* and *Neltneria* than between *Neltneria* and *Bondonella.* At this time additional families within the superfamily Judomioidea are not defined.

Finally, the rest of the taxa within the Olenellina are assigned to a paraphyletic "Nevadioidea," in order to avoid creating several new monotypic superfamilies. The "Nevadioidea" corresponds roughly to the Nevadiinae Hupé, 1953 as discussed by Hupé (1953), Harrington et al. (1959), and Bergström (1973), and the Nevadiidae as discussed by Ahlberg et al. (1986) and Palmer and Repina (1993, 1997). An alternative to defining a paraphyletic "Nevadioidea" would be to define several monotypic or depauperate superfamilies but this decision is not advocated. Further, at this time additional families within the "Nevadioidea" are not defined because it would result in the generation of several new, taxonomically depauperate families. However, two clades of moderate diversity, *Nevadella* and *Cirquella,* are recognized within the "Nevadioidea." Two smaller clades, one containing *Bradyfallotaspis* and *Paranevadella,* and one containing *Cambropallas* and *Andalusiana,* are also recognized.

Figure 1 predicts that the Judomioidea and the Olenelloidea were derived from the "nevadioids." This matches the predictions of Geyer (1996) who concluded that the "nevadioids" were the members of the Olenellina that had diverged the least from the "fallotaspidoids." Within the "nevadioids," *Pseudojudomia* Egorova *in* Goryanskii and Egorova, 1964 and *Nevadia* are relatively closely related, as predicted by Repina (1979), Ahlberg et al.

(1986), and Palmer and Repina (1993, 1997), though they are not sister taxa. *Nevadia* and *Nevadella* are also closely related, supporting the contention of every author who has considered this group previously, though they are not sister taxa. *Cambropallas* and *Andalusiana* are also closely related, matching the predictions of Geyer (1993) and Palmer and Repina (1997), though their superfamilial classifications for these taxa differ from that presented herein. Geyer (1993), Geyer and Palmer (1995), and Palmer and Repina (1993, 1997) concluded that these taxa were referable to the Holmiidae. Geyer and Palmer (1995) assigned this family to the Nevadioidea. Palmer and Repina (1993, 1997) assigned to this family to the Olenelloidea. Therefore, the phylogenetic placement of *Cambropallas* and *Andalusiana* presented herein agrees at the superfamilial level with that of Geyer (1993) and Geyer and Palmer (1995) and diverges from that of Palmer and Repina (1993, 1997). Lieberman (1998) suggested that *Cambropallas* and *Andalusiana* did not belong within the Olenelloidea because they lack the defining characters of that superfamily, and their failure to emerge as sister taxa to the Olenelloidea or *Gabriellus* plus the *Olenelloidea* reinforces this conclusion. However, the divergence from the conclusions of Palmer and Repina (1993, 1997) is not profound because herein it appears that *Cambropallas* and *Andalusiana* are closely related to a clade that includes the Olenelloidea.

Counter to the predictions of Palmer and Repina (1993, 1997), *Paranevadella* does not group with the judomioids but is rather part of a grade of "nevadioids." Finally, as discussed in Lieberman (1998), *Geraldinella* groups within the Olenellina rather than with the "fallotaspidoids." In particular, it has a relatively long (sag.) frontal lobe (character 9 state 2 in the list of characters used in phylogenetic analysis given above), and the ocular lobe merges smoothly with the lateral margin of the frontal lobe (character 13 state 1 in the list of characters used in phylogenetic analysis given above). Other characters that place *Geraldinella* up the tree relative to the "fallotaspidoids" include the following character states in the list of characters used in phylogenetic analysis given above: 8(1); 14(1); 17(2); 18(1); 19(1); 25(1); 27(1); 28(1); 38(2); and 57(2). A T-PTP test was conducted using the same protocol given above to determine the relative degree of support for this hypothesis. The *P*-value of this test was 0.02, implying that this hypothesis is well supported based on the character data given in Table 1.

Lieberman (1998) also suggested that within the Olenellina *Geraldinella* should be grouped with the judomioids; however, more detailed phylogenetic analysis suggests that this is not the case. Rather, this genus is part of a paraphyletic grade of "nevadioids." Specifically, it lacks the following character states typical of the Judomioidea from the list of characters used in phylogenetic analysis: 5(1), the taxon has 0 instead; 21(0), the taxon has 1 instead; 29(1 or 2), the taxon has 0 instead; and 40(1), the taxon has 2 instead. A T-PTP test was conducted using the same protocol given above, except that only ingroup taxa were randomized, to ascertain the relative degree of support for the hypothesis that *Geraldinella* groups with the "nevadioids" rather than with the Judomioids. The *P*-value determined using PAUP was 0.001, implying that there is strong evidence supporting placement of *Geraldinella* with the "nevadioids" rather than with the judomioids.

