

# *Paranephrolenellus*, a new genus of Early Cambrian olenelloid trilobite

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New field collections from the poorly-known Delamar Member of the Pioche Formation (*Bristolia* Zonule, Dyeran Stage, Lower Cambrian) from Klondike Gap in the Chief Range, Lincoln County, Nevada, reveal that at least 18 species of olenelloid trilobite occur within the unit. This diversity exceeds that documented within well-studied correlative units such as the Latham Shale and Carrara Formation. The first biostratigraphic range chart is presented for olenelloid trilobites within the Delamar Member, constructed from five incomplete but partially overlapping detailed sections. The succession of species generally matches that previously documented in correlative units, suggesting that a refinement to the biostratigraphy of the *Bristolia* Zonule in the southwestern United States may be possible. Three new biceratopsid species are described herein and assigned to *Paranephrolenellus* n. gen., distinguished from other biceratopsid genera by aspects of oculo-glabellar and thoracic morphology. *Paranephrolenellus klondikensis* n. sp. is the stratigraphically oldest member of the genus, and is known only from Klondike Gap and correlative horizons in the Delamar Member elsewhere in the Chief Range and in the Highland Range. *Paranephrolenellus inflatus* n. sp. and *Paranephrolenellus besti* n. sp., the stratigraphically youngest member of the genus, are also known from correlative intervals from other formations in the southwestern United States. These species exhibit ontogenetic trends in several aspects of cephalic morphology also found in closely related taxa such as *Nephrolenellus*.

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OVER the last decade, field work in the Pioche Formation of east-central Nevada has yielded a previously underappreciated diversity of Lower and Middle Cambrian trilobites (Sundberg & McCollum 1997, 2000, 2002, 2003; Eddy & McCollum 1998; Palmer 1998) and other invertebrates (Lieberman 2003). The abundance and high preservational quality of trilobites from many intervals within the Pioche Formation has provided insight into issues of phylogeny (Sundberg & McCollum 1997, 2000; Webster *et al.* 2001; Sundberg 2004; Paterson & Edgecombe 2006), palaeobiology (Palmer 1998; Webster *et al.* 2001; Webster & Zelditch 2005; Webster *in press*), and taphonomy (Webster & Hughes 1999), and has contributed towards an improved resolution of Delamaran biostratigraphy (Eddy & McCollum 1998; Sundberg & McCollum 2000).

To date, research attention has focused on the faunas in the Combined Metals Member (uppermost Dyeran Stage) and successively overlying Comet Shale, Susan Duster Limestone,

Log Cabin, and Grassy Spring members (all Delamaran Stage; lithostratigraphic nomenclature for subdivisions of the Pioche Formation follows the recent revisions proposed by Eddy & McCollum [1998] and Sundberg & McCollum [2000]). The fauna of the Delamar Member (the basal unit of the Pioche Formation, underlying the Combined Metals Member) has been little studied by comparison. Published reports have documented the presence of *Mesonacis fremonti* (Walcott, 1910), *Bristolia bristolensis* (Resser, 1928), *Bristolia insolens* (Resser, 1928), *Olenellus nevadensis* (Walcott, 1910) and *Peachella* Walcott, 1910 within the Delamar Member (Palmer *in Merriam* 1964; Sundberg & McCollum 2000); a faunal list sufficient to establish that the unit lies within the *Bristolia* Zonule (Palmer & Halley 1979), but of rather low diversity in comparison to correlative assemblages from elsewhere (e.g., in the Carrara Formation [Palmer & Halley 1979; Fowler 1999] and Latham Shale [Webster *et al.* 2003]). However,

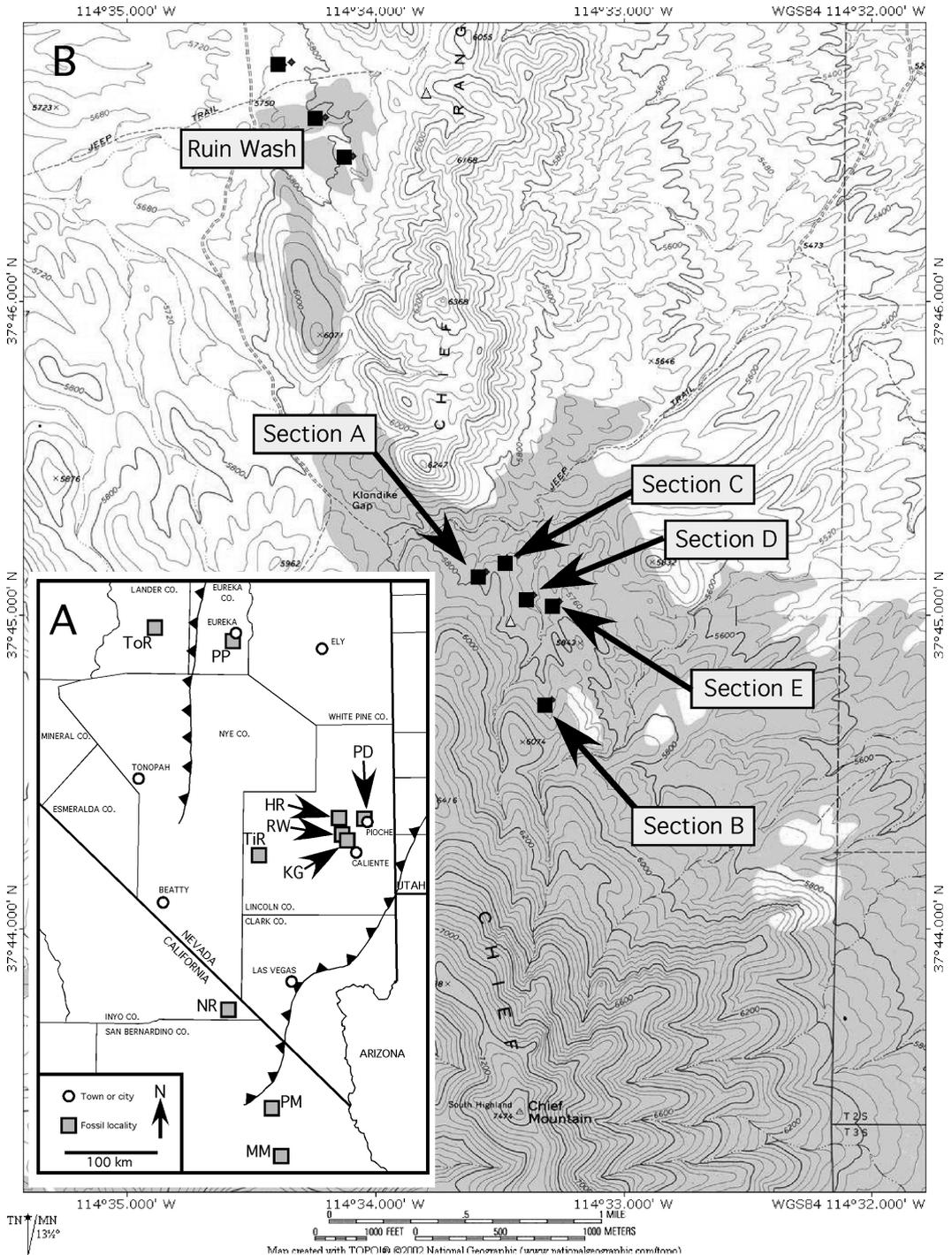


Fig. 1. A, Map of localities in SW U.S.A. from which *Paranephrolenellus* specimens have been recovered. Abbreviations: HR, Highland Range; KG, Klondike Gap; MM, Marble Mountains; NR, Nopah Range; PD, Pioche Divide; PM, Providence Mountains; PP, Prospect Peak; RW, Ruin Wash; TiR, Timpahute Range; ToR, Tiyoabe Range. Black lines with triangles mark eastern limits of thrusting (Antler Orogenic Belt in N, Sevier Orogenic Belt in SE; overthrust block to W in each case). B, Location of measured sections from which the composite log and biostratigraphic range chart (Fig. 2) of the Delamar Member of the Pioche Formation at Klondike Gap was constructed (see Appendix). The sites of three excavations at the Ruin Wash locality (Palmer 1998) are shown to the north. Map created with TOPO! software (© National Geographic, 2002).

mirroring results from the stratigraphically higher units of the Pioche Formation, recent field work by the present author has revealed the presence of a far greater trilobite diversity (at least 18 species) within the Delamar Member. The newly documented succession of olenelloid species at the most studied section (Klondike Gap, Chief Range; Figs 1-2) generally matches (and diversity even exceeds) that found in the *Bristolia* Zonule at sections elsewhere in the southwestern United States (Palmer & Halley 1979; Fowler 1999; Webster *et al.* 2003). At least eight new species are represented in the Delamar Member. A new species of *Mesonacis* Walcott, 1885, two new morphotypes of *Bristolia* Harrington, 1956, and two new morphotypes of *Olenellus* Hall, 1861 found at Klondike Gap (Fig. 2) are all represented by material of higher preservational quality and abundance from correlative formations at other localities and will be described elsewhere in a series of systematic papers (in preparation). The present paper describes three new species assigned to *Paranephrolenellus* n. gen. (Fig. 3). *Paranephrolenellus klondikensis* n. sp. is known only from Klondike Gap and correlative horizons in the Delamar Member elsewhere in the Chief Range and in the Highland Range. Specimens here assigned to *Paranephrolenellus inflatus* n. sp. and *Paranephrolenellus besti* n. sp. have also been recovered from correlative intervals from other formations in the southwestern United States (see below), and may offer some regional biostratigraphic utility.

## LITHOSTRATIGRAPHY AND BIOSTRATIGRAPHY

The Delamar Member (previously informally known as the D-shale member; Merriam 1964) of the Pioche Formation is a relatively thick (approximately 103 m at Klondike Gap) heterolithic sequence dominated by fine sandstones and bioturbated siltstones, with minor fissile shale intervals and thin sandy carbonate interbeds (Fig. 2). The sediments were deposited during a general relative deepening-to-shallowing cycle (see also Sundberg & McCollum 2000), which is recorded in correlative strata across the southwestern United States, and likely accumulated over approximately one million years. A single section through the entire Delamar Member could not be located at Klondike Gap owing to the structural complexity of the Chief Range. However, a complete composite section (simplified and summarised in Fig. 2) was constructed from the stitching together of several partially overlapping, incomplete sections (Fig. 1B, Appendix).

The initial deposits of the Delamar Member overlie the coarse siliciclastics of the Zabriskie

Quartzite (lithostratigraphic nomenclature for this quartzite here follows that applied by Rowley *et al.* [1994] and Sundberg & McCollum [2000]; Merriam [1964] and Palmer [1998] applied the term Prospect Mountain Quartzite in this region; see Stewart [1970] for a discussion of regional application of these terms), and consist of hackly, bioturbated siltstones with thin (centimetre- to decimetre-scale, sometimes cross-bedded) interbedded sandstones. Flat-pebble conglomerates and other thin, fining-up conglomerates were recovered from float in the lower 40 m. The sandstones become thinner and less frequent up section, and the highest prominent *in situ* sandstone ledge in the deepening interval was logged at 34 m above the base of the unit. The stratigraphically lowest body fossils, representing *Mesonacis fremonti* and *O. clarki* (Resser, 1928), were extracted from a thin shale interval 44 m above the base of the unit, although trace fossils (burrows, surface trails, and arthropod scratch marks) are abundant below this level. The stratigraphically lowest trilobite of biostratigraphic significance is *Bristolia mohavensis* (Crickmay in Hazzard, 1933). This is consistently the stratigraphically oldest species of *Bristolia* across the southwestern United States (Webster *et al.* 2003; also unpublished observations) and therefore marks the base of the *Bristolia* Zonule (Palmer & Halley 1979). Collections below this horizon are assigned to the underlying *Arcuolenellus arcuatus* Zonule (Palmer & Halley 1979) although the eponymous species has not been recovered at Klondike Gap. The succession of *Bristolia* species (Fig. 2) at Klondike Gap matches that of more continuously fossiliferous and thoroughly sampled correlative sections (e.g., the Latham Shale of the Marble Mountains and Providence Mountains; Webster *et al.* 2003; also unpublished observations). Biostratigraphic subdivision of the *Bristolia* Zonule and younger Dyeran strata utilising species-level biozones will be formally proposed elsewhere (see Webster 2003, 2005 for preliminary notes).

A relatively thin (1.3 m) interval of mudstone interrupted only by millimetre- to centimetre-thick micaceous siltstone stringers occurs 62 m above the base of the Delamar Member. Regional-scale correlation and facies interpretation suggest that this interval approximates the time of maximal flooding. This coincides with the attainment of relatively large size (over 5 cm sagittal cephalic length) and high preservational quality (including complete articulation) of some olenelloid trilobite species. The stratigraphically short-ranging olenelloid *Bristolia insolens* is confined to this interval, and provides a biostratigraphically

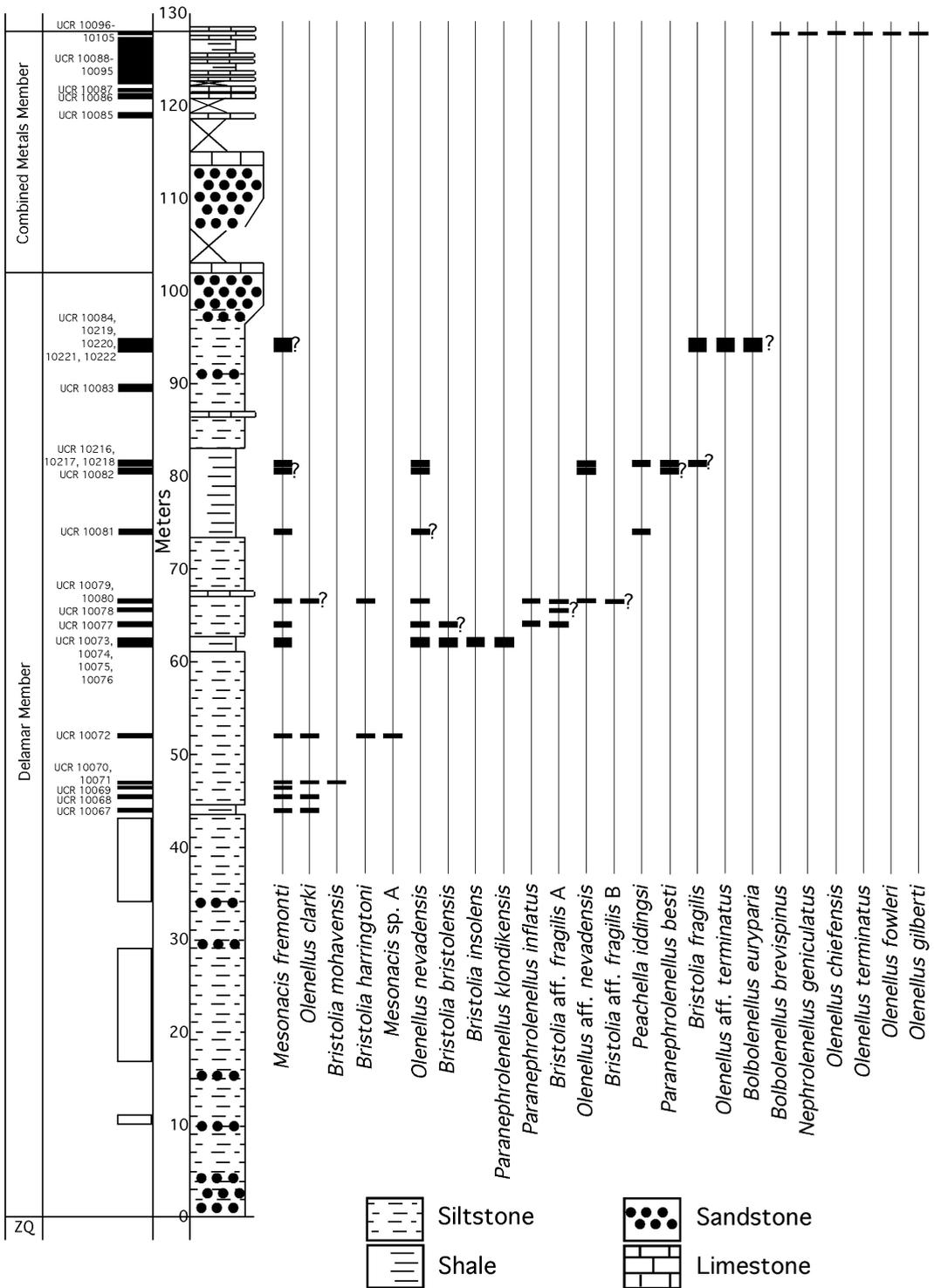


Fig. 2. Composite log and range chart for common olenelloid trilobite species in the Delamar Member of the Pioche Formation at Klondike Gap. Black bars to the left of the metre scale indicate provenience of stratigraphically constrained fossil collections housed in the Geology Museum, University of California, Riverside (UCR); empty bars indicate intervals of failed searches for body fossils. A question mark next to a black bar indicates a tentative identification due to poor preservation. Stratigraphic occurrences of specimens identifiable only to superspecific taxonomic level are not shown. ZQ, Zabriskie Quartzite.

useful marker (the ‘*Insolens* Beds’) of regional significance. The oldest representative of the new genus described herein, *Paranephrolenellus klondikensis* n. sp., also occurs in this interval.

The upper 41 m of the Delamar Member is a crudely coarsening-up succession of bioturbated siltstones, sandstones, thin shales, and thin carbonate interbeds. The stratigraphically lowest carbonate was found 5 m above the ‘*Insolens* Beds’. *Paranephrolenellus inflatus* n. sp., described herein, occurs between the ‘*Insolens* Beds’ and this carbonate ledge. *Paranephrolenellus besti* n. sp. was recovered from the upper portion of a poorly exposed interval of interbedded shale and siltstone approximately 11 to 21 m above the ‘*Insolens* Beds’. This interval also contains the distinctive and biostratigraphically useful *Peachella iddingsi* (Walcott, 1884). The uppermost 18 m of the Delamar Member are dominated by extensively burrowed, hackly siltstones and fine sandstones with thin (centimetre-scale) sandy carbonates. Olenelloids recovered from 8 m below the top of the Delamar Member include *Bristolia fragilis* Palmer in Palmer & Halley, 1979, and *Bolbolenellus euryparia?* (Palmer in Palmer & Halley, 1979; the identification is equivocal due to poor preservation). These species occur within the Chambless Limestone at the Marble Mountains (Webster *et al.* 2003).

The Delamar Member terminates in a thick (3 m) succession of calcareous sandstones, capped by a regionally developed erosion surface with centimetre- to decimetre-scale relief interpreted as a palaeokarst (Sundberg & McCollum 2000). The basal oncolitic carbonate ledge of the Combined Metals Member immediately overlies this erosion surface. The lithostratigraphy of the Combined Metals Member was recently refined and described by Sundberg & McCollum (2000). Silicified trilobites from several carbonate ledges in the upper portion of this unit have been recovered and will be described elsewhere. The diverse olenelloid faunal assemblage described by Palmer (1998) from nearby Ruin Wash (Fig. 1B) is also represented in the uppermost Combined Metals Member at Klondike Gap, but the fossils at Klondike Gap are disarticulated and of unremarkable preservational quality in comparison to those at Ruin Wash.

## SYSTEMATIC PALAEOLOGY

### Terminology

Morphological terminology follows that of Whittington and Kelly (1997), with modifications proposed by Palmer (1998) and Webster (in press). Genal spine advancement is measured by finding the point at which the axial furrow of the glabella is intersected by a transverse line

drawn between the adaxial margins of the genal spine bases where they contact the posterolateral cephalic margin (crudely, and with no intended implication of homology, the ‘armpits’ of the genal spines).

### Materials

Specimens listed here are housed in the collections of the Field Museum, Chicago (FMNH), the Institute for Cambrian Studies, Department of Geophysical Sciences, University of Chicago (ICS), the Geology Museum of the University of California, Riverside (UCR), the Smithsonian Institution, Washington D.C. (USNM), and the Yale Peabody Museum (YPM). Stratigraphic information (such as distance from marker beds) following UCR or ICS numbers refers to collateral field descriptions deposited with the geology museum at the University of California, Riverside, or the Institute for Cambrian Studies, Department of Geophysical Sciences, University of Chicago, respectively. A question mark preceding a specimen number indicates a tentative identification due to poor preservation.

Order REDLICHIIIDA Richter, 1932

Suborder OLENELLINA Walcott, 1890

Superfamily OLENELLOIDEA Walcott, 1890

Family BICERATOPSIDAE Pack & Gayle, 1971

### *Paranephrolenellus* new genus

*Type species. Paranephrolenellus besti* n. sp.

*Other species. Paranephrolenellus klondikensis* n. sp. and *Paranephrolenellus inflatus* n. sp.

*Diagnosis.* Biceratopsids with short, strongly divergent ocular lobes (posterior tip opposite or anterior to midlength of L1; line drawn from posterior tip of ocular lobe to contact between adaxial margin of ocular lobe and axial furrow forms angle of 25°–50° with sagittal axis). Glabella hourglass-shaped, constricted at S1 or L2; axial furrow shallow or absent at lateral margins of L1; S2 gently convex anteriorly, contacts axial furrow; S3 elongate furrow, oriented anterolaterally away from axis until contact with ocular lobes, contacts axial furrow; LA hemispherical to transversely oblate, summit slightly higher than more posterior glabellar lobes. Genal spine longer than length of LO (exsag.), base located at point of maximal cephalic width (tr., excluding genal spines). Fourteen prothoracic segments; pleural spine of T3 stout, macrospinous, blunt-tipped; first segment of opisthothorax with long axial spine. Summit of interocular area of

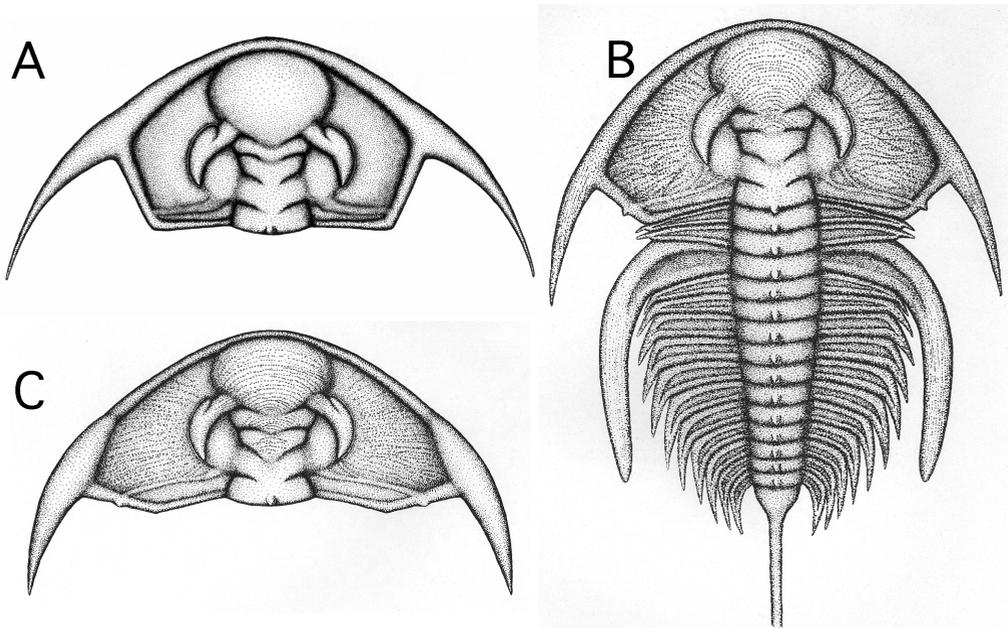


Fig. 3. Reconstructions of morphologically mature dorsal exoskeletal elements of the three new species described herein. A, cephalon of *Paranephrolenellus besti* new species. B, cephalon, prothorax, and first opisthothoracic segment of *Paranephrolenellus klondikensis* new species. Axial nodes are shown on all prothoracic segments based on analogy with the condition in closely related taxa (e.g., *Nephrolenellus* species), although their presence on segments posterior to T4 in *P. klondikensis* is unknown. C, cephalon of *Paranephrolenellus inflatus* new species. All reconstructions represent individuals with sagittal cephalic length of approximately 10 mm.

higher dorsal elevation than summit of ocular lobes at small cephalic size (approximately 1.5 mm sagittal length).

*Etymology.* Named for the close similarity of this genus to *Nephrolenellus* Palmer & Repina, 1993. Gender masculine.

*Occurrence.* Middle to upper *Bristolia* Zonule, upper Dyeran Stage, Lower Cambrian, U.S.A. (California, Nevada; Fig. 1A).

*Discussion.* Webster *et al.* (2001) recognised the close affinity of *Paranephrolenellus klondikensis* n. sp. with *Nephrolenellus* (indeed, they referred to the new species as “*Nephrolenellus?* n. sp.”; the other species assigned to *Paranephrolenellus* had not been discovered at the time). The ontogeny and mature morphology of the two known species of *Nephrolenellus*, *N. multinodus* (Palmer in Palmer & Halley, 1979) and *N. geniculatus* Palmer, 1998, is described elsewhere (Webster in press). *Paranephrolenellus* differs from *Nephrolenellus* in the possession of a slit-like (rather than pit-like) S3 which retains contact with the axial furrow, a less pronounced constriction of the glabella at S2 (Fig. 4A), fourteen (rather than thirteen) prothoracic segments, a stout, blunt-

tipped, macrospinous T3 pleural spine (rather than slender, sharp-tipped and hyperpleural), and a long axial spine on the anteriormost opisthothoracic segment. These thoracic characters are known only in *Paranephrolenellus klondikensis* n. sp. among *Paranephrolenellus* species. Differences in glabellar and thoracic characters are typically used to discriminate olenelloid genera (e.g., Palmer & Repina 1993, 1997; Lieberman 1998, 1999).

*Paranephrolenellus* also shares close similarity to *Bolbolenellus* Palmer & Repina, 1993 and *Arcuolenellus* Palmer & Repina, 1993. All known species of the latter genus are characterised by having genal spine bases located posterior and adaxial to the point of maximal cephalic width (tr.). *Bolbolenellus* species differ from *Paranephrolenellus* species in having longer and less divergent ocular lobes (Fig. 4B-C).

Species assigned to *Paranephrolenellus* are therefore excluded from current diagnoses of all closely related genera. However, discrete potential synapomorphies of *Paranephrolenellus* remain ambiguously resolved: e.g., the condition of the T3 pleural spine (stout, macrospinous, and blunt-tipped in *P. klondikensis* n. sp.) and of the interocular area relief at small cephalic sizes (of higher dorsal elevation than the summit

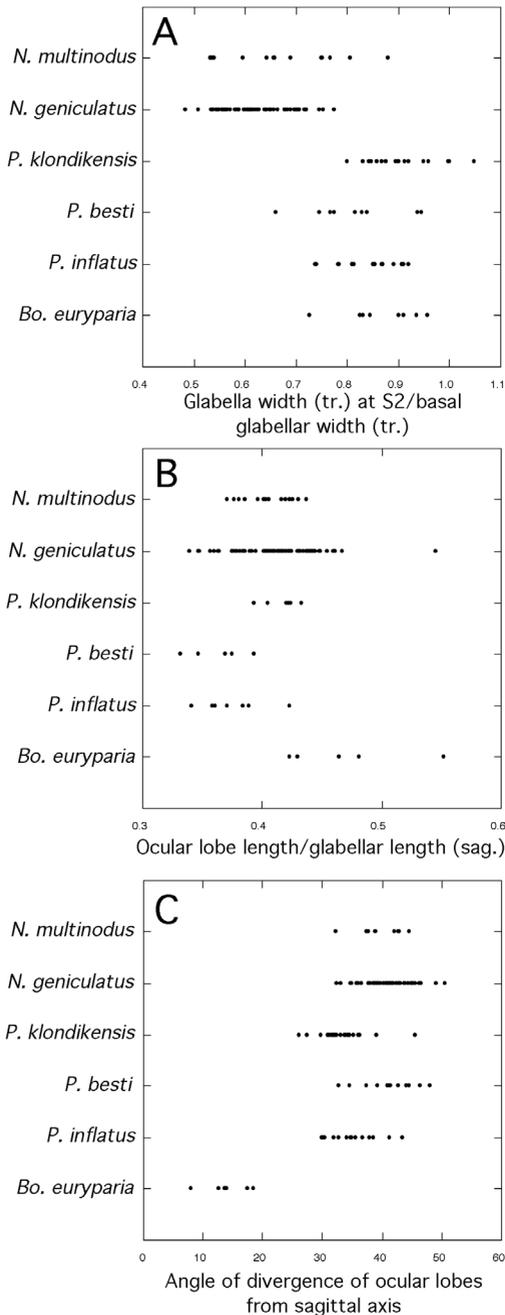


Fig. 4. Morphometric variables distinguishing mature cephalae of *Paranephrolenellus* species from those of closely related taxa. A, glabella width (tr.) at S2 relative to basal glabellar width (tr.) for *Nephrolenellus multinodus* (n = 14), *N. geniculatus* (n = 67), *Paranephrolenellus klondikensis* (n = 20), *P. besti* (n = 9), *P. inflatus* (n = 15) and *Bolbolenellus euryparia* (n = 8). B, ocular lobe length relative to sagittal glabellar length for *N. multinodus* (n = 14), *N. geniculatus* (n = 72), *P. klondikensis* (n = 8), *P. besti* (n = 5), *P. inflatus* (n = 9), and *Bo. euryparia* (n = 5). C, divergence of ocular lobes for *N. multinodus* (n = 9), *N. geniculatus* (n = 62), *P. klondikensis* (n = 21), *P. besti* (n = 14), *P. inflatus* (n = 15), and *Bo. euryparia* (n = 7). This variable was measured as the angle formed between the sagittal axis and a line drawn from the posterior tip of the ocular lobe to the point of contact between the adaxial margin of the ocular lobe and the axial furrow. In all plots, measurements were restricted to well preserved cephalae of sagittal length >5 mm. See text for details.

of the ocular lobes in *P. besti* n. sp.) is known for only one of the three *Paranephrolenellus* species and is unknown in relevant outgroup taxa such as *Bolbolenellus euryparia*. It is therefore possible that the *Paranephrolenellus* species form a paraphyletic grade with respect to the *Nephrolenellus* clade. Pending a cladistic analysis of all biceratopsid taxa (in preparation), a dramatic expansion of the diagnosis of *Nephrolenellus* to include the three *Paranephrolenellus* species is considered premature, and *Paranephrolenellus* is here recognised as a distinct genus diagnosed by a unique combination of (non-unique) character states and ambiguously resolved potential synapomorphies (above).

*Paranephrolenellus besti* n. sp. and *P. inflatus* n. sp. were two of the earliest olenelloid taxa to be discovered. Specimens now assigned to these species were figured by Walcott (1884, pl. 9, figs 15, 15b, pl. 21, figs 1, 3, 4, 6) under the name *Olenellus howelli* Meek in White, 1874, and have been refigured or listed under different names several times since (see synonymy lists below).

“*Olenellus abnormis*” and “*Olenellus barrandi*”, first mentioned by Hague (1883, p. 256-257) and later copied in faunal lists by Marcou (1885, p. 231) and Brögger (1886, pp. 183, 186 [the latter species referred to as “*Olenellus barrandei*”]), are invalid taxon names which likely refer to specimens later assigned by Walcott (1884) to his concept of *O. howelli*, which included specimens now assigned to *P. besti* n. sp. and *P. inflatus* n. sp., among other species.

***Paranephrolenellus besti* new species (Figs 3A, 5-6)**

- 1884 *Olenellus howelli* (part); Walcott, pl. 9, fig. 15b, pl. 21, figs 1, 3, 4 only.
- 1886 *Olenellus gilberti* (part); Walcott, pl. 20, figs 1, 1c, 1e, 1g only.
- 1890 *Olenellus gilberti* (part); Walcott, pl. 86, figs 1, 1c, 1e, 1g only.
- 1910 *Olenellus fremonti* (part); Walcott, pl. 37, figs 8, 11, 12 only, see also mention of form in caption to pl. 37, fig. 9.
- 1912 *Olenellus fremonti* (part); Walcott, p. 140,

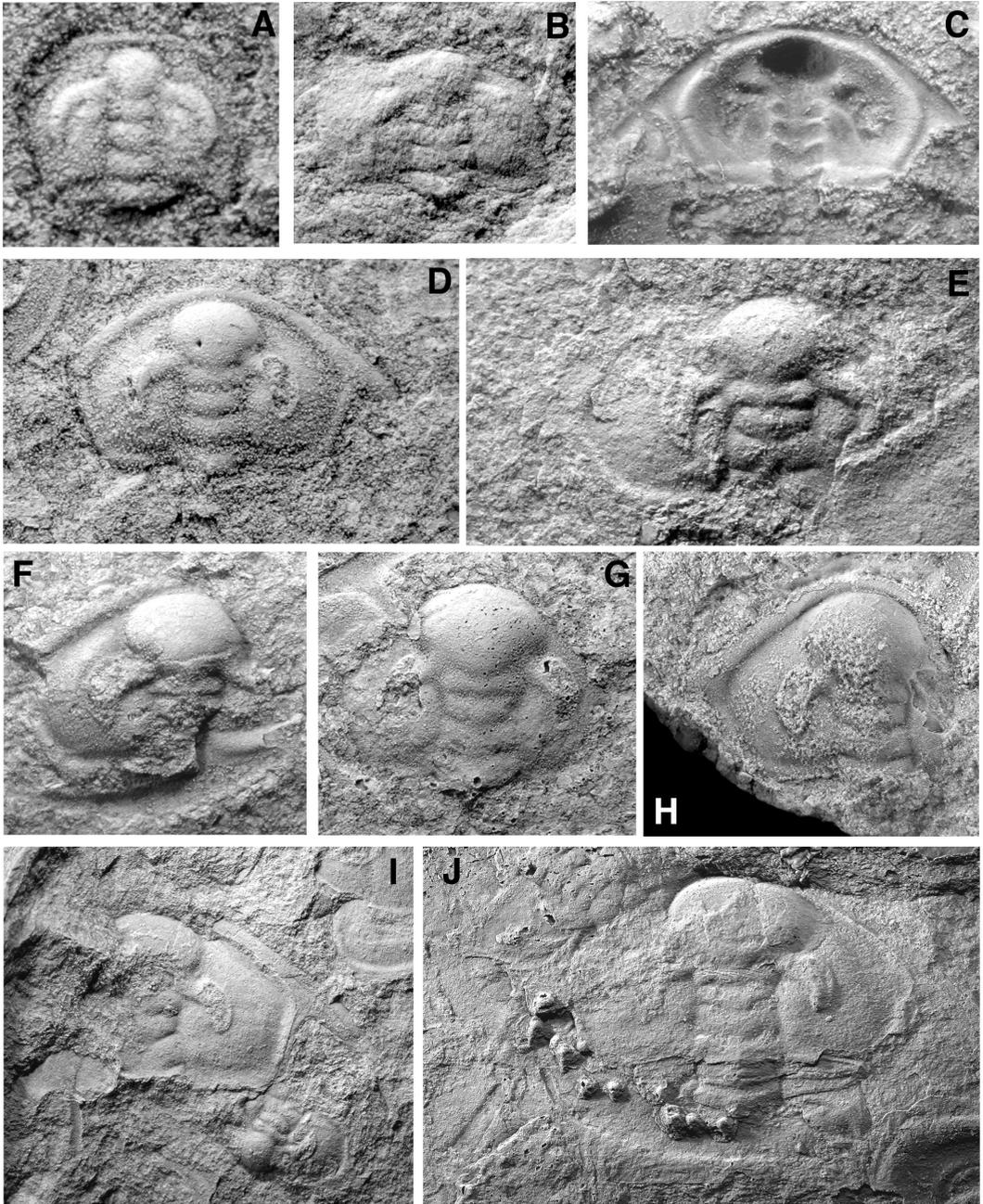


Fig. 5. Cephala of *Paranephrolenellus besti* n. sp. in dorsal view. A, small, coarsely preserved cephalon, latex cast of external mould, FMNH PE58003, x16. B, small, poorly preserved and incomplete cephalon, internal mould, UCR 10216.3, x9. C, small cephalon, external mould in limestone, USNM 15407, x9. D, small, coarsely preserved cephalon, latex cast of external mould, FMNH PE58002, x8. E, small, coarsely preserved and incomplete cephalon, internal mould, UCR 10218.6, x7. F, small, incomplete cephalon, internal mould in limestone, USNM 15407, x6. G, incomplete cephalon, latex cast of external mould, FMNH PE58001, x5. H, incomplete cephalon preserved in limestone with adherent matrix, FMNH PE58005, x4. I, incomplete cephalon, internal mould, UCR 10218.5, x3. J, incomplete cephalon and anterior thoracic segments, latex cast of external mould, UCR 10216.18, x3. A, D, and G from ICS-1010, Prospect Peak, Eureka district, Nevada; B, E, I, and J from various stratigraphic levels at Klondike Gap, Chief Range, Nevada (see Appendix); C and F from Walcott's (1910, 1912) locality 52, Prospect Peak, Eureka district, Nevada; H from ICS-1364, Toiyabe Range, Callahan Window, Lander County, Nevada.

- 158, 201, 246 (included within concept of "*Olenellus fremonti*" from localities 52 and 313g).
- ?1936 *Mesonacis fremonti* (sic)(part); Grabau, p. 67, 133 (probably included within concept of "*Mesonacis fremonti*" from the Eureka district and the southern end of the Timpahute Range).
- ?1956 *Olenellus fremonti* (part); Nolan *et al.*, 1956, p. 8 (probably included within concept of "*Olenellus fremonti*" from Prospect Peak).
- 1956 genus and species indet.; Harrington, p. 57-58 (reference to USNM 56819g = Walcott, 1910, pl. 37, fig. 11).
- 1979 "undescribed species related to *Bristolia anteros*"(part); Palmer & Halley, p. 71 (reference to Walcott, 1910, pl. 37, figs 8, 11 only; not fig. 10 = *Bristolia anteros*).
- 1999 Bristoliinae n. gen. 1 n. sp. 1; Fowler, p. 48.

*Diagnosis.* Species of *Paranephrolenellus* with very strong adgenal angle (deflecting posterior margin of cephalon anteriorly by 60°-80°), base of genal spine opposite L2, S2, or L3; S2 gently convex anteriorly either side of sagittal axis, abaxial and adaxial ends on roughly transverse line; L3 transverse to weakly 'V'-shaped.

*Description* (mature morphology). Cephalon subpentagonal in outline; proximal portion of posterior cephalic margin transverse or angled slightly posterolaterally away from axial furrow, distal portion flexing anteriorly by 60°-80° relative to proximal portion at distinct adgenal angle located approximately half the distance along posterior cephalic margin from axial furrow to base of genal spine. Greatest observed cephalic length approximately 14.9 mm (sag.). Genal spine slender, base opposite L2, S2, or L3 at point of maximal cephalic width (excluding spines, Fig. 6C-E), length approximately equal to glabella length (sag.), flares posterolaterally from cephalic border, distally curves more strongly posteriorly. Tiny intergenal node occasionally present, situated approximately one-third of distance between adgenal and genal angles (Fig. 6B). Cephalic border well defined around entire margin by distinct border furrow; rounded dorsally anteriorly, flattens slightly in profile abaxially; width of anterior border opposite junction of ocular lobe with LA approximately three-fifths to four-fifths length of LO (exsag.), proportionally widens laterally to base of genal spine; posterior border narrows adaxially. Glabella extends to anterior border, hourglass-shaped, strongly constricted at S1. Maximum width (tr.) of LA 1.3 to 1.6 times greater than basal glabellar width (tr.). Posterior

margin of glabella gently convex posteriorly. SO deep only abaxially, abaxial end slightly anterior to adaxial end. S1 deepest abaxially, oriented strongly anterolaterally abaxially. LO and L1 subtrapezoidal, narrowing anteriorly; axial furrow shallow or absent at lateral margins of L1. S2 deepest abaxially, gently convex anteriorly either side of sagittal axis, abaxial and adaxial ends on roughly transverse line. L2 subtrapezoidal, widens (tr.) slightly anteriorly. S3 deepest abaxially, oriented anterolaterally away from axis until contact with ocular lobes. L3 broadly transverse or weakly 'V'-shaped, lateral margins widen (tr.) anteriorly until contact with ocular lobes. LA hemispherical to transversely oblate, well inflated dorsally above extraocular area, slightly higher than posterior glabellar lobes; impinges onto anterior border; contact with L3 and ocular lobes marked by distinct break in slope. Axial node developed on LO (Figs 5G, 6A). Ocular lobes convex dorsally (tr.), strongly divergent, crescentic, tip widely separated from glabella, directed nearly straight posteriorly; posterior tip opposite midlength or anterior portion of L1 or S1, slightly shorter on larger cephalia (Fig. 6B); very short, shallow ocular furrow located abaxially on ocular lobe. Interocular area typically arched dorsally, rarely sloping down towards axial furrow (Fig. 6B), occasionally strongly inflated opposite L2 (Fig. 6E), width (tr.) opposite L2 slightly greater than that of ocular lobe. Width of extraocular area opposite posterior tip of ocular lobe approximately 1.5 times that of interocular area. Extraocular area with weak intergenal ridge, rarely also with very weak posterior ocular line (Fig. 6A). Terrace lines developed on cephalic doublure and ventral surface of genal spine (Figs 5J, 6E). A single specimen (Fig. 6F) preserves widely-spaced bertillon markings on LA. Hypostome unknown.

Thorax known from one specimen, preserving only first three segments (Fig. 5J). Width (tr.) of axis approximately equal to width (tr.) of inner pleural region on T1. Tiny axial node may be developed on T1, condition unknown on other segments. Inner pleural regions of T1 and T2 transverse, tapering distally; pleural spines sentate and divergent. T3 hyperpleural; length of pleural spine unknown but probably macrospinous or dolichospinous. Pleural furrows of all known segments well developed, more steep-sided adjacent to anterior pleural band; tapering to point short of pleural spine on T1 and T2, passing onto pleural spine of T3. Base of pleural spine of T3 bears bertillon markings dorsally. Rest of thorax and pygidium unknown.

*Ontogeny.* Specimens with sagittal cephalic

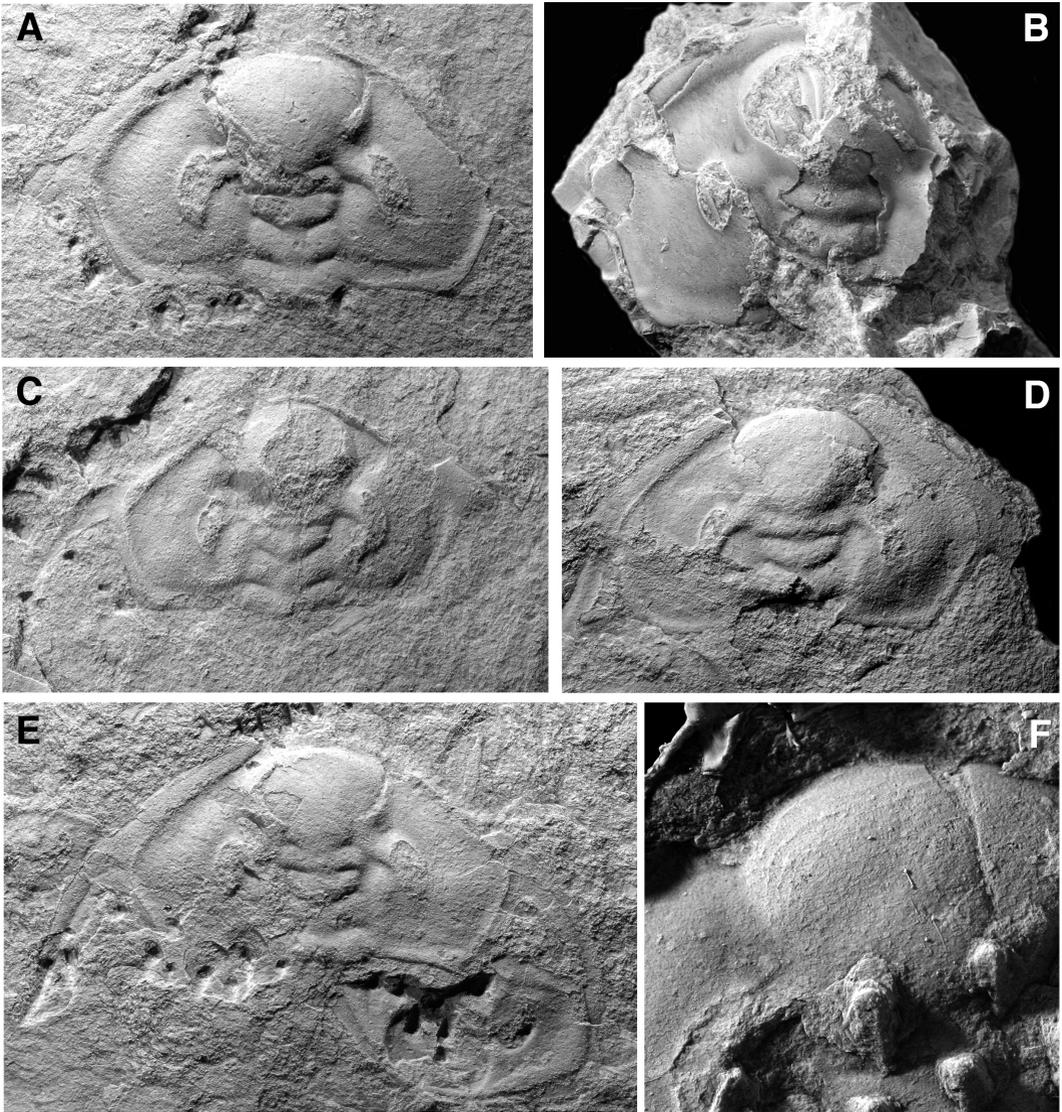


Fig. 6. Cephalons of *Paranephrolenellus besti* n. sp. in dorsal view. A, holotype cephalon, internal mould, UCR 10216.2, x3. B, incomplete and partially exfoliated cephalon preserved in limestone, FMNH PE58004, x3. C, slightly worn cephalon, internal mould, UCR 10218.13, x3. D, incomplete, coarsely preserved cephalon, internal mould, UCR 10218.4, x3. E, mostly complete cephalon, internal mould, UCR 10218.9, x3. F, details of bertillon markings on LA, latex cast of external mould, UCR 10218.25, x7. A, C-F from various stratigraphic levels at Klondike Gap, Chief Range, Nevada (see Appendix); B from ICS-1364, Toiyabe Range, Callahan Window, Lander County, Nevada.

lengths ranging from approximately 1.5 mm to 14.9 mm preserved in sandy carbonates and siltstones from Klondike Gap and Prospect Peak provide information regarding morphological changes in the cephalon over mid- to late stages of ontogeny.

The smallest known specimen (Fig. 5A) is coarsely preserved, but shows a progressive narrowing (tr.) of the glabella from LO to S3. L3 is subrectangular, laterally defined by an axial furrow which does not contact the adaxial margin

of the ocular lobe. A prominent intergenal ridge extends onto the base of the intergenal spine (length unknown), which is located at or adjacent to the anterior deflection in posterior cephalic margin. Preservation is of insufficient quality to determine whether this deflection represents an intergenal angle or an adgenal angle *sensu* Webster (in press). The interocular area is strongly inflated, with a summit higher than the dorsal surface of the ocular lobes; weak interocular nodes and furrows are present. The genal region is

poorly preserved, but genal spines appear to have been present, with bases developed approximately opposite the cephalic midlength.

A cephalon with sagittal length of 2.4 mm (Fig. 5B) shows a subtrapezoidal L3 (wider anteriorly), defined laterally by an axial furrow which contacts and is deflected adaxially (when traced anteriorly) by the ocular lobe. The glabella is most constricted at L2 or S2. The interocular area is arched dorsally, and bears no interocular nodes or furrows. Progressively larger cephalia demonstrate that LA expanded dorsally and proportionally lengthened, causing S3 to adopt a progressively more posterior orientation when traced adaxially from the contact with the ocular lobes (Figs 5C-I). Over the same ontogenetic interval, L3 widened (tr.) and L2 became progressively more trapezoidal in outline (wider anteriorly), such that the glabella became most constricted at S1. On some large cephalia (over 13 mm sagittal length) S2 shallows at the contact with the axial furrow (Fig. 6B), but S2 was never observed to be entirely isolated from the axial furrow. A weak axial node is occasionally present on L1 on cephalia up to 3.5 mm (questionably 3.9 mm) sagittal length, in addition to the node consistently present on LO. A slight swelling is present on the axis of L1 and L2 on specimens with sagittal glabellar length of up to 5.8 mm (Figs 5B, D, G); whether these slight swellings represent greatly reduced axial nodes or taphonomic artefact is unclear. A preglabellar field is absent on all known cephalia, although the anterior border furrow progressively narrows as LA enlarges during late ontogeny (a trend found in the late stages of ontogenetic loss of a preglabellar field in other taxa, e.g., *Bristolia* and *Arcuolenellus*; unpublished observations). The genal spines on cephalia smaller than 3.5 mm sagittal length are typically less advanced than on larger cephalia, the spine bases being opposite L1 or L2 (Figs 5C, E). This suggests an ontogenetic trend towards increasing advancement of the genal spines during cephalic development. There may also be an ontogenetic trend towards increased angularity of the adgenal angle, with an anterior deflection of the distal portion of the posterior cephalic border (relative to the proximal portion) of typically 45°-60° on small cephalia, and up to 80° on some larger cephalia (sagittal length greater than 13 mm). However, considerable variation in these features exists among similar-sized cephalia.

*Etymology.* Named for R. V. Best, for his work on the olenelloids of the Laurentian Cordillera.

*Holotype.* UCR 10216.2 (Fig. 6A).

*Other material examined.* FMNH PE58001-58005; ?UCR 10082.19; UCR 10216.1, 3, 4, 9, 12, ?13, 14, 18, ?40; UCR 10218.?1, 2-11, 13-17, 22, 24, 25, 47; USNM 15407 (two cephalia, in type lot of *Peachella iddingsi*); USNM 15412 (14 cephalia plus two poor specimens); USNM 56819g; USNM 137633 and USNM 137634 (specimens housed in the biological collections); 55 cephalia total. UCR 10216.18 (Fig. 5J) also shows the first three thoracic segments. Photographs of three additional cephalia from Emigrant Pass were provided by Ed Fowler (specimens in his private collection).

*Occurrence.* California: Nopah Range, Inyo County: Emigrant Pass, 52-54 m above the base of the Carrara Formation, Thimble Limestone Member (Fowler 1999). Nevada: Chief Range, Lincoln County: Klondike Gap, ?UCR 10082 (21.2 m below base of Combined Metals Member; a tentative identification), UCR 10216 (21 m below base of Combined Metals Member) and UCR 10218 (21.2-20.9 m below base of Combined Metals Member); all in the Delamar Member of the Pioche Formation. Eureka District, Eureka County: ICS-1010, float from below 1-2 m thick quartzite rib, east side of Prospect Peak; Walcott's (1910, 1912) locality 52, "arenaceous shales above the Prospect Mountain sandstones, summit of Prospect Mountain, Eureka District" (these strata are typically referred to the "Pioche Formation", but warrant distinct lithostratigraphic recognition). [USNM 15412 is a lot collection containing specimens from two localities. Specimens of *P. besti* in this lot are preserved in a sandy, micaceous limestone and were collected from Walcott's locality 52. However, USNM 15412 also includes specimens of *Olenellus gilberti* Meek in White, 1874, *O. terminatus*? Palmer, 1998, and *Olenellus* sp. indet. preserved in a lithology identical to the type lot of *O. gilberti* (collected from Walcott's [1910, 1912] locality 31a; Pioche Divide, Lincoln County, Nevada). The latter collection is from a stratigraphically higher horizon than the former.] Timpahute Range, Lincoln County: Walcott's (1910, 1912) locality 313g, a limestone from the southern end of the range. Toiyabe Range, Callahan Window, Lander County: ICS-1364, cephalic fragments in shaly limestone. All occurrences are in the upper *Bristolia* Zonule, Dyeran, Lower Cambrian, where the species co-occurs with *Peachella iddingsi*, *Olenellus nevadensis* and *Mesonacis fremonti* (Fig. 2). This is the stratigraphically youngest of the known species of *Paranephrolenellus*.

*Discussion.* Development of the base of the genal spines opposite L2, S2, or L3 distinguishes

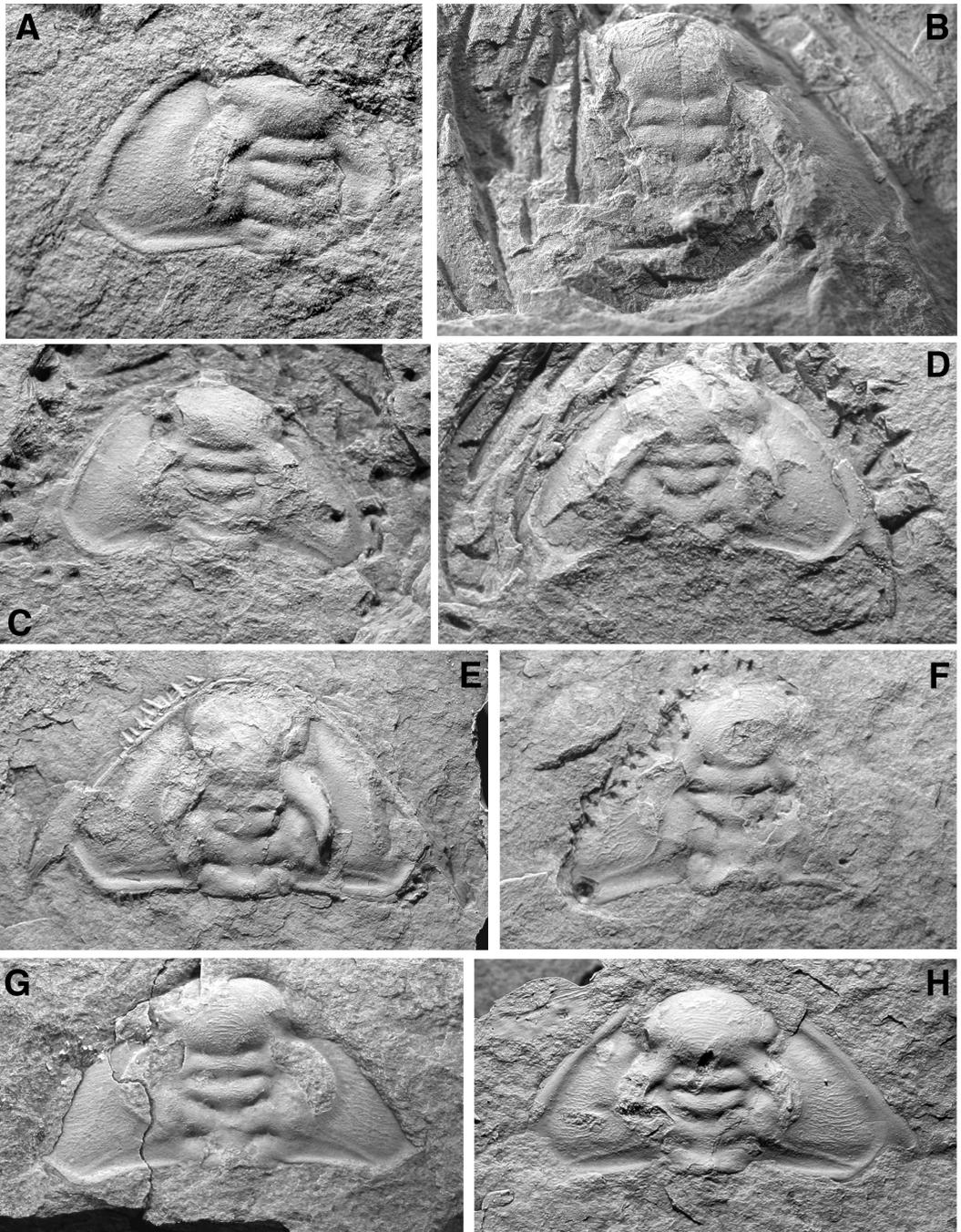


Fig. 7. Cephalons of *Paranephrolenellus klondikensis* n. sp. in dorsal view. A, relatively small morphologically mature cephalon, internal mould, FMNH PE58006, x5. B, incomplete, poorly preserved, relatively small morphologically mature cephalon showing prominent bertillon markings on LA, internal mould, UCR 10074.34, x4. C, internal mould, UCR 10075.33, x3. D, internal mould, UCR 10074.25, x3. E, almost complete cephalon, latex cast of external mould, FMNH PE58007, x3. F, incomplete cephalon showing prominent ornament, internal mould, UCR 10074.33, x3. G, partially obscured cephalon showing well preserved ornament, internal mould, FMNH PE58008, x3. H, cephalon with prominently developed ornament, latex cast of external mould, FMNH PE58009, x3. All from the 'Insolens Beds' at Klondike Gap, Chief Range, Nevada (see Appendix).

morphologically mature cephalo of *P. besti* from all closely related taxa. The most similar species is *P. klondikensis* n. sp., from which *P. besti* differs by possessing more advanced genal spines and a stronger adgenal angle. *Paranephrolenellus besti* also lacks the prominent extraocular genal caeca typical of *P. klondikensis*. *Bristolia anteros* Palmer in Palmer & Halley, 1979 differs from *P. besti* by having more advanced genal spines (bases opposite LA) and a pit-like S3 isolated from the axial furrow (similar to the condition seen in *Nephrolenellus*). Although the anterolateral cephalic border is moderately wide in *P. besti*, it is not dorsally inflated in the manner of *P. inflatus* n. sp.

Ontogenetic changes in the cephalon of *P. besti* are similar to those documented in *Nephrolenellus* (Webster in press), suggesting that at least some aspects of the four-phase subdivision of cephalic ontogeny recognised in the latter genus (Webster in press) may be applicable on a broader phylogenetic scale. The oculo-glabellar morphology of the smallest known cephalon of *P. besti* (Fig. 5A) is typical of similarly sized cephalo in early phase 3 of development in both *Nephrolenellus* species (*sensu* Webster in press). The subsequent proportional lateral expansion of L3 (with a progressive increase in the extent of anterolateral contact between the axial furrows and ocular lobes) is typical of similarly sized cephalo in early phase 4 of development in both *Nephrolenellus* species (*sensu* Webster in press), although in *P. besti* S3 retains contact laterally with the axial furrow rather than becoming an isolated dimple (i.e., the anterolateral portion of L3 does not merge with the posterolateral portion of LA). Other aspects of cephalic ontogeny shared between *P. besti* and the two *Nephrolenellus* species include: (1) the loss of interocular nodes and furrows from the interocular area during phase 3 of cephalic development; (2) the progressive loss of glabellar axial nodes (anteriormost first); (3) the progressive proportional expansion (in all dimensions) of LA during phase 4 of development; (4) the progressive reduction in proportional size of the intergenal spines (which are often lost at large cephalic size in *N. geniculatus* and *P. besti*); (5) the progressive anterior migration of the genal spine bases; and (6) the progressive increase in angularity of the adgenal angle. Very small cephalo of both *Nephrolenellus* species bear axial nodes on LO, L1, L2, and L3 (*N. multinodus* also bears a node on LA), which became progressively lost during phase 3 of development (see trend 2 above). Relatively small cephalo of *P. besti* bear an axial node on LO and L1 (and questionably L2; see above); larger cephalo bear a node only on LO. It is unknown whether *P. besti* cephalo equivalent

in size to *Nephrolenellus* cephalo in phase 1 or 2 of development bore axial nodes anterior to L1 (or L2). Notable differences in cephalic ontogeny between *P. besti* and the two *Nephrolenellus* species include: (1) the interocular area being of higher dorsal relief than the summit of the ocular lobes at small cephalic size in *P. besti*; and (2) the lack of merger of the anterolateral portion of L3 and the posterolateral portion of LA at large cephalic size in *P. besti*.

Large, mildly tectonised specimens from Emigrant Pass (Nopah Range, Inyo County, California) assigned to “*Bristoliinae* n. gen. 1 n. sp. 1” by Fowler (1999) are here assigned to *P. besti*. The Emigrant Pass specimens possess slightly more advanced genal spines (bases opposite S3 or the posterior portion of LA) and S2 is shallow at its contact with the axial furrow. Such differences are considered ontogenetic in nature (see above).

Best (unpublished work) examined specimens now assigned to *P. besti* collected from USNM locality 313g (Timpahute Range, Groom district, Nevada) and informally referred to the species as “*Bristolia glabrata* n. sp.” (informally proposed holotype USNM 137633). However, the stratigraphic and geographic data associated with the Timpahute Range specimens are very poor. The holotype of *P. besti* designated herein was collected *in situ* from a well documented section (Fig. 2, Appendix).

Four specimens of “*Olenellus howelli*” from Prospect Peak originally figured by Walcott (1884, pl. 9, fig. 15b, pl. 21, figs 1, 3-4) were reassigned by Palmer (in Palmer & Halley 1979, p. 71) to a new species now recognised as *P. besti*. However, one of these specimens (USNM 56819f; Walcott 1884, pl. 21, fig. 2; 1886, pl. 20, fig. 1d; 1890, pl. 86, fig. 1d; 1910, pl. 37, fig. 10) is here assigned to *Bristolia anteros* on the grounds that the base of the genal spine is more advanced (developed opposite mid-LA), and therefore the anterior cephalic border is straighter, than in *P. besti*. Two specimens of *P. besti* occur on a slab bearing *Peachella iddingsi* in the type lot of that species (USNM 15407; Fig. 5C, F), also collected from Prospect Peak.

***Paranephrolenellus klondikensis* new species** (Figs 3B, 7-10)

2001 *Nephrolenellus?* n. sp.; Webster *et al.*, p. 111, 113.

*Diagnosis.* Species of *Paranephrolenellus* with strong adgenal angle (deflecting posterior margin of cephalon anteriorly by 40°-70°), base of genal spine opposite LO, SO, or L1; S2 gently convex

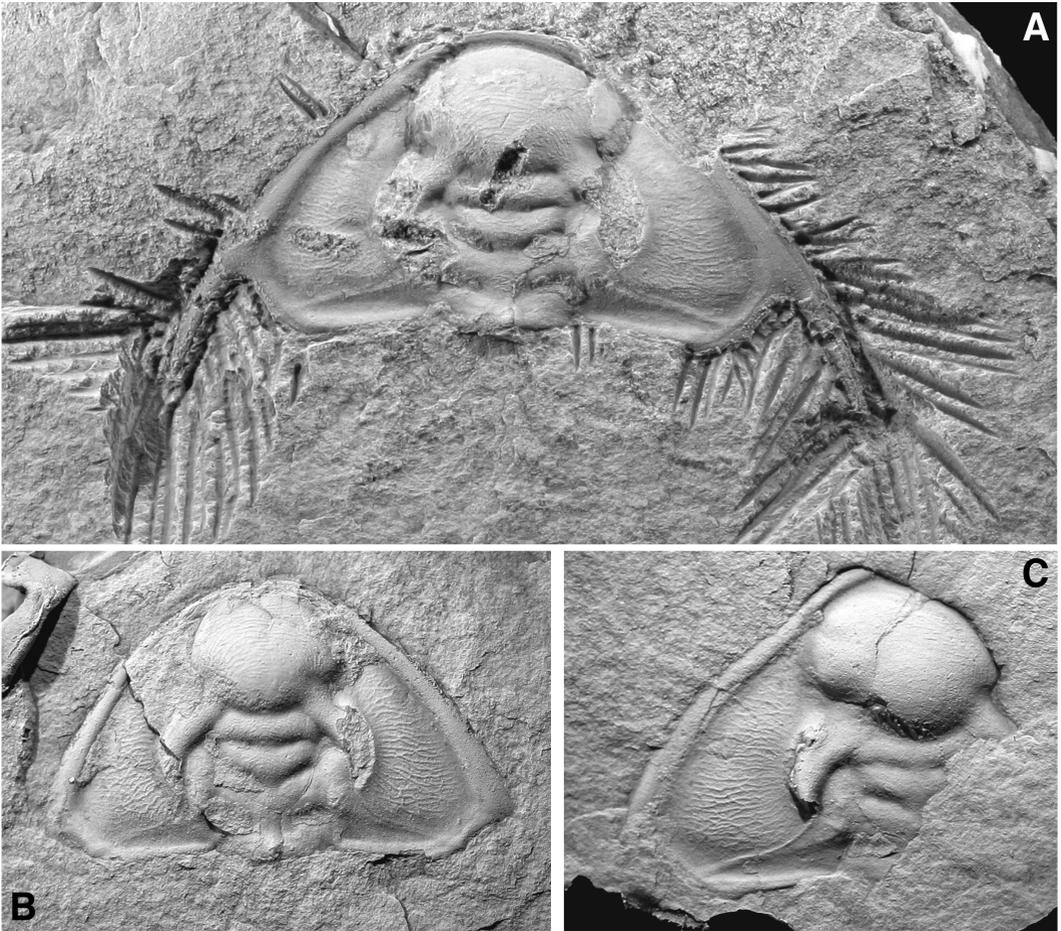


Fig. 8. Cephalon of *Paranephrolenellus klondikensis* n. sp. in dorsal view. A, holotype cephalon, internal mould, UCR 10074.237, x4. B, cephalon with well preserved ornament, latex cast of external mould, FMNH PE58000, x3. C, incomplete cephalon with well preserved ornament, latex cast of external mould, FMNH PE58010, x3. All from the 'Insolens Beds' at Klondike Gap, Chief Range, Nevada (see Appendix).

anteriorly either side of sagittal axis, abaxial and adaxial ends on roughly transverse line; L3 roughly transverse to weakly 'M'-shaped. Fourteen prothoracic segments; T3 weakly hyperpleural, macrospinous, pleural spine stout, broad (tr.), blunt-tipped; long axial spine on T15.

*Description* (mature morphology). Cephalon semi-parabolic to sub-pentagonal in outline; proximal portion of posterior cephalic margin angled posterolaterally away from axial furrow by 5°-20° relative to transverse line, distal portion flexes anteriorly by 40°-70° relative to proximal portion at distinct adgenal angle located approximately two-thirds distance along posterior cephalic margin from axial furrow to base of genal spine. Greatest observed cephalic length approximately 14.3 mm (sag.). Genal spine slender, base opposite LO, SO, or L1 (Figs 7E,

9A, 10A) at point of maximal cephalic width (excluding spines), length slightly more than half sagittal length of cephalon, proximally follows curvature of anterolateral cephalic border, distally curves more strongly posteriorly. Small intergenal spine situated approximately one-third of distance between adgenal and genal angles (Figs 10C, 9F), reduced to small node or swelling on some large individuals (Fig. 8A). Cephalic border well defined around entire margin by distinct border furrow, rounded dorsally anteriorly, flattens slightly in profile abaxially; width of anterior border opposite junction of ocular lobe with LA approximately one-half to two-thirds length of LO (exsag.), proportionally widens laterally to base of genal spine; posterior border narrows adaxially. Glabella extends to anterior border, hourglass-shaped, strongly constricted at S1. Maximum width (tr.) of LA 1.35 to 1.75 times greater than basal glabellar width (tr.). Posterior margin of

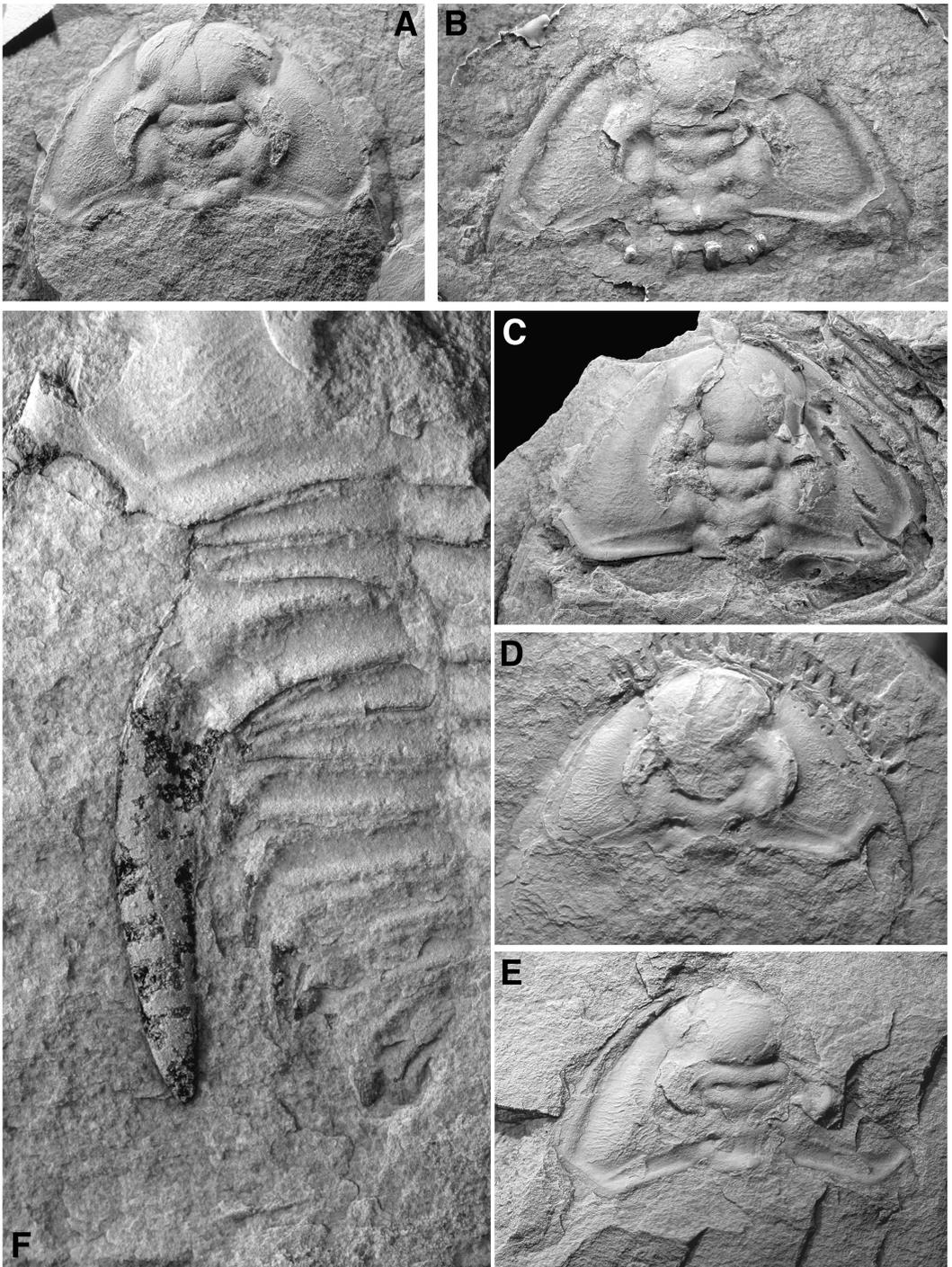


Fig. 9. A-E, cephalons of *Paranephrolenellus klondikensis* n. sp. in dorsal view. A, internal mould, FMNH PE58011, x2.5. B, latex cast of external mould, UCR 10074.23, x2.5. C, internal mould, UCR 10074.4, x2.5. D, internal mould, FMNH PE58012, x2.5. E, partially obscured internal mould, FMNH PE58013, x2.5. F, details of left thoracic pleural region and T3 pleural spine, internal mould, UCR 10076.3, x7 (see also Fig. 10C). All from the 'Insolens Beds' at Klondike Gap, Chief Range, Nevada (see Appendix).

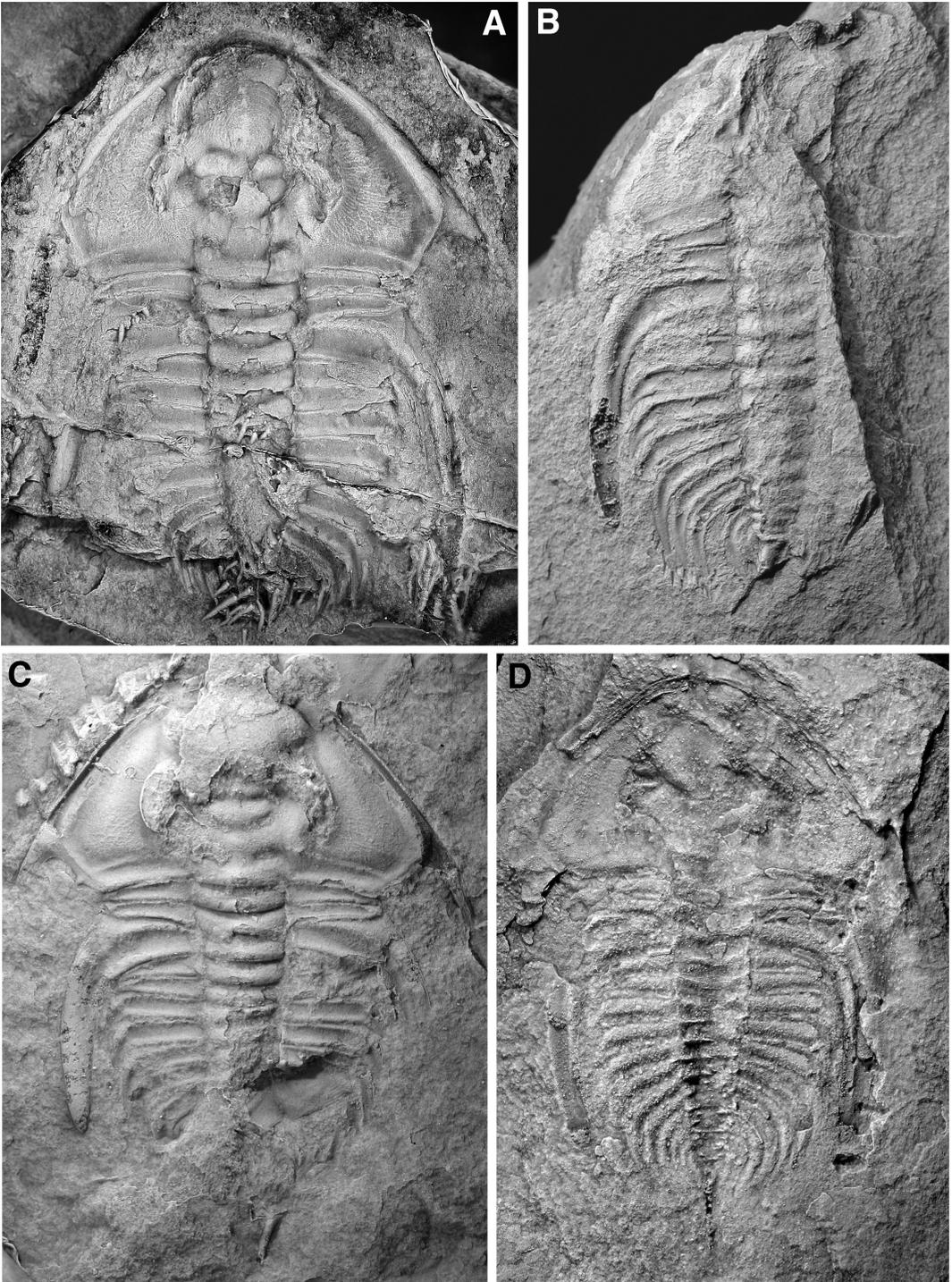


Fig. 10. Articulated dorsal exoskeletons of *Paranephrenellus klondikensis* n. sp. A, cephalon and partial prothorax, latex cast of external mould, FMNH PE58014, x3. B, poorly preserved cephalon, prothorax, and first opisthothoracic segment, internal mould, FMNH PE58015, x3. C, cephalon and partial prothorax, latex cast of external mould, UCR 10076.3, x3 (see also Fig. 9F). D, coarsely preserved cephalon, prothorax, first opisthothoracic segment, and impression of hypostome in life position, composite mould, UCR 10076.2, x3. All from the “*Insolens Beds*” at Klondike Gap, Chief Range, Nevada (see Appendix).

glabella straight (Fig. 9B) or gently convex posteriorly (Fig. 8B). SO deep only abaxially, abaxial end slightly anterior to adaxial end. S1 deepest abaxially, oriented strongly anterolaterally abaxially. LO and L1 subtrapezoidal, narrowing anteriorly; axial furrow shallow or absent at lateral margins of L1. S2 deepest abaxially, shallows at contact with axial furrow in some individuals (Fig. 9E), gently convex anteriorly either side of sagittal axis, abaxial and adaxial ends on roughly transverse line. L2 subtrapezoidal, widens (tr.) slightly anteriorly. S3 deepest abaxially, oriented slightly anterolaterally away from axis until contact with ocular lobes. L3 broadly transverse or weakly "M"-shaped (with distal tips slightly wrapping around anterolateral margins of L2), distal portion between L2 and ocular lobes shorter (exsag.) than axial portion. LA hemispherical to transversely oblate, well inflated dorsally above extraocular area, slightly higher than posterior glabellar lobes; impinges onto and slightly deflects anterior border; contact with L3 and ocular lobes marked by distinct break in slope. Axial node developed on LO. Ocular lobes convex dorsally (tr.), strongly divergent, crescentic, tip widely separated from glabella, directed nearly straight posteriorly; posterior tip opposite midlength or anterior portion of L1; very short, shallow ocular furrow rarely located abaxially on ocular lobe (Fig. 8B), although typically not developed. Interocular area arched dorsally, inflated into distinct swelling opposite L1, rarely also into second swelling opposite L2 (Fig. 7E); width (tr.) opposite L2 about equal to that of ocular lobe. Width of extraocular area opposite posterior tip of ocular lobe approximately twice that of interocular area. Extraocular area with intergenal ridge and posterior ocular line, which merge into single ridge before passing over posterior border (Figs 7F-G, 8A, C, 9D). Weak genal ridge occasionally developed (Fig. 7G). Genal caeca prominently developed on extraocular and rarely on interocular area (Fig. 7H). Bertillon markings on LA, occasionally extending onto anterior portion of ocular lobes and axial portion of L3, rarely also onto axes of L2, L1, and LO (Figs 7H, 8A-B, 9C). Terrace lines developed on cephalic doublure and genal spine. Hypostome present on several specimens, but preservation too poor for details to be seen (Fig. 10D).

Prothorax of 14 segments; width (tr.) of axis approximately equal to width (tr.) of inner pleural on T1, gently tapering posteriorly. Axial nodes developed on each segment at least as far posteriorly as T4 (Fig. 10C), condition on T5 and more posterior segments unknown. Inner pleural regions of T1 and T2 transverse, taper distally; pleural spines sentate and divergent. T3 weakly

hyperpleural; macrospinous spine stout, broad (tr.), blunt-tipped, terminates approximately opposite end of prothoracic axis. Inner pleural regions of T4 and to lesser extent T5 taper distally; pleural spines sentate, posterolaterally divergent. Inner pleural regions of T6 to T8 transverse, parallel-sided, with straight margins. Inner pleural regions of T9 to T14 increasingly divergent to pendent, parallel-sided, margins increasingly curved in more posterior segments. Pleural spines of T6 to T14 falcate; increasing in length posteriorly to T12, spines of T13 and T14 progressively decrease slightly in length. Pleural furrows of all segments well developed, more steep-sided adjacent to anterior pleural band; taper to point short of pleural spine on T1, T2, T4 and T5, pass onto pleural spine of T3 and T6 to T14. Pleural spines of T3, T5 to T7 and T10 to T14 occasionally bear granulations or bertillon markings dorsally (Figs 9F, 10C). T3 occasionally bears terrace lines ventrally. Axis of T15 bears long axial spine (Figs 10B, D), full length unknown. Rest of opisthothorax and pygidium unknown.

*Ontogeny.* Cephalia of this species range from approximately 6 mm to 14.3 mm in sagittal length. The smallest cephalia (Fig. 7A-D) exhibit lateral extension (tr.) of L3 beyond the abaxial margins of L2, with the anterolateral margins of L3 contacting (and being deflected by) the adaxial margins of the ocular lobes. This oculo-glabellar morphology is typical of similarly sized cephalia of *Nephrolenellus* in phase 4 of cephalic development (*sensu* Webster, in press), although in *P. klondikensis* S3 retains contact laterally with the axial furrow rather than becoming an isolated dimple (i.e., the anterolateral portion of L3 does not merge with the posterolateral portion of LA). Little allometry appears to take place during this late portion of cephalic ontogeny in *P. klondikensis*. An axial node is present only on LO, and the presence or absence of axial nodes on more anterior glabellar lobes during earlier ontogeny is unknown. On all known cephalia, LA touches the anterior cephalic border and the border furrow is narrow; there is no trace of a preglabellar field (although secondary loss of such a feature is common in closely related taxa, e.g., *Bristolia*, *Nephrolenellus* and *Arcuolenellus*; unpublished observation).

*Etymology.* Named for Klondike Gap, Chief Range, where the species was first discovered.

*Holotype.* UCR 10074.237 (Fig. 8A).

*Other material examined.* FMNH PE58000,

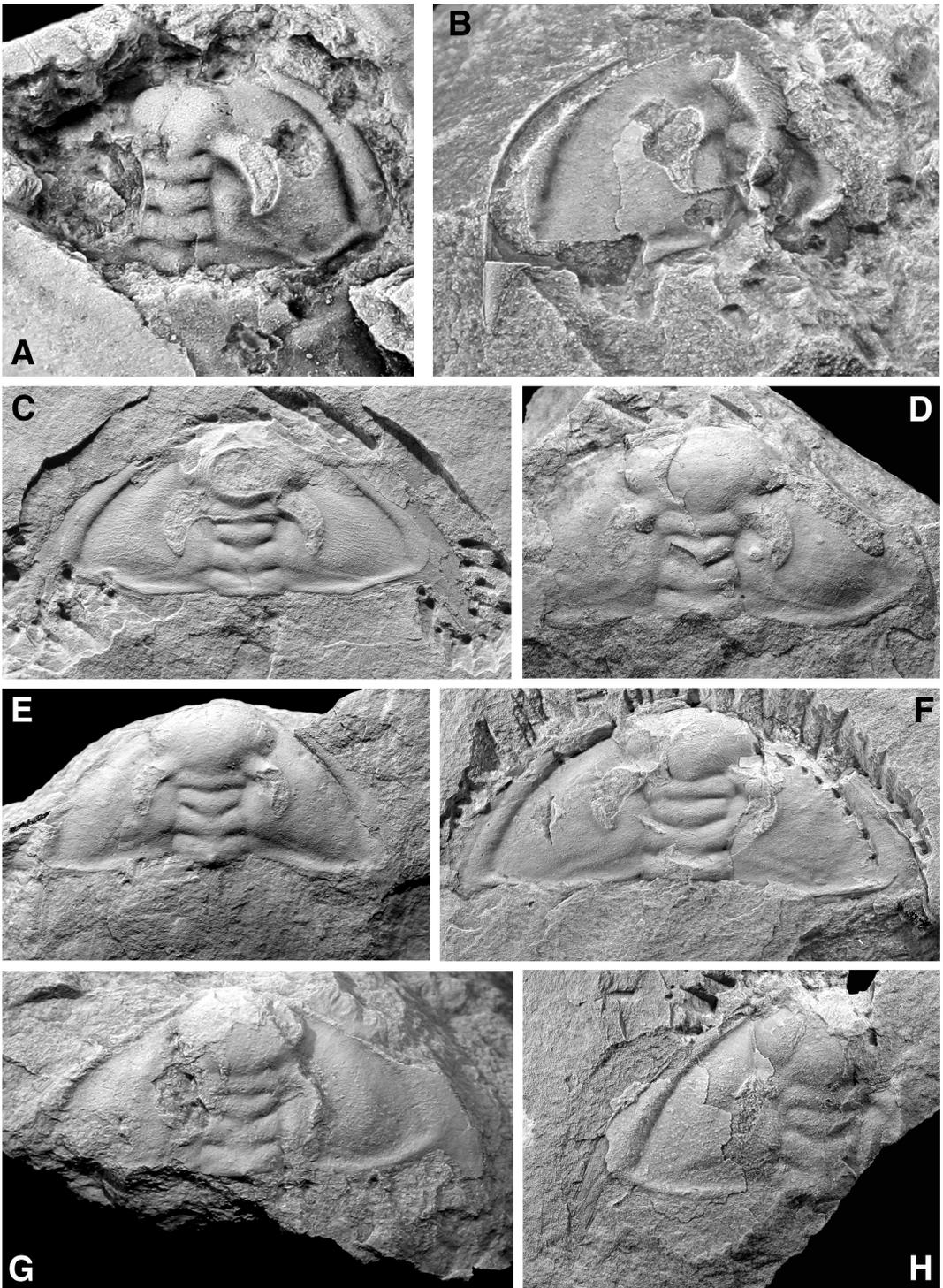


Fig. 11. Cephalons of *Paranephrolenellus inflatus* n. sp. in dorsal view. A, small, incomplete cephalon, composite mould, UCR 10574.3, x12. B, small, incomplete and crushed cephalon, composite mould, UCR 10565.4, x8. C, holotype cephalon, internal mould, UCR 10077.49, x3. D, incomplete cephalon, internal mould, UCR 10077.53, x2.5. E, almost complete cephalon, internal mould, UCR 10080.4, x2. F, internal mould, UCR 10080.13, x2.5. G, coarsely preserved internal mould, UCR 10077.3, x2.5. H, incomplete internal mould, UCR 10080.26, x2.5. A-B from the Latham Shale, Marble Mountains, San Bernardino County, California. C-H from various stratigraphic levels at Klondike Gap, Chief Range, Nevada (see Appendix).

FMNH PE58006-15; ICS-1098.2, 7-11, 16-21, 23; UCR 10073.50; UCR 10074.4, 12, 21, 23-38, 44, 45, 47, 48, 197, 212, 224; UCR 10075.33-35; UCR 10076.1-3, 6, 7, 9; YPM 163844: 62 cephalia total. FMNH PE58014, FMNH PE58015, ICS-1098.2, and UCR 10076.1-3 also preserve thoracic information.

*Occurrence.* Nevada: Chief Range, Lincoln County: Klondike Gap, UCR 10073 (62 m above top of Zabriskie Quartzite), and correlative horizons ICS-1098, ICS-1172, UCR 10074, UCR 10075, and UCR 10076 (39.5 m below base of Combined Metals Member). Poorly preserved specimens of *Paranephrolenellus* from a correlative horizon at Ruin Wash may also represent this species. Highland Range, Lincoln County: Comet Mine, Log Cabin Mine, and One Wheel Canyon sections. All occurrences are in the Middle *Bristolia* Zonule, Delamar Member of the Pioche Formation, Dyeran, Lower Cambrian, where the species co-occurs with *Bristolia insolens*, *B. bristolensis*, *Olenellus nevadensis*, and *Mesonacis fremonti* (Fig. 2). This is the stratigraphically oldest of the known species of *Paranephrolenellus*.

*Discussion.* Differences between *P. klondikensis* and *P. besti* n. sp. are discussed under the latter species. Lack of an inflated cephalic border at the base of the genal spines differentiates *P. klondikensis* from *P. inflatus* n. sp.

*Paranephrolenellus klondikensis* is similar to *Bolbolenellus euryparia*, from which it differs most obviously by possessing slightly shorter and more divergent ocular lobes (the posterior tips of which are more widely separated from the lateral margin of L1; Fig. 4B-C), in lacking a deep axial furrow at the lateral margin of L1, and in L3 morphology (which is much more strongly 'M'-shaped in *Bo. euryparia*, with S2 correspondingly more strongly convex anteriorly). L2 is proportionally longer in *P. klondikensis* (typically 8-10% of glabella length) than in *Bo. euryparia* (typically 7-8% of glabella length), and LA is also typically proportionally wider in *P. klondikensis*, although this may be exaggerated through taphonomic compaction.

The thorax of *P. klondikensis* is unique among known biceratopsids in possessing stout, blunt-ended pleural spines on T3 (Figs 9F, 10B-D).

***Paranephrolenellus inflatus*** new species (Figs 3C, 11-12)

1884 *Olenellus howelli* (part); Walcott, pl. 9, fig. 15, pl. 21, fig. 6 only.

1886 *Olenellus gilberti* (part); Walcott, pl. 20,

figs 1b, 1i only;

1890 *Olenellus gilberti* (part); Walcott, pl. 86, figs 1b, 1i only.

1910 *Olenellus fremonti* (part); Walcott, pl. 37, figs 13-14 only;

1912 *Olenellus fremonti* (part); Walcott, p. 140, 201 (included within concept of "*Olenellus fremonti*" from locality 52);

?1936 *Mesonacis fremonti* [sic] (part); Grabau, p. 67, 133 (probably included within concept of "*Mesonacis fremonti*" from the Eureka district).

1952 *Olenellus (Fremontia) fremonti* (part); Lochman in Cooper *et al.*, p. 93 (reference to Walcott, 1910, pl. 37, fig. 13).

?1956 *Olenellus fremonti* (part); Nolan *et al.*, p. 8 (probably included within concept of "*Olenellus fremonti*" from Prospect Peak).

