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by Bruce S. Lieberman

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New olenelline trilobites from the Northwest Territories, Canada, and the phylogenetic placement of *Judomia absita*

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Abstract

The Early Cambrian olenelline trilobites are a diverse clade that have been the subject of several phylogenetic analyses. Here, three new species of *Bradyfallotaspis* Fritz, 1972 (*B. coriae, B. nicolascagei,* and *B. sekwiensis*) and one new species of *Nevadia* Walcott, 1910 (*N. saupeae*) are described from the Sekwi Formation of the Mackenzie Mountains, Northwest Territories, Canada. In addition, new specimens potentially referable to *Nevadia ovalis* were recovered that may expand that species' geographic range, which was thought to be restricted to Sonora, Mexico. A phylogenetic analysis incorporating several olenelline taxa, including *Judomia absita* from the Sekwi Formation, is also presented herein. This species has been assigned to various olenelline genera, including *Judomia* Lermontova, 1951 and *Paranevadella* Palmer & Repina, 1993. Phylogenetic

analysis suggests this species is closely related to *Judomia tera* Lazarenko, 1960 from Siberia. This phylogenetic relationship provides further support for the hypothesis that a close biogeographic relationship existed between Laurentia and Siberia during the Cambrian.

Introduction

Cambrian trilobites have served as foci for several phylogenetic studies (e.g., Cotton 2001; Lieberman 2002; Paterson & Edgecombe 2006). Among Cambrian trilobites, the Olenellina Walcott, 1890, is a diverse and widely distributed suborder of trilobites from the Early Cambrian. Further, these have provided important data used in various evolutionary and biogeographic studies of the Cambrian radiation (e.g., Fortey et al. 1996; Smith & Lieberman; Lieberman 2003; Meert & Lieberman 2004). Phylogenetic studies suggest olenellines are a basal suborder within Trilobita (see Lieberman & Karim 2010 for a recent discussion of phylogenetic studies of trilobites). In particular, Lieberman (1998) reassessed the group, making it monophyletic, by removing the superfamily "Fallotaspidoidea" (quotation marks denoting paraphyly after Wiley 1979), and a phylogenetic analysis of the suborder was conducted by Lieberman (2001).

Olenelline trilobites are known from several localities in the Sekwi Formation, Mackenzie Mountains, Northwest Territories, Canada (Fig. 1, 2). The Sekwi Formation is between 715 and 770 m thick in the Mackenzie Mountains, and can be constrained to the late Early Cambrian, Cambrian series 2, stages 3 and 4 (Fritz 1972; Randell et al. 2005; Dilliard et al. 2007, 2010). The formation consists of interbedded carbonate, shale, and sandstone, comprising mainly weathered limestone and dolostone (Dilliard et al. 2007, 2010) and was deposited during the *Fallotaspis, Nevadella,* and *Bonnia-Olenellus* trilobite zones. Recent collections recovered three new species of *Bradyfallotaspis* Fritz, 1972, and one new species of *Nevadia* Walcott, 1910. Additional material tentatively referred to ?*Nevadia ovalis*, McMenamin, 1987, previously known only from Mexico, was also recovered. Finally, *Judomia absita* Fritz, 1973, which Fritz (1973) treated as closely similar to *J. tera* Lazarenko, 1960, a Siberian platform trilobite, was also found. The phylogenetic affinities of this species have been debated. For instance, Palmer &

Repina (1993) informally suggested *J. absita* belonged to *Paranevadella* Palmer & Repina, 1993. To resolve the position of this taxon, a phylogenetic analysis, based on Lieberman's (2001) earlier analysis, was conducted.

Phylogenetic Analysis

Taxa analyzed. A total of 20 taxa within the Olenellina were subjected to phylogenetic analysis; these were chosen to best consider the phylogenetic placement of *J. absita*. The two outgroups used were *Nevadella mountjoyi* Fritz, 1992 and *N. perfecta* (Walcott, 1913); these 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 57 holaspid exoskeletal characters and character states based on Lieberman (2001). Morphological terminology follows Palmer & Repina (1993), Whittington et al. (1997), and Lieberman (1998). 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. Character state distributions are given in Table 1.

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: (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: (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: (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 LA: (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 LA: (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 where 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 where 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: (0) converging where proceeding from anterior to posterior (1) sub-parallel.

50) Single nodes on median part of thoracic axial rings (0) present (1) 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 (non-additive) because there were no clear criteria for ordering them. Three most parsimonious trees were recovered of length 198 steps, and a strict consensus of these is shown in Figure 3. 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, which implies strong phylogenetic signal in these data (Hillis 1991).

To further assess the quality of the overall phylogenetic signal and the significance of the recovered phylogenetic placement of *J. absita* with *Judomia* Lermontova, 1951, as opposed to with *Paranevadella*, tPTP tests (Faith 1991) were performed using PAUP. 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 obtained. The second test was run with all nodes collapsed except for *J. absita* and *J. tera*; this resulted in a *P*-value of 0.026, supporting the hypothesis that *J. absita* groups with *J. tera* instead of *P. subgroenlandicus*.

Support for each node was determined using a bootstrap analysis in TNT (Goloboff et al. 2008). 10,000 replications were employed using a standard (sample with replacement) analysis. A jacknife analysis was also performed using TNT (Goloboff et al. 2008) that involved 10,000 replicates with 36 percent removal (corresponds to 20 characters) probability (Fig. 3).

Finally, a Bremer branch support analysis (Bremer 1994) was 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 (Fig. 3). The total support index (Bremer 1994) for the tree is at least 0.07.

Systematics

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

Order Redlichiida Richter, 1933

Suborder Olenellina Walcott, 1890

***Bradyfallotaspis* Fritz, 1972**

Type species. *B. fusa* Fritz, 1972.

Discussion. The three new species of *Bradyfallotaspis* presented here are assigned to the genus based on their possession of diagnostic features identified by Fritz (1972) and Lieberman (2001). These include a cylindrical glabella with high relief and rounded anterior end, elevated ocular lobes that are connected to the glabella via ocular ridges, and genal spines that taper back rapidly. Species presented here have a cephalic width that is relatively wider than that of *B. fusa* Fritz, 1972 and *B. patula* Fritz, 1972. Also, *B. fusa* and *B. patula* have very short genal spines compared to the new species of *Bradyfallotaspis*. Lastly, the ocular ridges of *B. fusa* and *B. patula* are connected with the glabella via an ocular ridge at the anterior part of the glabella unlike the new species, which have the connection at S3. Important characters that vary among species include the presence or absence of a preglabellar area, position of the posterior margins of the ocular lobes (in contact or not with the posterior cephalic border), and the relative width (tr.) of the anterior cephalic border.

Bradyfallotaspis coriae **n. sp.**
(Fig. 4)

Type material. Holotype PWNHC-2009.20.1. Assigned specimens KUMIP 320696-320700 and PWNHC-2009.20.2-2009.20.8 from *Nevadella* zone, Early Cambrian, Sekwi Formation, Mackenzie Mountains, Northwest Territories, Canada (Section 2, 345-375 m above base of formation and in float; Section 14 in float). There are a total of 13 specimens.

Etymology. Named in honor of Corrine Myers, University of Kansas, for her assistance with laboratory techniques that facilitated the completion of this research.

Diagnosis. Anterior cephalic border (sag.) equal to length (sag.) L0, unlike broad anterior cephalic border ([sag.] greater than twice length [sag.] L0) of *B. sekwiensis*; differs from *B. sekwiensis* by possession of preglabellar area; differs from *B. fusa* and *B. patula* by possession of ocular ridges connected to glabella at L3, extraocular region very

broad, and genal spines length (exsag.) greater than length (sag.) of cephalon rather than possession of ocular ridges connected to glabella at anterior end of glabella, extraocular area narrow, and short genal spines, respectively; differs from *B. patula, B. nicolascagei,* and *B. sekwiensis* by possession of ocular lobes in contact with posterior border; 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 and genal spine angle 65-100 percent 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; S2, S3 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 spine length (exsag.) approximately six to ten times length (sag.) of L0, sweeping posterolaterally at roughly 10 degree angle relative to 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.

***Bradyfallotaspis nicolascagei* n. sp.**
(Fig. 5)

Type material. Holotype KUMIP 320701. Assigned specimens KUMIP 320702-320707 and PWNHC-2009.20.9-2009.20.17 from *Nevadella* zone, Early Cambrian, Sekwi

Formation, Mackenzie Mountains, Northwest Territories, Canada (Section 1, 200-400 m above base of formation; Section 2 in float; Section 14 in float). There are a total of 16 specimens.

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

Diagnosis. Differs from all other species of *Bradyfallotaspis* by possession of anterior cephalic border (sag.) equal to approximately half length (sag.) L0 and preglabellar area equal to combined length (sag.) L3 and LA; differs from *B. fusa* and *B. patula* by possession of ocular ridges connected to glabella at L3, extraocular region very broad, and genal spines length (exsag.) greater than or equal to length (sag.) of cephalon; ocular lobes not in contact with posterior border, unlike *B. coriae* and *B. fusa*.

Description. Cephalic length (sag.) 45-50 percent of width (tr.). Anterior cephalic border narrow, raised ridge, length (exsag.) between lateral margins of LA and genal spine angle 65-100 percent 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 of 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; S2, S3 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 spine length (exsag.) approximately six to ten times length (sag.) of L0, sweeping posterolaterally at roughly 5 degree angle relative to 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.

Bradyfallotaspis sekwiensis **n. sp.**

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(Fig. 6)

?*Bradyfallotaspis* sp. 3 FRITZ, 1973, p. 11, pl. 6, figs. 25-27.

Type material. Holotype PWNHC-2009.20.18. Assigned specimens KUMIP 320708-320710 and PWNHC-2009.20.19-2009.20.20. from *Nevadella* zone, Early Cambrian, Sekwi Formation, Mackenzie Mountains, Northwest Territories, Canada (Section 1, 175.6-288 m above base of formation; Section 2 in float). There are a total of six new specimens.

   Etymology. Named after the species occurrence in the Sekwi Formation.

   Diagnosis. Differs from all other species of *Bradyfallotaspis* by possession of anterior cephalic border (sag.) equal to twice length (sag.) L0 and preglabellar area absent; differs from *B. fusa* and *B. patula* by possession of ocular ridges connected to glabella at L3 and genal spine length (exsag.) greater than length (sag.) of cephalon; ocular lobes not in contact with posterior border, unlike *B. coriae* and *B. fusa*.

   Description. Cephalic length (sag.) 45-50 percent of width (tr.). Anterior cephalic border wide, raised ridge, length (exsag.) between lateral margins of LA and genal spine angle 65-100 percent length (sag.) of L0. Frontal lobe about 20 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 of 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; S2, S3 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 posterior border furrow; ocular lobes elevated from extraocular area; posterior margin of L0 subparallel; genal spines of length (exsag.) approximately six to ten times length (sag.) of L0, sweeping posterolaterally at roughly 10 degree angle relative to sagittal line; genal spine angle opposite L0; extraocular area

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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.

Discussion. *Bradyfallotaspis* sp. 3 from Fritz (1973), which is based on early ontogenetic stages, is questionably placed within *B. sekwiensis* based on its glabella with high relief, wide (sag.) cephalon with a broad (exsag.) anterior cephalic border, and posterior cephalic border that tapers to a point proximally.

Nevadia **Walcott, 1910**

Type species. *N. weeksi* Walcott, 1910.

Discussion. *Nevadia saupeae* n. sp. was assigned to *Nevadia* based on its possession of key diagnostic features including the lack of a macropleural third thoracic segment, the relatively long (as opposed to species of *Nevadella*) length (sag.) of LA, and the possession of straight S0 and S2 (additional discussion of criteria for assigning species to *Nevadia* is given in Lieberman 2001). Important distinctions between *N. saupeae* and other species of *Nevadia/Nevadella* include a very broad (tr.) extraocular area, very short (exsag.) genal spines (about the length [sag.] of L0), presence of a preglabellar field, and absence of a macropleural third thoracic segment.

Nevadia saupeae n. sp.
(Fig. 7)

Type material. Holotype KUMIP 320711 and PWNHC-2009.20.21 from *Nevadella* zone, Early Cambrian, Sekwi Formation, Mackenzie Mountains, Northwest Territories, Canada (Sections 2 and 14 in float). There are a total of 2 specimens.

Etymology. Named in honor of Erin Saupe, University of Kansas, for her assistance with laboratory techniques that facilitated the completion of this research.

Diagnosis. Differs from *N. weeksi* and *N. fritzi* due to lack of plectrum and possession of very short (exsag.) genal spines; differs from *N. fritzi* and *N. ovalis* by possession of

posterior cephalic border approximately parallel to transverse line; has relatively wide (tr.) cephalon and extraocular area.

Description. Cephalic length (sag.) 40-50 percent of width (tr.). Anterior cephalic border wide, flattened ledge, length (exsag.) between lateral margins of LA 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 length (sag.) of L0, sweeping posterolaterally at roughly 40 degree angle relative to 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.

Discussion. Fritz (1973) figured early ontogenetic stages of cephala he referred to as *Nevadia*? sp. but it was not possible to determine if these were conspecific with *N. saupeae*.

?Nevadia ovalis **McMenamin, 1987**
(Fig. 8)
Nevadia ovalis McMenamin, 1987, p. 744, figs. 5.2, 5.5, 5.6, 6.1, 6.3, 6.4, 6.6.

Material examined. PWNHC-2009.20.22 and KUMIP-320712-320713 and 320738 from *Nevadella* zone, Early Cambrian, Sekwi Formation, Mackenzie Mountains, Northwest Territories, Canada (Section 1, 199.5-300 m above base of formation and in float) and (following McMenamin 1987) base of the middle shaley interval of unit 3 of the Puerto Blanco Formation, Cerro Rajón area, Mexico.

   Discussion. These specimens maybe referable to *Nevadia ovalis* McMenamin 1987 originally described from the Puerto Blanco Formation of Sonora, Mexico. For instance, the material from the Sekwi Formation appears to match that species in possessing the anterior and posterior cephalic borders much wider and extraocular area much narrower than other species of *Nevadia*, as well as a cephalon that has an ovate shape along its anterolateral margins. However, because neither McMenamin's (1987) original material, nor the new material from the Sekwi Formation, is particularly well preserved, our assignment is considered tentative and questionable, and awaits discovery and identification of new material from each of these localities. The material from the Sekwi appears distinct from the aforementioned early ontogenetic stages of cephala Fritz (1973) referred to as *Nevadia*? sp., differing principally in the outline and overall geometry of the cephalon.

   Most olenellinid species tend to have very limited geographic ranges and are often endemic to narrowly defined areas. One of the rare exceptions is *Elliptocephala logani* (Walcott 1910), which straddles both the western and eastern parts of North America (Lieberman 1999); therefore, *Nevadia ovalis*, from southwestern North America, may comprise another such exception, if it is ultimately confirmed to be present in northwestern North America.

Genus *Judomia* Lermontova, 1951

***Judomia absita* Fritz, 1973**
(Fig. 9)
Judomia? absita FRITZ, 1973, p. 14, pl. 8, figs. 1-11.

Material examined. PWNHC-2009.20.23-2009.20.46, KUMIP-320714-320737, from *Nevadella* zone, Early Cambrian, Sekwi Formation, Mackenzie Mountains, Northwest Territories, Canada (Section 1, 196.1-378 m above base of formation and in float; Section 2 in float; Section 3, lower 100 m of formation; Section 4, 195-215 m above base of formation; Section 14 in float).

   Discussion. Nelson (1976, 1978) commented on the presence of various species he referred to *Judomia* in the Lower Cambrian of the present day White-Inyo region of California. However, his definition of *Judomia* did not always accord with a phylogenetically constrained, monophyletic conception of the genus (see Lieberman 2001for more detailed discussion). Still, the present study provides additional evidence that species of *Judomia* are indeed present in Laurentia; the genus was originally described from Siberia. This indicates there is potential for a biostratigraphic link between Siberia and Laurentia. Specifically, *J. absita* occurs in the *Nevadella* zone in Laurentia and other species of *Judomia* occur in the *Judomia* zone of the Atdabanian stage of Siberia (Palmer & Repina 1993); thus, these biostratigraphic divisions might be coeval. Based on the higher-level phylogeny presented in Figure 3, the Laurentian *J. absita* is sister to the Siberian *J. tera*. This provides further support for the close biogeographic and tectonic relationship between these two cratons in the late Proterozoic and early Cambrian (see also McKerrow et al. 1992; Pelechaty 1996; Lieberman 1997; and Meert & Lieberman 2004, 2008).

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FIGURE CAPTIONS

FIGURE 1—Map of the Sekwi Formation, from Dilliard et al. (2007).

FIGURE 2—Schematic cross-section of the Sekwi Formation, from Dilliard et al. (2010). Specimens in this study came from the *Nevadella* zone at sections 1, 2, 3, and 14 (63° 26' 22.2"N, 129° 22' 20.4"W; 63° 24' 27.4"N, 129° 7' 31. 8"W; 63° 33' 3.8"N, 129° 11' 51.2"W; 63° 37' 3.6"N, 128° 37' 32.2"W, respectively).

FIGURE 3—The strict concensus of three most parsimonious trees of length 198 steps produced from analysis of character data in Table 1 using 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 0.54, 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 0.07. Character states are placed at nodes (using MacClade v. 3.0.4 [Maddison & Maddison 1992]), with the characters given in the text. The apomorphic state is given in parentheses. Brackets indicate equivocal character states that are ambiguous because of missing data, polymorphisms, or multiple equally parsimonious resolutions. Equivocal characters are placed only at their basal phylogenetic position, and only unambiguous reversals are shown, 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 4—Specimens of *Bradyfallotaspis coriae* n. sp., from section 2 in float, *1* – holotype PWNHC-2009.20.1, X4; *2* – KUMIP 320696, X2.5.

FIGURE 5— Specimens of *Bradyfallotaspis nicolascagei* n. sp., *1* – holotype KUMIP 320701, X2.8, from section 2 in float; *2* – PWNHC-2009.20.9, X2, from section 1, 260-288 m above the base of the section.

FIGURE 6— Specimens of *Bradyfallotaspis sekwiensis* n. sp., *1* – holotype PWNHC-2009.20.18, X2.3, from section 1, 260-288 m above the base of the section; *2* – KUMIP 320708, X2, from section 1, 200-210 m above the base of the section.

FIGURE 7— Specimens of *Nevadia saupeae* n. sp., *1* – holotype KUMIP 320711, X1.8, from section 14 in float; *2* – PWNHC-2009.20.21, X4, from section 2 in float.

FIGURE 8— Specimens of ?*Nevadia ovalis* McMenamin, 1987, *1* – KUMIP 320712, X8.5, from section 1 in float; *2* – KUMIP 320738, X7.5, from section 1 in float.

FIGURE 9— Specimens of *Judomia absita* Fritz, 1973, *1* – KUMIP 320714, X4, from section 2 in float; *2* – PWNHC-2009.20.23, X4.7, from section 1, 208-210 m above
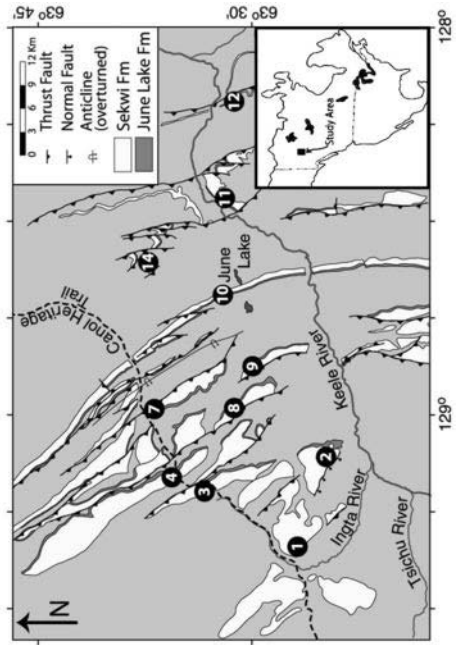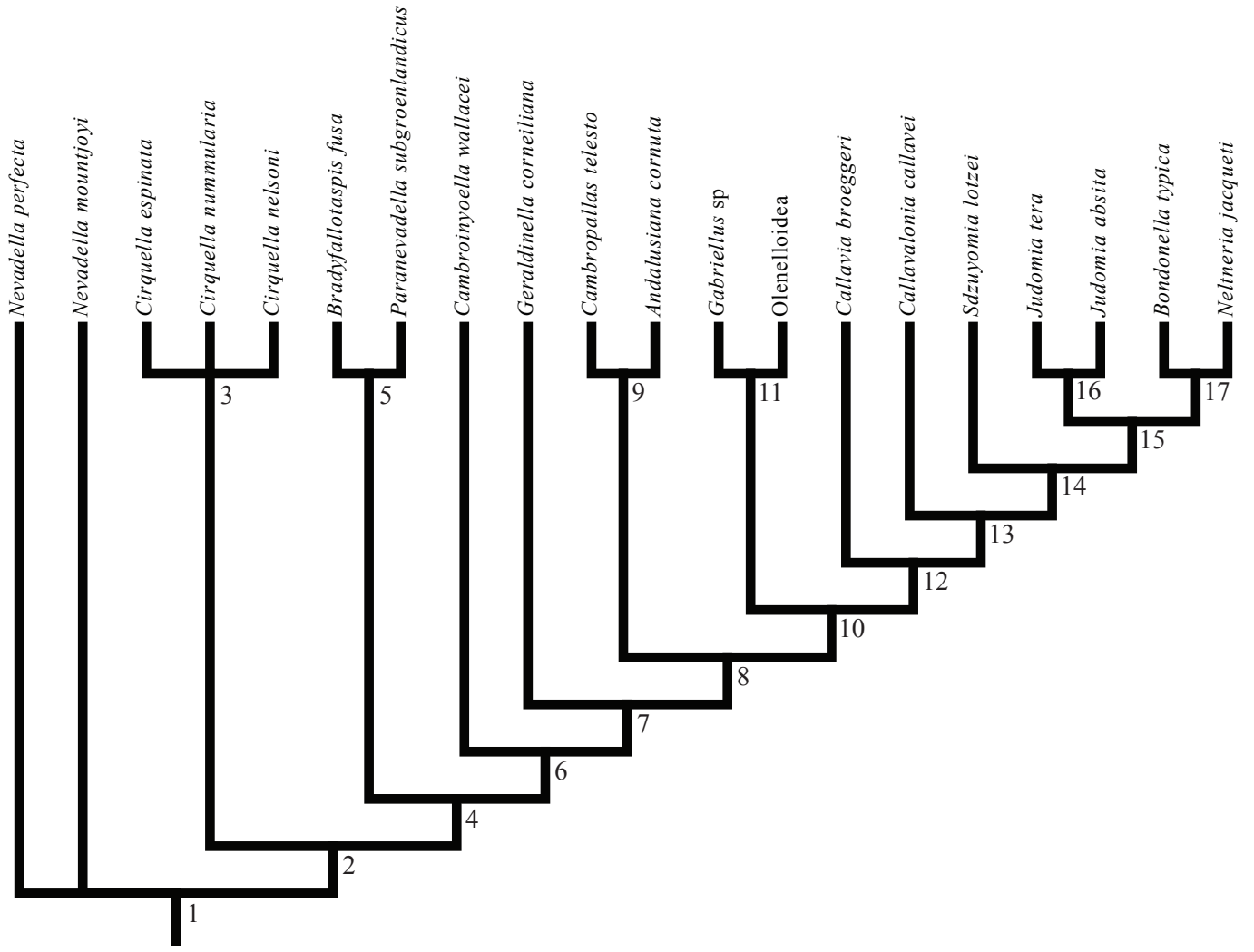
the base of the section.