ANCESTRAL MORPHOLOGY OF THE OLENELLINA

Based on phylogenetic analysis and parsimonious optimizations of characters using MacClade v. 3.0.4 (Maddison and Maddison, 1992) it is possible to make predictions about the ancestral morphology of the Olenellina when it diverged from the rest of the Trilobita, either some time during the pre-trilobitic (Placentian in Avalonia) part of the Early Cambrian, or in the Neoproterozoic. The following are the predicted character states using the characters listed above and in Table 1 (character states marked with one or more asterisks are realistically questionable due to missing data, with the number of asterisks referring to the number of basal taxa within the Olenellina for which this character is missing, and character states marked? indicate that the basal taxon within the Olenellina, or the basal taxon in terms of those that have that character preserved, bear a different state): 1(1); 2(0); 3(0); 4(1)**; 5(0); 6(0)*; 7[0, 1]*; 8(1); 9(0); 10(0); 11(1); 12(1); 13(0); 14(0); 15(2)?; 16(0); 17(0)?; 18(0); 19(0)*; 20(0)*; 21[0, 1]*; 22(0); 23(0); 24(0); 25(0); 26[0, 1]; 27(0); 28[0, 1]; 29[0, 1]; 30(0); 31(0); 32(1); 33(0)?; 34(0)*; 35(2)?; 36(1); 37(0)?; 38(0); 39(0); 40(1)?; 41(0); 42(0)***?; 43(0)***?; 44(0)***; 45(0)***; 46(0)***; 47(0)***; 48[0, 2]; 49(0)***; 50[0, 1]; 51[0, 1]; 52(0)***; 53[0, 1]; 54(0)***; 55[0, 1]; and 56(0)***. On the basis of these character states, the ancestral morphology of the Olenellina most resembles the morphology of *Pseudojudomia egregia* and *Plesionevadia burri.*

In this discussion, one character that deserves further mention is the condition of the pygidium because Fortey and Whittington (1989) and Ramsköld and Edgecombe (1991) offered the pygidium as a potential synapomorphy of the Trilobita. Later, Edgecombe and Ramsköld (1999) concluded that a pygidium with a specific type of thoracic/pygidial tagmosis was a synapomorphy of the Trilobita, the naraoiids, and the helmetiids. Ramsköld and Edgecombe (1991) recognized a distinction between species with a pygidium consisting of a single segment plus a fused telson-like area and species with a pygidium having multiple segments, and they also discussed the condition of the pygidium in some members of the Olenellina. The condition of this character in many representatives of the Olenellina that were considered herein could not be determined because of poor preservation. For the same reason, this character was also difficult to evaluate in "fallotaspidoid" outgroups to the Olenellina. Therefore, it was not included in phylogenetic analysis. However, because the condition of this character potentially has some bearing on synapomorphies characterizing the base of the Trilobita, it merits some comment, in the context of the Olenellina. The following taxa have a pygidium with a single free segment and then a second segment fused to a telson (the size of the telson does vary in these taxa): *Nevadia weeksi*; *Geraldinella corneiliana*; *Cambropallas telesto*; *Gabriellus* sp.; *Callavalonia callavei*; *Judomia tera*; *Sdzuyomia lotzei*; and *Neltneria jacqueti.* (For other taxa, the state of this character could not be determined.) By contrast, some representatives of the Olenelloidea have pygidia with multiple segments. This would suggest that at least within the Olenellina, primitively the pygidium consisted of a single segment plus a second segment fused to a terminal telson. Geyer (1996) illustrated a pygidium of the "fallotaspidoid" *D. ambroggii.* It consists of only a single segment fused to a telson, closely matching the condition found in most of the Olenellina, exclusive of the Olenelloidea.

TAXA ANALYZED AND SYSTEMATIC PALEONTOLOGY

Some of the taxa treated in phylogenetic analysis do not need a detailed synonymy list or discussion and they are simply listed below. For these taxa, previous diagnoses are sufficient, although these can be augmented using the character codings detailed above and in Table 1. Other taxa are treated in a systematic paleontology section. Of these other taxa, some from western Laurentia occur within the *Fallotaspis* zone. Geyer (1996) has presented cogent arguments as to why the *Fallotaspis* zone in Laurentia may not represent a vaild biostratigraphic zone, at least when compared to other sections outside of Laurentia. However, because no alternative zonal terminology exists at this time, this zonal name is used.

Collections from the following institutions were examined: