

NEW EARLY CAMBRIAN OLENELLINE TRILOBITES FROM THE SEKWI
FORMATION, MACKENZIE MOUNTAINS, NORTHWEST TERRITORIES,
CANADA, AND NEW INSIGHTS INTO OLENELLINID EVOLUTIONARY
HISTORY AND BIOGEOGRPHY

by

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ABSTRACT

The olenellinid trilobites of the Early Cambrian are a diverse clade that has been an ideal group used in phylogenetic analyses. Recently, new specimens from the Sekwi Formation of the Mackenzie Mountains, Northwest Territories, Canada, were collected to add more material, to help paleontologists to better understand this group. This thesis presents three new species of *Bradyfallotaspis* and one new species of *Nevadia*. Further, new specimens of *Nevadia ovalis* expand the known geographic range for this species, only known previously from a locality in Senora, Mexico. This expansion is unusual for olenellinid trilobites, which generally have very restricted ranges. A phylogenetic analysis of *Judomia absita* was performed to help ameliorate confusion regarding its generic assignment between *Judomia* and *Paranevadella*, providing further support for a close biogeographic relationship between Laurentia and Siberia.

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DEDICATION

I would like to dedicate this thesis to the memory of Bill Fritz, of the Canadian Geological Survey, who passed away this past year. Much of the early trilobite collection and systematics from the Sekwi Formation was done by Bill in the early 1970s.

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THESIS INTRODUCTION

The Cambrian radiation represents a significant event in the history of life: the sudden appearance of nearly all major metazoan phyla in the fossil record. Despite its importance as being a major radiation involving metazoan cladogenesis, there has been debate regarding the uniqueness of the event that dates back to Darwin's *On the Origin of Species* (1859), where he mused on the problematic aspects of this event. In his chapter entitled "On the Imperfection of the Fossil Record," he writes a section "On their sudden appearance in the lowest known fossiliferous strata." Darwin hypothesized a slow and gradual evolution of metazoans before the Cambrian, citing trilobites as an example:

...it cannot be doubted that all the Cambrian and Silurian trilobites are descended from some one crustacean, which must have lived long before the Cambrian age, and which probably differed greatly from any known animal.

...if the theory be true, it is indisputable that before the lowest Cambrian stratum was deposited long periods elapsed, as long as, or probably far longer than, the whole interval from the Cambrian age to the present day; and that during these vast periods the world swarmed with living creatures.

This view was later argued against by Gould (1989), who contended that the sudden appearance of these organisms reflects real events in evolutionary history. This view is one that fits with the ideas of Simpson (1944) that evolutionary patterns are preserved in the paleontological record. He wrote:

That it is true of most, perhaps all, of the phyla well recorded as fossils is another indication that they may really have arisen not long before the time when they enter the record, rather than far back in the pre-Cambrian.

These opposing views of the Cambrian radiation have been designated as the Darwinian and Simpsonian views, respectively (Lieberman, 1999). Throughout the past 150 years

since *On the Origin of Species* was first published, other questions have emerged and been tested, regarding this great evolutionary event. These include studying rates of speciation during the Cambrian and examining paleobiogeographic patterns for specific taxa.

Just as trilobites have become the representative fossil for Paleozoic faunas, the olenellinid trilobites have come to be iconic of the Early Cambrian. This clade of trilobites was widely distributed and highly diverse. For these reasons (coupled with their complex morphology that make them ideal for phylogenetic analysis) the olenellinids have been useful to test questions regarding the Cambrian radiation.

The Olenellina was originally held to be the basal group of trilobites, because they lacked facial sutures, and possessed a nonfulcrate thorax and a narrow pygidium with few segments. This was, however, based on the traditional diagnosis of the group. Phylogenetic analysis by Lieberman (1998) hypothesized that the traditional “Olenellina” was paraphyletic. To create a monophyletic clade “Fallotaspidea” (including the oldest known trilobites) were removed from Olenellina and placed sister to Redlichiina.

Studies regarding the identification of the Olenellina suborder date back to the work of Walcott (1890). Since then, many others have been involved in the identification of olenellinid taxa collected from all over the world, including Hupé and Geyer (Morocco), Repina (Siberia), Kiaer and Ahlberg (Scandinavia), Samsonowicz and Orłowski (Poland), Fritz (Canada), and Nelson and Palmer (United States) just to name a few. Much of this early work was strictly taxonomic, with a large focus on biostratigraphy and a smaller focus on biogeography. From this, parts of the Early Cambrian have been subdivided into *Fallotaspis*, *Nevadella*, and *Olenellus* zones.

The timing of the Cambrian radiation and biogeographic patterns-

As the collective knowledge of the Olenellina grew, some began using these data to test questions regarding the Cambrian radiation. As stated earlier, timing of the radiation has been a topic that many have addressed and debated. The first to use Early Cambrian trilobites to address this topic were Fortey et al. (1996) who argued for a long evolutionary history of trilobites, prior to their appearance in the fossil record. Their argument stems from paleobiogeographic patterns of these trilobites that were divided into two distinct biogeographic provinces, one, the suborder Olenellina (encompassing Laurentia [presentday North America and Greenland], Siberia, and Baltica), the other the suborder Redlichiina (encompassing Gondwana). They argued this divergence was the result of a vicariant event associated with the breakup of Rodinia 750 Ma. Subsequent work by Lieberman (1997, 1999, 2001, 2002, 2003), and Meert and Lieberman (2004, 2008) incorporated phylogenetic data to study the biogeographic patterns in olenellinid trilobites. The patterns shown in these studies were well resolved vicariance trees of and poorly resolved geodispersal trees, indicating that vicariance was the major mode of speciation within this clade.

The vicariance trees presented by Lieberman revealed three major biogeographic groupings: 1) Siberia, marginal western Gondwana, and present-day southwestern North America; 2) Baltica and what was formerly the eastern margin of Laurentia; and 3) parts of East Gondwana. The pattern of splitting fits well with the pattern of fragmentation of the supercontinent Pannotia that began 550-600 Ma, well before the start of the Cambrian at 543 Ma. When combined with paleomagnetic data, Meert and Lieberman (2008) placed the origins of trilobites in Siberia at about 570 Ma.

Thesis Results-

This thesis addresses newly collected material of olenelline trilobites from the Early Cambrian Sekwi Formation of the Makenzie Mountains, Northwest Territories, Canada and aims to place them into a detailed phylogenetic and biogeographic context. These faunas had previously been studied by Fritz (1972, 1973, 1991) but the new material could not be considered in Lieberman's earlier analyses so this work extends the breadth and scope of our knowledge of evolutionary patterns during this key time period in the history of life. Specimens collected during two field seasons by colleagues at The University of Kansas and Washington State University were examined; trilobites from the *Nevadella* zone were the principal focus because these are quite diverse and well preserved. Three new species of *Bradyfallotaspis* and one of *Nevadia* are described here and material of pre-existing species are also figured and discussed. For instance, new data is presented that expands the range of *Nevadia ovalis*, which until now had only been thought to be present in Sonora, Mexico. Most olenellines are geographically highly restricted so this is somewhat unusual. Further, a higher-level phylogeny for the Olenellina was reconstructed, incorporating new material of *Judomia absita*. (Earlier authors had suggested that this material was referable to *Paranevadella* rather than *Judomia* but the phylogeny made it possible to test that contention.) *Judomia* was thought to be restricted to Siberia, so this result provides further support for a close biogeographic relationship between Siberia and Laurentia.

INTRODUCTION

The *Olenellina* Walcott, 1890, is a diverse and widely geographically distributed suborder of trilobites from the Early Cambrian. Lieberman re-diagnosed the group as to make it monophyletic by removal of the superfamily “fallotaspidoidea,” (1998) and a higher-level phylogeny was conducted to assess the relative position of taxa within the suborder, recognizing four new genera (2003). Previous studies of the group have focused on phylogenetic patterns as a means of testing detailed paleobiogeographic distributions and speciation rates during the Cambrian radiation (Lieberman, 1998, 2001, 2003).

During the summer of 2003, paleontologists from the University of Kansas and Washington State University collected trilobites from the Sekwi Formation in the Mackenzie Mountains, Northwest Territories, Canada. The Sekwi Formation is between 715 and 770m thick in the Mackenzie Mountains of northwestern Canada, and dates from the late early Cambrian (Fritz, 1972; Randell et al., 2005; Dillard et al. 2007). The unit of interbedded carbonate, shale, and sandstone, consists mainly of weathering dolostone and limestone (Handfield, 1968) deposited through the *Fallotaspis*, *Nevadella*, and *Bonia-Olenellus* zones (Dillard et al. 2007). Specimens from this site revealed new olenellinid species and provided new material for further revisions of the *Olenellina*.

Specimens found include *Judomia absita*, originally assigned to the genus *Judomia*, Lermontova, 1951, by Fritz (1973), citing a close resemblance to *J. tera*, a Siberian platform trilobite. It was later moved to *Paranevadella* Palmer and Repina, 1993, based on a glabella that is weakly tapered forward to nearly parallel-sided, a present preglabellar field, ocular lobes that extend opposite L0, and a distinctly developed

interocular area. This study included a phylogenetic parsimony analysis to resolve the positioning of this taxon.

Among the new taxa collected from the Sekwi Formation, four are described here. They include three new species of *Bradyfallotaspis* Fritz, 1972, and one new species of *Nevadia* Walcott, 1910. Also figured are two new specimens of *Nevadia ovalis*, McMenamin, 1987, which had previously only been from Mexico.

PHYLOGENETIC ANALYSIS

Taxa analyzed.—A total of 20 taxa within the Olenellina were subjected to phylogenetic analysis. This included 18 ingroup taxa. *Judomia absita* was incorporated into Lieberman's (2001) higher-level phylogeny of the Olenellina. *Daguinaspis ambroggii*, *Parafallotaspis grata*, *Pseudojudomia egregia*, *Nevadia weeksi*, and *Nevadella perfecta* were removed from the analysis because they were basal and not necessary for determining the position of *J. absita*.

The two outgroups chosen are *Nevadella mountjoyi* and *N. perfecta* since they were shown by Lieberman (2001) to be basal to the 18 ingroup taxa.

Characters and character states—Phylogenetic patterns were determined by parsimony analysis of the following 57 holaspid exoskeletal characters taken from Lieberman's higher-level phylogeny of the Olenellina (2001). 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.

1) Anterior border near but not directly anterior of frontal lobe (LA) (0) moderately long, length (exsag.) equal to length (sag.) of L0 (1) very short, length (exsag.) less than or equal to one-half 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) prominently separated from extraocular area by furrow (1) not prominently separated from extraocular area by furrow

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

5) Frontal lobe (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 40 degree angle relative to transverse line (1) roughly 10–20 degree angle

relative to transverse line.

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

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 posterior part of frontal lobe (1) at anterior and posterior parts of frontal lobe.

12) Outer band of ocular lobe near lateral margin of L4 (0) does not expand prominently exsagittally (1) expands 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) narrow (tr.), nearly in contact (1) broad (tr.), 25–33 percent width of glabella at L1.

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

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

margin of L1 (2) medial part of distal margin of L0

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

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

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

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

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

- 28) S1 (0) conjoined medially (1) not conjoined medially.
- 29) Distal sector of S0 (0) convex anteriorly (1) straight to concave 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) with node present (1) smooth (2) with spine present.
- 33) Glabellar furrows (0) some moderately to strongly incised (1) all weakly incised.
- 34) Medial of eye, intergenal ridge (0) not visible (1) prominently developed.
- 35) Extraocular region opposite L1 (0) broad, width (tr.) greater than or equal to 65–75 percent of the width of the glabella at L1 (1) narrow, width (tr.) 35–50 percent of the width of the glabella at L1.
- 36) Length (exsag.) of genal spine (0) equal to length (sag.) of first three to five thoracic segments (1) genal spine not well developed or absent (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) first thoracic segment (1) distal margin of L0 (2) distal margin of L1 (3) distal margin of L2.
- 38) Intergenal angle developed (0) posterior of point half way between ocular lobes and genal spine (1) adjacent to or directly behind genal spine (2) posterior of lateral margins

of ocular lobes (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) deflected at roughly -10 to 10 degree angle (1) directed anteriorly at roughly 30 degree angle (2) directed anteriorly at roughly $60-70$ 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) directed anteriorly (1) parallel to a transverse line or very weakly directed posteriorly.

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

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) developed as broad sweeping projections extending back six to eight thoracic segments (1) developed as short projections extending two to four thoracic segments back (2) do not sweep significantly back.

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

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

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

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

53) Length (exsag.) of thoracic pleural furrows at medial part of thoracic segment relative to length at distal part of segment (0) equal to one to 1.3 times length of pleural furrows on distal part of segment (1) equal to twice 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) very short (sag.), equal to half the length of the posterior band (1) long, greater than or equal to 1.5 times the length of the posterior band (2) short, equal to the length of the posterior band.

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

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

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

Parsimony Analysis—These data were 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 198 steps. The retention index of the most parsimonious trees is 0.54, and the consistency index (when uninformative characters are excluded) is 0.40.

To assess overall phylogenetic signal within the database, 1,000 random trees were generated from the character data 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 –0.47. 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, of the grouping of *J. absita*, tPTP tests (Faith, 1991) were performed using PAUP. The *P*-value

calculated by the test is normally compared to a 0.05 significance level, however since these tests are being done *a posteriori*, a Bonferonni correction was applied, dividing the significance level by 16 ingroup taxa. Two tPTP tests were implemented. In the first, all nodes were collapsed except for *P. subgroenlandicus* and *J. absita*. A *P*-value of 0.260 was calculated. The second test was run with all nodes collapsed and *J. absita* grouped with *J. tera*, resulting in a *P*-value of 0.026. The results of these two tests were not statistically significant with the Bonferonni correction, however they do show a higher level of significance when *J. absita* is grouped with *J. tera*.

Support for each node was determined using a bootstrap analysis using TNT (Goloboff et al., 2008). 10,000 replications were employed using a standard (sample with replacement) analysis. A jackknife analysis was also performed using TNT (Goloboff et al., 2008) of 10,000 replicates was performed with 36% removal probability.

A Bremer branch support analysis (Bremer, 1994) was also conducted to examine the support of the different individual nodes of the cladogram. 30 trees of length less than or equal to 199 steps, and 246 trees of length less than or equal to 200 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. The total support index (Bremer, 1994) for the tree is at least 0.01.

SYSTEMATIC PALEONTOLOGY

BRADYFALLOTASPIS CORIAE new species

Figure 3

Diagnosis—Anterior cephalic border (sag.) equal to length (sag.) L0, preglabellar area present, ocular ridges connect to glabella at L3, ocular lobes in contact with posterior boarder, extraocular region very broad, genal spines length (exsag.) greater than length (sag.) of cephalon, occipital spine present in some specimens.

Description—Cephalic length (sag.) 45-50 percent of width (tr.). Anterior cephalic border wide, raised ridge, length (exsag.) between lateral margins of LA(L4) and genal spine angle 65-100% length (sag.) of L0. Frontal lobe about 40 percent length (sag.) of glabella; frontal lobe does not contact anterior border furrow; plectrum is not visible; anterior margin of frontal lobe at each side of midline deflected posteriorly at roughly 40 degree angle relative to transverse line; lateral margins of LA directly anterior lateral margins of L0; lateral margins of LA convergent anteriorly; ocular lobes connected to frontal lobe via ocular ridges at posterior part of frontal lobe; ocular lobes maintain constant dorso-ventral elevation between axial furrow and mid-point of ocular lobes; S3 not conjoined medially; S2 not conjoined medially; L2 and L3 do not merge distally; line from anterior to posterior edge of ocular lobe forms roughly sub-parallel to sagital line; S1 not conjoined medially, S0 conjoined medially; width (tr.) of glabella opposite margins of L1 subparallel relative to width at lateral margins of L0; posterior edge of ocular lobe opposite medial margin of L0, contacting the posterior border furrow; ocular lobes elevated from extraocular area; posterior margin of L0 subparallel; genal spines of length (exsag.) approximately 6-10 times the length (sag.) of L0, sweeping posterolaterally at roughly 10 degree angle relative to the

sagittal line; genal spine angle opposite L0; extraocular area opposite L1 broad, width (tr.) approximately equal width of glabella at L1; posterior margin of cephalic posterior border between L0 and genal angle flexing posterolaterally.

Etymology—Named in honor of Corrine Myers for her continued support regarding lab techniques and discussions.

Occurrence—*Nevadella* zone, Sekwi Formation, Mackenzie Mountains, Northwest Territories, Canada (sections 2 and 14).

BRADYFALLOTASPIS NICOLASCAGEI new species

Figure 4

Diagnosis—Anterior cephalic border (sag.) equal to approximately half the length (sag.) L0, preglabellar area equal to combined length (sag.) L3 and L4, ocular ridges connect to glabella at L3, ocular lobes not in contact with posterior boarder, extraocular region very broad, genal spines length (exsag.) greater than or equal to length (sag.) of cephalon.

Description—Cephalic length (sag.) 45-50 percent of width (tr.). Anterior cephalic border narrow, raised ridge, length (exsag.) between lateral margins of LA(L4) and genal spine angle 65-100% length (sag.) of L0. Frontal lobe about 30 percent length (sag.) of glabella; frontal lobe does not contact anterior border furrow; plectrum is not visible; anterior margin of frontal lobe at each side of midline deflected posteriorly at roughly 40 degree angle relative to transverse line; lateral margins of LA directly anterior lateral margins of L0; lateral margins of LA

convergent anteriorly; ocular lobes connected to frontal lobe via ocular ridges at posterior part of frontal lobe; ocular lobes maintain constant dorso-ventral elevation between axial furrow and mid-point of ocular lobes; S3 not conjoined medially; S2 not conjoined medially; L2 and L3 do not merge distally; line from anterior to posterior edge of ocular lobe forms roughly sub-parallel to sagittal line; S1 not conjoined medially, S0 conjoined medially; width (tr.) of glabella opposite margins of L1 subparallel relative to width at lateral margins of L0; posterior edge of ocular lobe opposite medial margin of L0, contacting the posterior border furrow; ocular lobes elevated from extraocular area; posterior margin of L0 subparallel; genal spines of length (exsag.) approximately 6-10 times the length (sag.) of L0, sweeping posterolaterally at roughly 5 degree angle relative to the sagittal line; genal spine angle opposite L0; extraocular area opposite L1 broad, width (tr.) approximately equal width of glabella at L1; posterior margin of cephalic posterior border between L0 and genal angle flexing posterolaterally.

Etymology—Named in honor of trilobite enthusiast and Hollywood actor, Nicolas Cage.

Occurrence—*Nevadella* zone, Sekwi Formation, Mackenzie Mountains, Northwest Territories, Canada (sections 1, 2, and 14).

BRADYFALLOTASPIS SEKWIENSIS new species

Figure 5

Diagnosis—Anterior cephalic border (sag.) equal to twice the length (sag.) L0, preglabellar area absent, ocular ridges connect to glabella at L3, ocular lobes not

in contact with posterior boarder, extraocular region very broad, genal spines length (exsag.) greater than length (sag.) of cephalon.

Description—Cephalic length (sag.) 45-50 percent of width (tr.). Anterior cephalic border wide, raised ridge, length (exsag.) between lateral margins of LA(L4) and genal spine angle 65-100% length (sag.) of L0. Frontal lobe about 40 percent length (sag.) of glabella; frontal lobe in contact with anterior border furrow; plectrum is not visible; anterior margin of frontal lobe at each side of midline deflected posteriorly at roughly 40 degree angle relative to transverse line; lateral margins of LA directly anterior lateral margins of L0; lateral margins of LA convergent anteriorly; ocular lobes connected to frontal lobe via ocular ridges at posterior part of frontal lobe; ocular lobes maintain constant dorso-ventral elevation between axial furrow and mid-point of ocular lobes; S3 not conjoined medially; S2 not conjoined medially; L2 and L3 do not merge distally; line from anterior to posterior edge of ocular lobe forms roughly sub-parallel to sagittal line; S1 not conjoined medially, S0 conjoined medially; width (tr.) of glabella opposite margins of L1 subparallel relative to width at lateral margins of L0; posterior edge of ocular lobe opposite medial margin of L0, contacting the posterior border furrow; ocular lobes elevated from extraocular area; posterior margin of L0 subparallel; genal spines of length (exsag.) approximately 6-10 times the length (sag.) of L0, sweeping posterolaterally at roughly 10 degree angle relative to the sagittal line; genal spine angle opposite L0; extraocular area opposite L1 broad, width (tr.) approximately equal width of glabella at L1; posterior margin of cephalic posterior border between L0 and genal angle flexing posterolaterally.

Etymology—Named after the Sekwi Formation, where the trilobites in this study were collected.

Occurrence—*Nevadella* zone, Sekwi Formation, Mackenzie Mountains, Northwest Territories, Canada (sections 1 and 2).

NEVADIA SAUPEAE new species

Figure 6

Diagnosis.—Anterior cephalic border prominently separated from extraocular area, long (exsag.), length about length (sag.) of L0; plectrum is absent; LA (L4) about 2.5 times the length (sag.) of L0; ocular lobes gradually increase dorsoventral elevation between axial furrows and mid-point of ocular lobes; posterior tips of ocular lobes developed opposite medial part of distal margin of L1; extraocular region very broad, width (tr.) opposite L1 more than 200% width of glabella at L1; genal spine angle developed opposite medial part of first thoracic segment; medial part of cephalic posterior border between intergenal angle and L0 flexes posteriorly.

Description.—Cephalic length (sag.) 40-50 percent of width (tr.). Anterior cephalic border wide, flattened ledge, length (exsag.) between lateral margins of LA(L4) and genal spine angle equal to length (sag.) of L0. Frontal lobe about 35-45 percent length (sag.) of glabella; frontal lobe does not contact anterior border furrow; plectrum is not visible; anterior margin of frontal lobe at each side of midline deflected posteriorly at roughly 40 degree angle relative to transverse

line; lateral margins of LA proximal to lateral margins of L0; lateral margins of LA convergent anteriorly; ocular lobes contact frontal lobe at posterior part of frontal lobe; ocular lobes gradually increase dorso-ventral elevation between axial furrow and mid-point of ocular lobes; anterodistal margins of L3 formed by axial furrows, distal margins of L3 straight; S3 straight, not conjoined medially; S2 straight, conjoined medially; L2 and L3 do not merge distally in internal mold but do in external mold; line from anterior to posterior edge of ocular lobe forms roughly 10 degree angle relative to sagittal line; S0, S1 straight, 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 medial margin of L1; ocular lobes elevated from extraocular area; posterior margin of L0 convex posteriorly; genal spines of length (exsag.) approximately 1-1.5 times the length (sag.) of L0, sweeping posterolaterally at roughly 40 degree angle relative to the sagittal line; genal spine angle opposite first thoracic segment; intergenal angle developed adjacent to genal spine; extraocular area opposite L1 broad, width (tr.) approximately 200 percent width of glabella at L1; posterior margin of cephalic posterior border between L0 and genal spine flexing posterolaterally.

Etymology—Named in honor of Erin Saupe for her continued support regarding lab techniques and discussions.

Occurrences— *Nevadella* zone, Sekwi Formation, Mackenzie Mountains, Northwest Territories, Canada (sections 2 and 14).

NEVADIA OVALIS McMEnamin, 1987

Figure 7

Discussion—Anterior and posterior cephalic borders much wider and extraocular area much narrower than other species of *Nevadia*. Ovate shape of cephalon is typical of this species. New specimens from the Sekwi Formation are diagnosably indistinguishable from specimens identified by McMEnamin (1987).

Occurrence—*Nevadella* zone, Sekwi Formation, Mackenzie Mountains, Northwest Territories, Canada (sections 1 and 2) and base of the middle shaly interval of unit 3 of the Puerto Blanco Formation, Cerro Rajón area, Mexico.

JUDOMIA ABSITA Fritz, 1973

Figure 8

Discussion—For diagnosable characters, see Table 1.

Occurrence—*Nevadella* zone, Sekwi Formation, Mackenzie Mountains, Northwest Territories, Canada (sections 1, 2, 3, and 14).

DISCUSSION

Biogeographic patterns of Laurentia and Siberia—

Based on the higher-level phylogeny generated in this study, we see that the Laurentian *J. absita* is sister to *J. tera* of the Siberian platform. This provides further

support for the notion that there is a close biogeographic relationship between these two continents, and further that they were likely in close association at the end of the Proterozoic and into the early Cambrian. In particular, this issue has been considered by several authors.

Some of the early support for a close relationship between Laurentia and Siberia during this time period came from McKerrow et al. (1992). They reconstructed these two continents in close association during the Early Cambrian based on sedimentary facies, faunal distributions (including archeocyathans, olenellid and redlichiid trilobites, and small shelly fossils), as well as paleomagnetic data. Baltica was also nearby each of these, whereas by contrast the parts of Gondwana seemed to be fundamentally distinct from these on paleontologic, sedimentologic, and paleomagnetic grounds. McKerrow et al. (1992) argued that rifting between Siberia, Laurentia, and Baltica had initiated before the start of the Cambrian; however, Pelechaty (1996) argued that some rifting between Siberia and Laurentia may have continued after the start of the Cambrian.

Animals, especially trilobites, suggested that diversification had begun back in the Precambrian and before the start of the fracturing of Precambrian supercontinents (Fortey et al., 1996). Phylogentic analysis of the diverse Olenellina (Lieberman, 1998) and other groups has allowed for more detailed testing of this proposition. In particular, biogeographic patterns of the Early Cambrian (Lieberman, 1997, 1999, 2001, 2002, 2003; Meert and Lieberman, 2004, 2008) were analyzed using modified Brooks Parsimony Analysis as described by Lieberman and Eldredge (1996) and Maguire and Stigall (2008). These analyses suggested that the earlier defined “olenellid” biogeographic

province was paraphyletic, and further there was a relatively close biogeographic relationship between Siberia and parts of Laurentia (Fig. 9).

Species ranges of olenellid trilobites—

For many of the olenellids, the species ranges tend to be very limited, often endemic to specific areas or even existing as point occurrences. Very rarely do we see a case of species with biogeographic ranges that expand across more than a single tectonic basin. One of the rare cases can be found in *Elliptocephala logani*, which has the largest geographic range at least within the olenelloid clade and straddles both the western and eastern parts of North America (Lieberman, 1999). One of the surprising and interesting results of my study is that another one of these rare instances of geographically far-flung olenelline species was recovered. In particular, new material I examined from the Sekwi Formation expands the range of *Nevadia ovalis*, which was previously thought to occur at only a single point location from the Puerto Blanco Formation in Sonora, Mexico (McMenamin, 1987). Although neither the material McMenamin nor I studied was well preserved, they are diagnosably indistinguishable from each other, and are therefore best treated as comprising a single species.

CONCLUSION

This study provides interesting implications in regards to trilobite paleobiogeography. The placement of *J. absita* with *J. tera* in my phylogeny provides further support for the idea that there is a close biogeographic (and probably tectonic)

relationship between Laurentia and Siberia. In the case of *N. ovalis*, an expanded geographic range represents an unusual example for the Olenellina.

The Sekwi Formation continues to yield new and interesting trilobites from the Early Cambrian. My future work will involve a focus on describing a large number of new species of olenelloids, and placing these within a phylogenetic context. This will also include studies of some clades of Ordovician-Silurian trilobites. The latter will be used as a point of comparison in order to focus on some of the differences between patterns and processes of evolution during the Cambrian and post-Cambrian intervals. The latter will particularly emphasize how biogeographic patterns and the tempo of evolution may have differed during these two time periods, one associated with the dramatic Cambrian radiation, one associated with the more protracted Ordovician radiation and the catastrophic end Ordovician mass extinction.

THESIS CONCLUSION

The results of this thesis provide new insight into the evolutionary history and biogeography of the Early Cambrian olenelline trilobites. Results involve the description of new taxa, a phylogenetic analysis, and information about biogeographic patterns based on the phylogeny. In particular, descriptions of three new species of *Bradyfallotaspis* are provided which add to the knowledge of the Sekwi Formation trilobite fauna, established by Fritz (1972, 1973, 1991). New data from *Nevadia ovalis* creates an expanded geographic range for this species and also provides new information useful for future phylogenetic studies.

A higher-level phylogenetic analysis that incorporated *Judomia absita* supports Fritz's (1973) hypothesis of placement of that taxon in *Judomia*, contrary to the predictions of Palmer and Repina (1993). In addition, the phylogenetic analysis, in conjunction with patterns of geographic distribution, supports the findings of Meert and Lieberman (2004, 2008) that there was a close biogeographic relationship between Siberia and Laurentia during the Early Cambrian.

My future research will partly continue to focus on Early Cambrian trilobites. As this thesis concentrated on Olenellina taxa outside the Olenelloidea, future research will shift toward the Olenelloidea. Specifically, I plan to pay particular attention to macroevolutionary patterns within the diverse superfamily Olenelloidea Walcott, 1890, concentrating on material collected from the Sekwi Formation, McKenzie Mountains, Northwest Territories, Canada. This will include identifying new and existing species, and inserting the new taxa into a phylogenetic framework. Preliminary analysis of the specimens shows new species of *Olenellus*, *Eliptocephalus*, *Bolbolenellus*, and *Bristolia*.

The second aspect of my future olenelloid research includes the study of trilobites from the Holy Cross Mountains of Poland. These trilobites have been well studied for many years by Czarnocki (1927), Samcinowicz (1959), and Orłowski (1974, 1985); however, due to the inaccessibility of this material and poor illustration quality of communist-era Polish journals, many of these taxa could not be included in Lieberman's (1999) revision of the Olenelloidea. I recently traveled to Warsaw, Poland to closely study and photograph the specimens of the genera *Holmia*, *Kjerulfia*, and *Scmidtellus*. It is already apparent from these observations that *H. marginata* Orłowski (1974) is a distinct species, contrary to Ahlberg et al. (1986), who argued that it belongs with the Scandinavian species, *H. kjerulfi* Linnarsson (1871).

Once *H. marginata*, *K. orcina*, and *S. panowi* are inserted into a phylogenetic framework, I hope to better understand the Early Cambrian biogeographic patterns of the Scandinavian and Baltic regions. This will be done using a modified Brooks Parsimony Analysis, as described by Lieberman and Eldredge (1996).

By incorporating Canadian and Polish taxa into Lieberman's (1999) phylogenetic analysis of the Olenelloidea, I intend to use these data to better understand speciation rates during the Cambrian radiation, to build on previous analyses conducted by Lieberman (2001, 2003). Speciation rates are viewed in a stochastic framework, testing the null hypothesis that rates of speciation during the Cambrian radiation were not significantly higher than any other period in the history of life. Analyses will use three different models: two-continuous time models (the Yule model and the birth and death model) and a discrete-time model (the Bienaymè—Galton—Watson branching process model). Results from Lieberman's study showed high speciation rates for Early

Cambrian trilobites, but these were not statistically distinguishable from the rates prevailing at other times. Thus, Lieberman concluded that evolutionary processes may have not been unique during the Cambrian radiation. The additional rate information that I collect will allow this issue to be considered in greater detail.

It is also useful to compare macroevolutionary patterns of trilobites during the Early Cambrian with those from other time periods, and this will be another focus of my Ph.D. research. In particular, I propose to investigate phylogenetic patterns in Ordovician-Silurian trilobites, concentrating on the diverse cheirurid trilobites. My future work will include revising phylogenies for cheirurid trilobites associated with the Ordovician mass extinction and hypothesizing biogeographic patterns for this time period and comparing speciation rates to those of the Early Cambrian.

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TABLES

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).

Nevadella_perfecta	000000000000000000X0X00000000X000X0000000000X0000000000000000?
Nevadella_mountjoyi	0001100000000000X0X000000000000X000000100000000000000111000?
Cirquella_espinata	110001201010000X000000000000000000100101010??????????????????
Cirquella_nummularia	110001211010000100000000000000000100121021??????????????????
Cirquella_nelsoni	11000??01010000X00??0001?00?0001011020??????????????????????
Bradyfallotaspis_fusa	011?0000020000121100010001201000001?00000????????????????????
Paranevadella_subgroenlandicus	1100000010100012111??11001?0?01?000?10030????????????????????
Cambroinyoella_wallacei	0100001?101111120112000000101?00000?02010?0100011111010??
Geraldinella_corneiliana	00010010101010010111000000101000000?00000?????????????????0
Cambropallas_telesto	211110110011100121110100001001000012100000000012001111010
Andalusiana_cornuta	01101001001111XZ0112011010110010011202000??00020011X21??
Gabriellus_sp	110110101010100Z11020010101101010010301221001120002112001
Olenelloidea	100111000W00100W011210XX1X11X10000000X100101X101002X0100W
Callavia_broeggeri	01011010101010022111101010100?02011011100?0110010011101?0
Callavalonia_callavei	20011010201010022111101010110102011?11100?????1?0100?00
Sdzuyomia_lotzei	010000?0121010002001?010?0?1?1?1?11131?000?011002?100?011?
Judomia_tera	00111000121010121102111010212111100?130000011011110011?11
Bondonella_typica	01011001021010101113?10010Y10X101010020011011011000011101
Neltneria_jacqueti	001110011210101111121101111101111010010011011012000011001
Judomia_absita	010X000012010020X111111010200001000?13001??????????????????

FIGURES

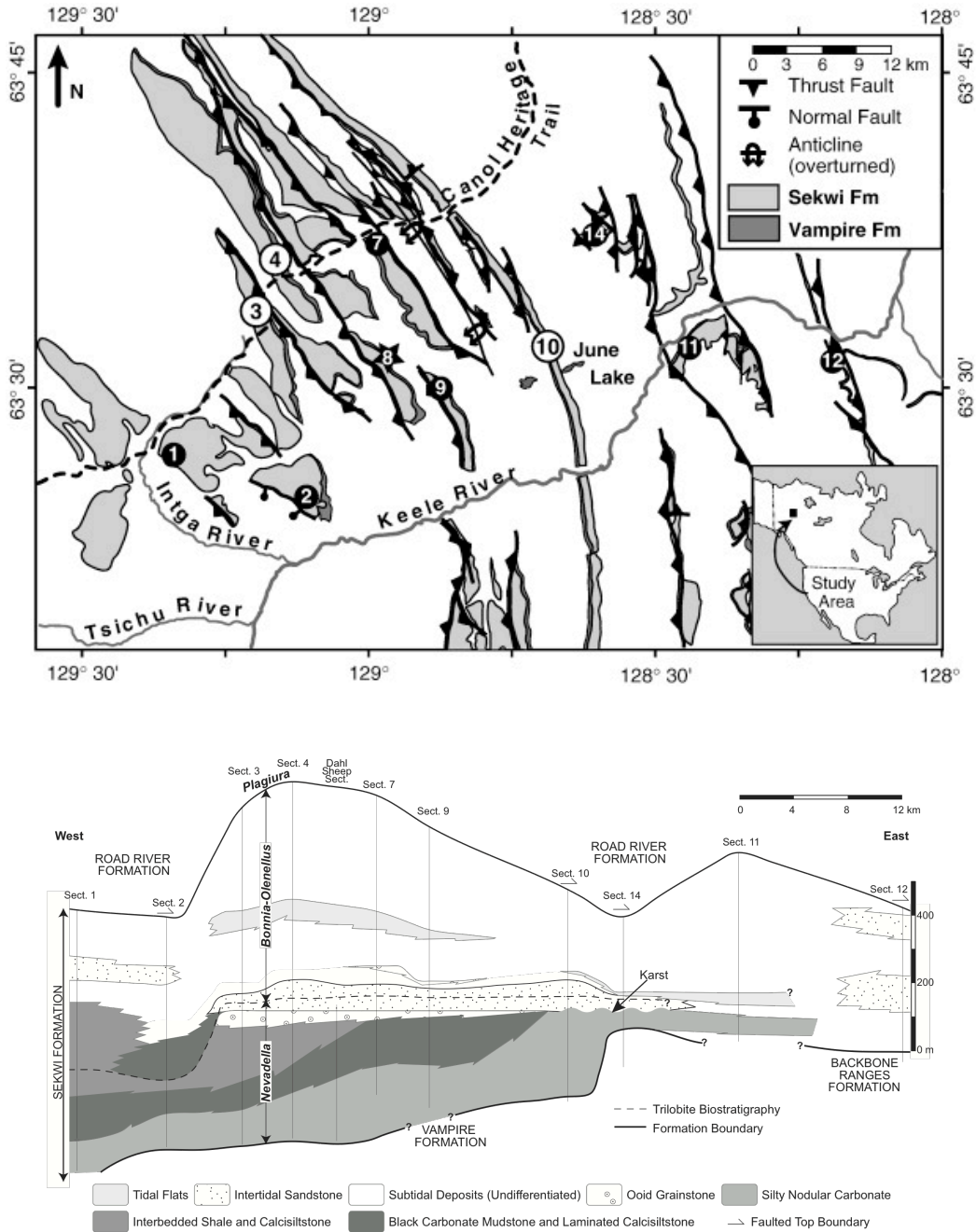


FIGURE 1—(a) Map of the Sekwi Formation, taken from Dilliard et al. 2007. (b) Schematic cross-section of the Sekwi Formation, taken from Dilliard et al. 2009. Specimens in this study came from the *Nevadella* zone of localities 1, 2, 3, and 14 ($63^{\circ} 26' 22.2''N$, $129^{\circ} 22' 20.4''W$; $63^{\circ} 24' 27.4''N$, $129^{\circ} 7' 31.8''W$; $63^{\circ} 33' 3.8''N$, $129^{\circ} 11' 51.2''W$; $63^{\circ} 37' 3.6''N$, $128^{\circ} 37' 32.2''W$ respectively).

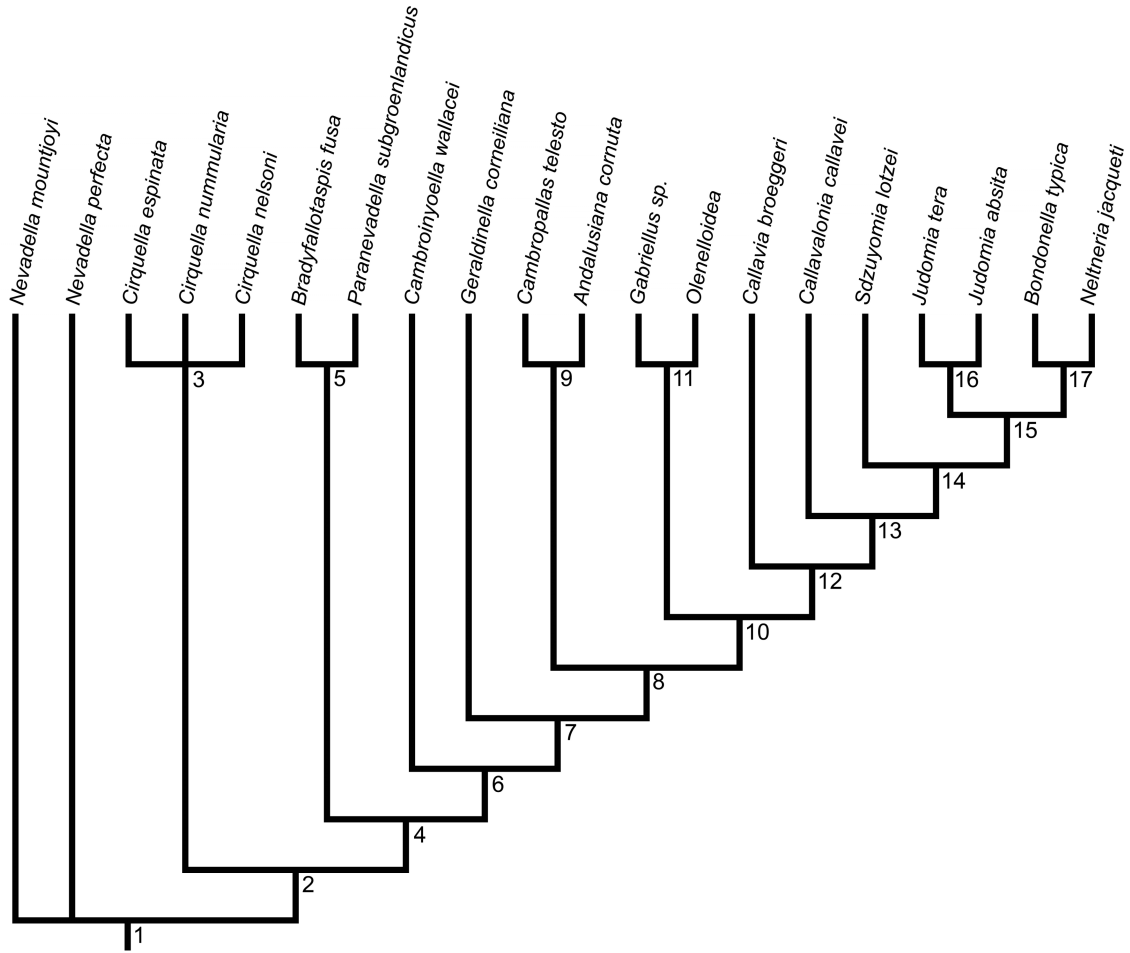


FIGURE 2—The strict consensus of three most parsimonious trees of length 198 steps produced from analysis of character data in Table 1 with PAUP 4.0 (Swofford, 1998). Cladogram constructed using a heuristic search with a stepwise addition sequence and 100 random replications. All characters were treated as unordered. 0.54, and the consistency index (when uninformative characters are excluded) is 0.40. The following nodes of the tree were supported by the following jackknife confidence values (see text for jackknife procedure utilized): Node 1 = 100; Node 2 = 32; Node 3 = 81; Node 4 = 4; Node 5 = 3; Node 9 = 19; Node 11 = 28; Node 17 = 32. The following nodes of the tree were supported by the following bootstrap confidence values (see text for bootstrap procedure utilized): Node 1 = 100; Node 2 = 32; Node 3 = 77; Node 4 = 4; Node 5 = 6; Node 9 = 12; Node 11 = 23; Node 17 = 27. The following branch support values (Bremer, 1994) were recovered for the following nodes: Node 1 = 1; Node 2 = 1; Node 3 = 2; Node 4 = 1; Node 5 = 1; Node 8 = 1; Node 9 = 2; Node 10 = 1; Node 12 = 1; Node 14 = 1; Node 15 = 1; Node 17 = 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. Node 1, 18[0,1], 51(1), 52(1), 53[0,1]; Node 2, 2(1), 9(1), 11(1), 44[0,1], 48[0,1], 54[0,1]; Node 3, 1(1), 6(1), 7(2), 18(0), 33(1), 36(1), 38(1), 40[0,1,2]; Node 4, 15[0,1], 16(2), 18(1), 19[0,1], 27[0,1,2], 29(1); Node 5, 15(1), 17(1), 22(1), 26(1); Node 6, 7(1), 13(1), 20[0,1,2], 27(1), 48(1), 54(1); Node 7, 4(1), 15(0), 20[1,2]; Node 8, 5(1), 23[0,1], 25[0,1], 28[0,1], 29(0), 30[0,1], 35(1), 53(1); Node 9, 3(1), 8(1), 9(0), 12(1), 22(1), 36(2), 48(2), 56[0,1]; Node 10, 21[0,1], 23(1), 25(1), 30[0,1], 39(1), 42[0,1], 45(1); Node 11, 1(1), 20(2), 28(1), 42(1), 46(1), 51(2), 57[0,1]; Node 12, 17(2), 20(1), 21(1), 32(2), 34(1), 37(1), 38(1), 44(1), 54(0), 55(1); Node 13, 28(1), 50[0,1], 51(0); Node 14, 7[0,1], 10(2), 16(1), 31[0,1], 32[0,1], 33(1), 39(0), 52(0), 56[0,1], 57[0,1]; Node 15, 7(0), 15(1), 17(2), 20[0,1], 22(1), 32(1), 34(0), 41[0,1], 47(1), 54(1), 57(1); Node 16, 27(2), 35(0), 38(3); Node 17, 8(1), 20[1,2,3], 23(0), 31(0), 37(0), 41(1), 42(1), 50(0), 56(0).



FIGURE 3—*Bradyfallotaspis coriae*. (1 = 3.9X; 2 = 2.6X)



FIGURE 4—*Bradyfallotaspis nicolascagei*. (1 = 3.2X; 2 = 2.8X)



FIGURE 5—*Bradyfallotaspis sekwiensis*. (1 = 2.6X; 2 = 5.4X)



FIGURE 6—*Nevadia saupeae*. (1 = 1.5X; 2 = 1.6X)