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).

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                    0000000000111111111122222222223333333333444444444455555555
                    1234567890123456789012345678901234567890123456789012345 67
Nevadella_perfecta
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Nevadella_mountjoyi
                    000110000000000X0X00000000000X00000010000000000000000111000?
Cirquella_espinata
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Cirquella_nummularia
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Cirquella_nelsoni
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Bradyfallotaspis_fusa
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Paranevadella_subgroenlandicus
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Cambroinyoella_wallacei
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Geraldinella_corneiliana
                    000100101010100101110000001 01000000?00000????????????????0
Cambropallas_telesto
                    211110110011100121110100001001000012100000000012001111010
Andalusiana_cornuta
                    01101001001111XZ011201101011001001120200 0???00020011X21??
Gabriellus_sp
                    110110101010100Z1102001010110101001030122100112 0002112001
Olenelloidea
                    100111000W00100W011210XX1X11X10000000X100101X101002X0100W
Callavia_broeggeri
                    01011010101010022111101010100?02011011100?0110010011101?0
Callavalonia_callavei
                    200110102010100221111010101101020 11?11100??????1??0100?00
Sdzuyomia_lotzei
                    010000?01210100020 01?010?0?1?1??11131?000?011002?100?011?
Judomia_tera
                    001110001210101211021110102121 11100?1300 0011011110011?11
Judomia absita
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Bondonella_typica
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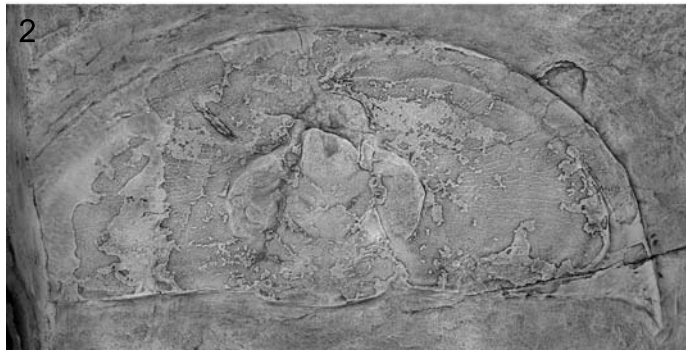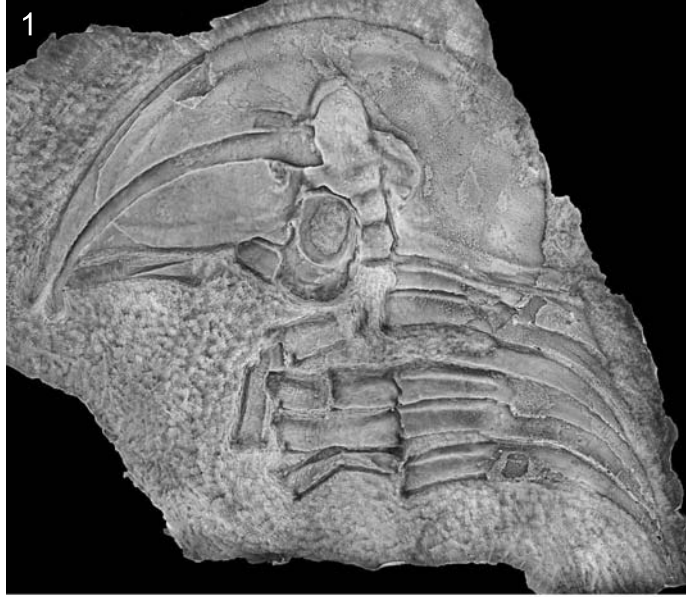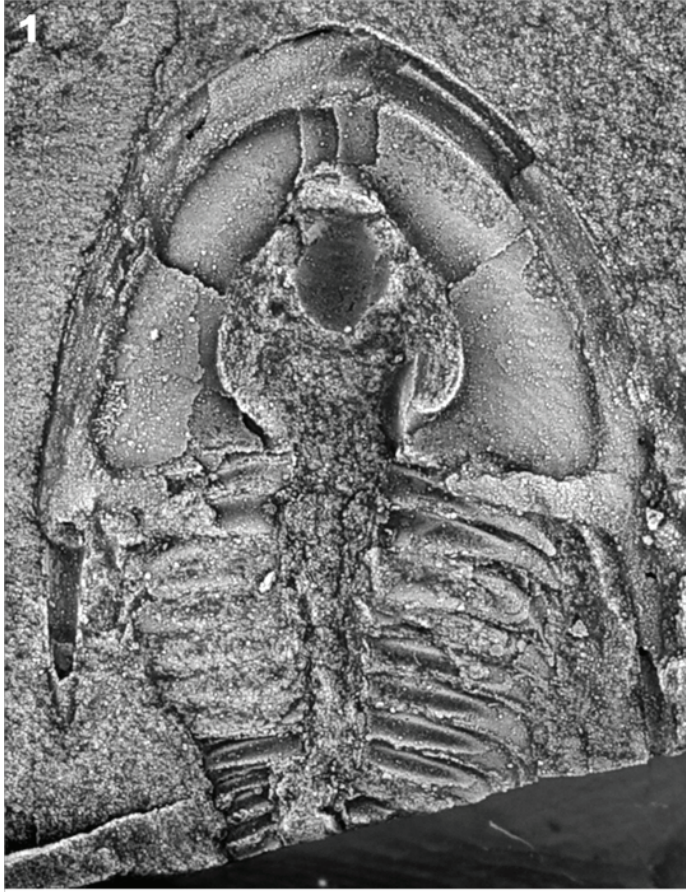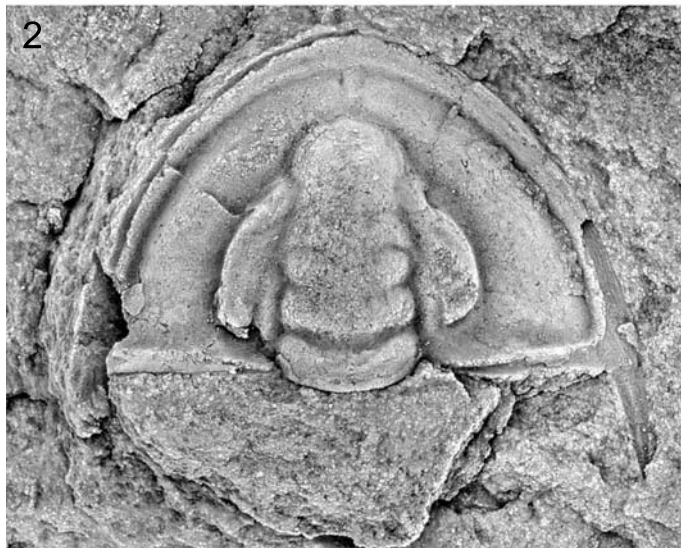
Neltneria_jacqueti
001110011210101111121101111011110100100110110120000011001