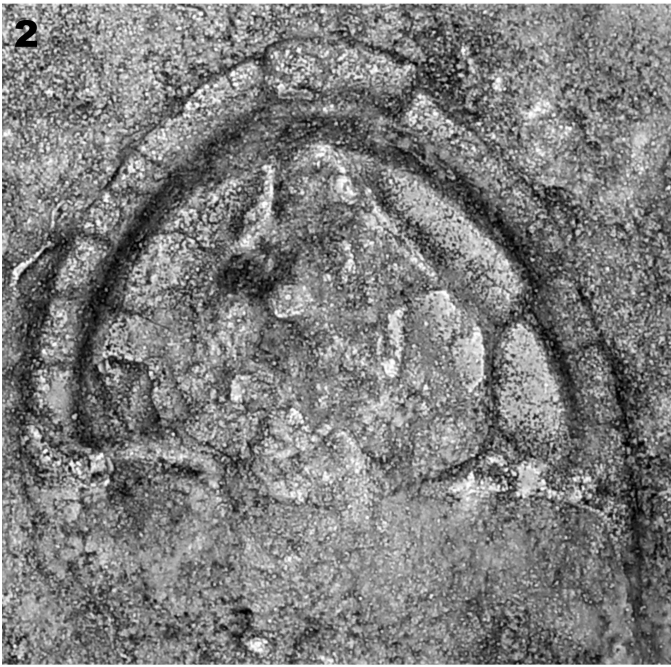
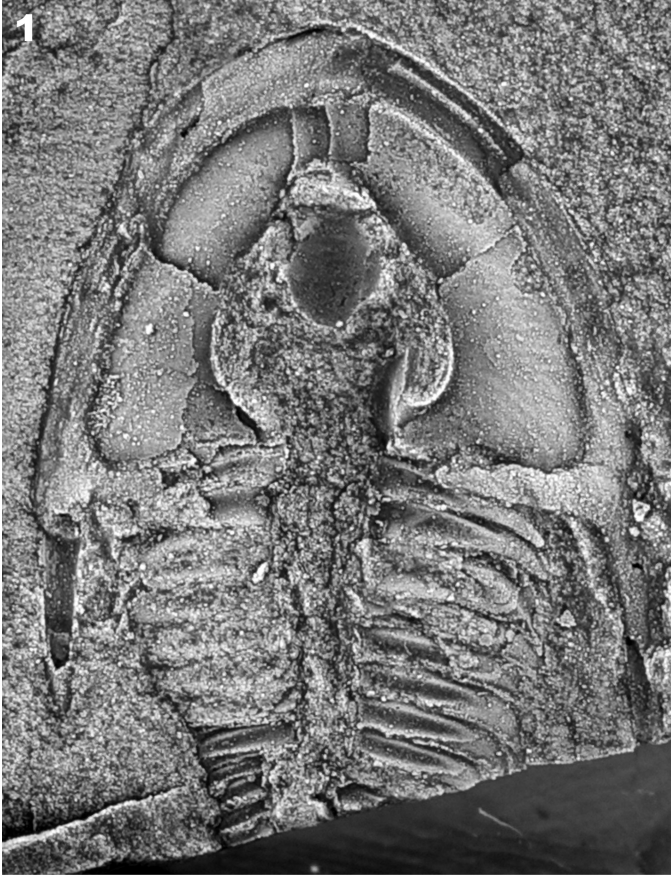


FIGURE 7—*Nevadia ovalis*. (1 = 8.4X; 2 = 7.7X)

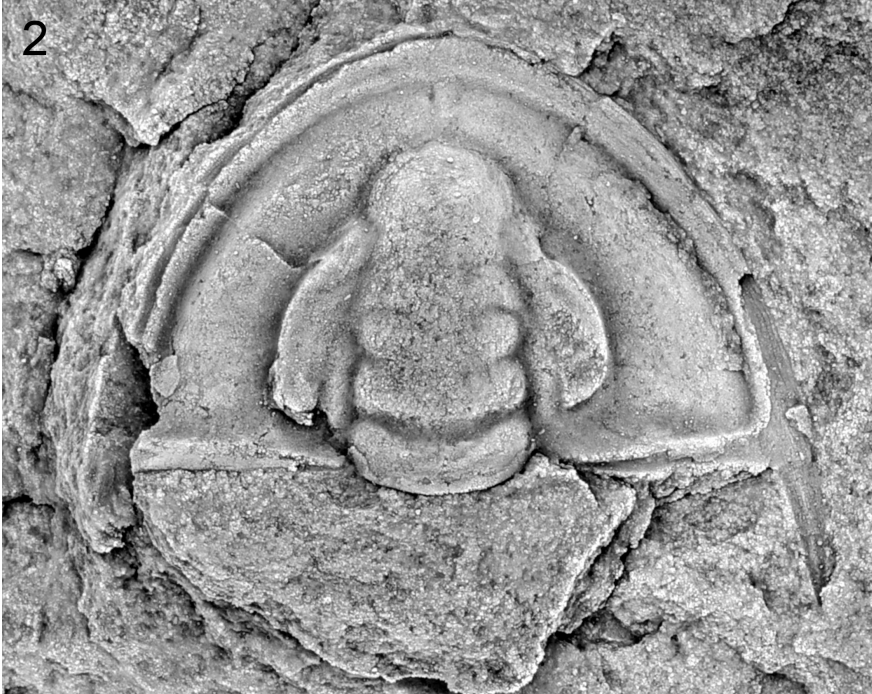


FIGURE 8—*Judomia absita*. (1 = 5.0X; 2 = 6.0X)

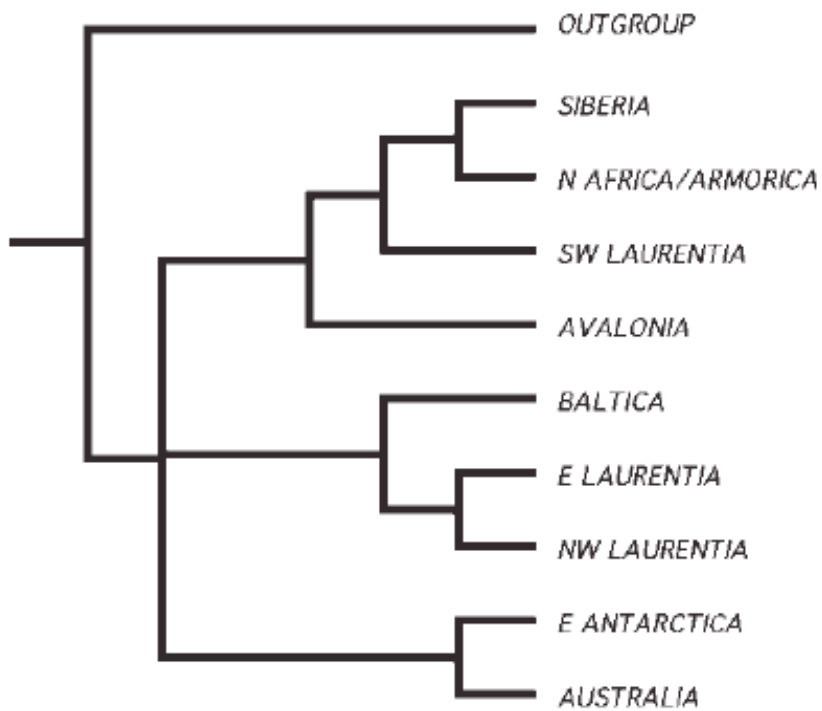


FIGURE 9 – Strict consensus of vicariance area cladograms for olenellid trilobites [taken from Meert and Lieberman (2004)]. The geodispersal cladogram is poorly resolved, indicating a lack of congruence. Therefore, it appears that vicariance was the major mode of speciation at this time.