1979 another undescribed species; Palmer & Halley, p. 71 (reference to Walcott, 1910, pl. 37, fig. 14).

*Diagnosis.* Species of *Paranephrolenellus* with weak adgenal angle developed approximately half distance along posterior cephalic margin from axial furrow to base of genal spine, base of genal spines opposite or slightly posterior to LO; cephalic border prominently inflated at base of genal spines; axial furrow shallow or absent at lateral margins of L1; S2 gently convex anteriorly either side of sagittal axis, abaxial and adaxial ends on roughly transverse line; L3 roughly transverse.

*Description* (mature morphology). Cephalon semi-parabolic in outline; proximal portion of posterior cephalic margin angled posterolaterally away from axial furrow by 3°-21° relative to transverse line, distal portion flexes anteriorly by 10° to 35° relative to proximal portion at distinct adgenal angle located approximately half distance along posterior cephalic margin from axial furrow to base of genal spine. Greatest observed cephalic length approximately 14.3 mm (sag.). Genal spine stout, pointed, base opposite LO (Figs 11C, G, 12C) or slightly posterior to LO (Figs 11E, F, 12E) at point of maximal cephalic width (excluding spines), length slightly more than half sagittal length of cephalon, curvature follows that of anterolateral cephalic border. Small intergenal node situated approximately halfway between adgenal and genal angles. Cephalic border well defined around entire margin by distinct border furrow, rounded dorsally anteriorly, flattens slightly in profile abaxially; width of anterior border opposite junction of ocular lobe with LA approximately two-fifths to three-fifths length of LO (exsag.). Lateral cephalic border and

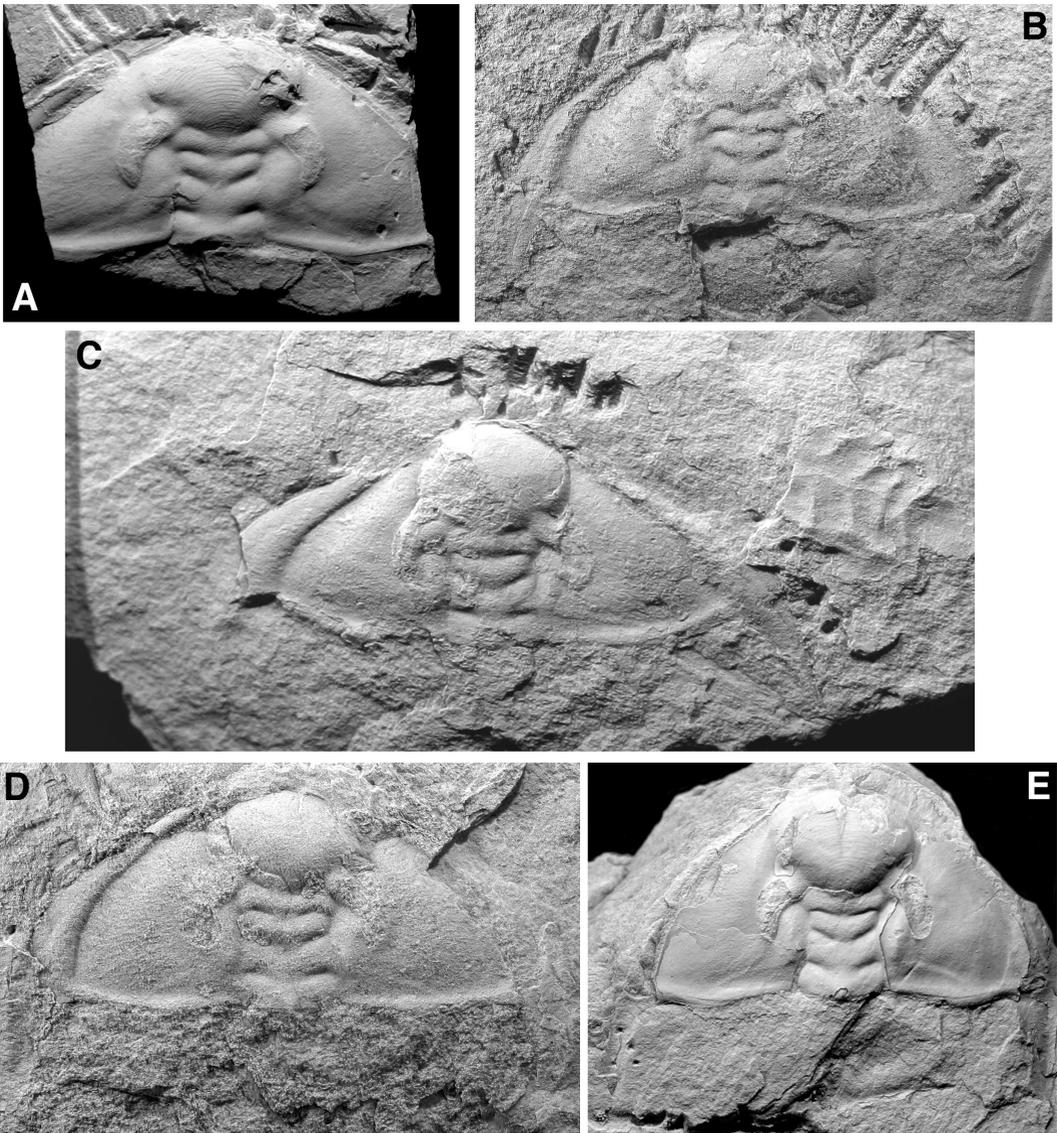


Fig. 12. Cephalons of *Paranephrenellus inflatus* n. sp. in dorsal view. A, finely preserved but incomplete internal mould, UCR 10080.1, x2.5. B, coarsely preserved internal mould, UCR 10080.25, x2.5. C, internal mould, UCR 10077.51, x3. D, internal mould, UCR 10077.45, x2.5. E, finely preserved, almost complete internal mould, UCR 10080.2, x2. All from various stratigraphic levels at Klondike Gap, Chief Range, Nevada (see Appendix).

base of genal spine distinctly inflated dorsally and laterally posterior to point opposite lateral margin of L3, maximum inflation at base of genal spine; width (tr.) of border at point of maximum inflation approximately twice length (exsag.) of LO. Posterior border narrows adaxially. Glabella extends to anterior border, hourglass-shaped, strongly constricted at S1. Maximum width (tr.) of LA 1.35 to 1.75 times greater than basal glabellar width (tr.). Posterior margin of glabella straight (Fig. 11C) or gently convex posteriorly (Figs 11E, 12B, E). SO deep only abaxially, abaxial

end slightly anterior to adaxial end. S1 deepest abaxially, oriented strongly anterolaterally abaxially. LO and L1 subtrapezoidal, narrowing anteriorly; axial furrow shallow or absent at lateral margins of L1. S2 deepest abaxially, gently convex anteriorly either side of sagittal axis, abaxial and adaxial ends on roughly transverse line. L2 subtrapezoidal, widens (tr.) slightly anteriorly. S3 deepest abaxially, oriented slightly anterolaterally away from axis until contact with ocular lobes. L3 broadly transverse or weakly "M"-shaped, widens (tr.) slightly anteriorly until

contact with ocular lobes. LA transversely oblate, well inflated dorsally above extraocular area, slightly higher than posterior glabellar lobes; impinges onto and slightly deflects anterior border; contact with L3 and ocular lobes marked by distinct break in slope. Axial node developed on LO. Ocular lobes convex dorsally (tr.), strongly divergent, crescentic, tip widely separated from glabella, directed nearly straight posteriorly; posterior tip opposite midlength or anterior portion of L1; very short, shallow ocular furrow located abaxially on ocular lobe. Interocular area gently arched dorsally (may appear shelf-like on taphonomically compacted specimens), width (tr.) opposite L2 about equal to that of ocular lobe. Width of extraocular area opposite posterior tip of ocular lobe approximately 2.5 times that of interocular area. Extraocular area typically with intergenal ridge and posterior ocular line, which merge into single ridge before passing over posterior border. Weak genal ridge occasionally developed (Figs 11C, 12C, D). Genal caeca developed on extraocular area (Fig. 11C, D). Interocular area occasionally bears faint “wrinkled” ornament of bertillon markings or granulations (Figs 11C, 12A). Bertillon markings on LA, L3, L2, and rarely axis of L1, occasionally also extending onto anterior portion of ocular lobes (Fig. 12A) and rarely developed dorsally on posterior border between genal and intergenal spines. Terrace lines developed on cephalic doublure and genal spine. Hypostome, thorax, and pygidium unknown.

*Ontogeny.* Observed cephalia range from approximately 2.6 mm to 14.3 mm sagittal length. The smallest known cephalon (Fig. 11A) is incomplete, but clearly shows the inflated cephalic border at the base of the genal spine. L3 is slightly wider (tr.) than L2, and the anterolateral margin of L3 abuts against the adaxial margin of the ocular lobe. An intergenal ridge and posterior ocular line cross the posterior cephalic border and run onto a small intergenal spine (length unknown) located just distal to a weak adgenal angle. An axial node is developed on LO. The frontal area is not preserved, but a small preglabellar field was probably present (based on an estimated projection of the curvature of the anterolateral cephalic border). The interocular area is strongly arched opposite S1. A slightly larger cephalon (Fig. 11B) is crushed, but shows a markedly inflated lateral cephalic border and genal spine base, and bertillon markings on at least LA, L3, and L2. Terrace lines are present on the cephalic doublure. Over the known portion of ontogeny, LA inflated dorsally and expanded laterally, and both L3 and L2 widened (tr.), particularly

anteriorly.

*Etymology.* Named for the distinct inflation of the lateral cephalic border and base of the genal spines.

*Holotype.* UCR 10077.49 (Fig. 11C).

*Other material examined.* UCR 10077.1-4, 45, 47, 51-54, ?59, 67, 73-75; UCR 10079.1, ?2; UCR 10080.1, 2, 4, 7-9, 11, 13, 16, 17, 25, 26, 46; UCR 10565.4; UCR 10574.3; USNM 56819i, USNM 56819j: 35 cephalia total.

*Occurrence.* California: Marble Mountains, San Bernardino County: UCR 10565 (1.3-1.4 m above marker bed K of LaGrange [2002]) in the Latham Shale at the southern end of the range; UCR 10574 (2.3-2.5 m above marker bed K of LaGrange [2002]) in the Latham Shale at the southern end of the range. Nevada: Chief Range, Lincoln County: Klondike Gap, UCR 10077 (2 m above *Bristolia insolens* beds; ?64 m above top of Zabriskie Quartzite), UCR 10079 (35.5 m below base of Combined Metals Member), and UCR 10080 (4.5 m above *B. insolens* beds; ?66.5 m above top of Zabriskie Quartzite); all in the Delamar Member of the Pioche Formation. Eureka District, Eureka County: Walcott’s (1910, 1912) locality 52, “arenaceous shales above the Prospect Mountain sandstones, summit of Prospect Mountain, Eureka District” (these strata are typically referred to the “Pioche Formation”, but warrant distinct lithostratigraphic recognition). All occurrences are in the middle to upper *Bristolia* Zonule, Dyeran, Lower Cambrian, where the species range overlaps with that of *Bristolia bristolensis*, *Olenellus nevadensis*, *Mesonacis fremonti*, *Bristolia harringtoni* Lieberman, 1999 (the stratigraphically “late occurrence”; Webster *et al.*, 2003), and *Bristolia* aff. *fragilis* A. *Paranephrolenellus inflatus* is found stratigraphically above *P. klondikensis* n. sp. and below *P. besti* n. sp. (Fig. 2).

*Discussion.* The elongate (tr.) cephalic outline and the distinctly inflated cephalic border at the base of the barely advanced genal spines differentiate *P. inflatus* from all other closely related species. The inflation of the base of the genal spines is reminiscent of the inflated genal spines of *Peachella* species. However, in *Peachella* species the glabella is effaced at morphological maturity, the ocular lobes do not strongly diverge from the lateral margins of the glabella (and the interocular area is therefore much narrower), and the genal spines are paddle-shaped and blunt-tipped (except in a newly discovered species, to be described

elsewhere).

The oculo-glabella morphology of the smallest known *P. inflatus* cephalon is typical of similarly sized cephalons of *Nephrolenellus* in early phase 4 of cephalic development (*sensu* Webster in press). The ontogenetic expansion (in all dimensions) of LA, and the lateral expansion of L3 and L2, is typical of other *Paranephrolenellus* and *Nephrolenellus* species. In contrast to *P. besti* n. sp. and both *Nephrolenellus* species, no traces of axial nodes on glabella lobes anterior to LO are known on cephalons of *P. inflatus* at any size (of course, the presence or absence of such structures during earlier ontogenetic stages cannot be determined). As in all other *Paranephrolenellus* species (and unlike both *Nephrolenellus* species), the anterolateral portion of L3 does not merge with the posterolateral portion of LA at large cephalic size (and S3 therefore retains contact with the axial furrow) in *P. inflatus* n. sp.

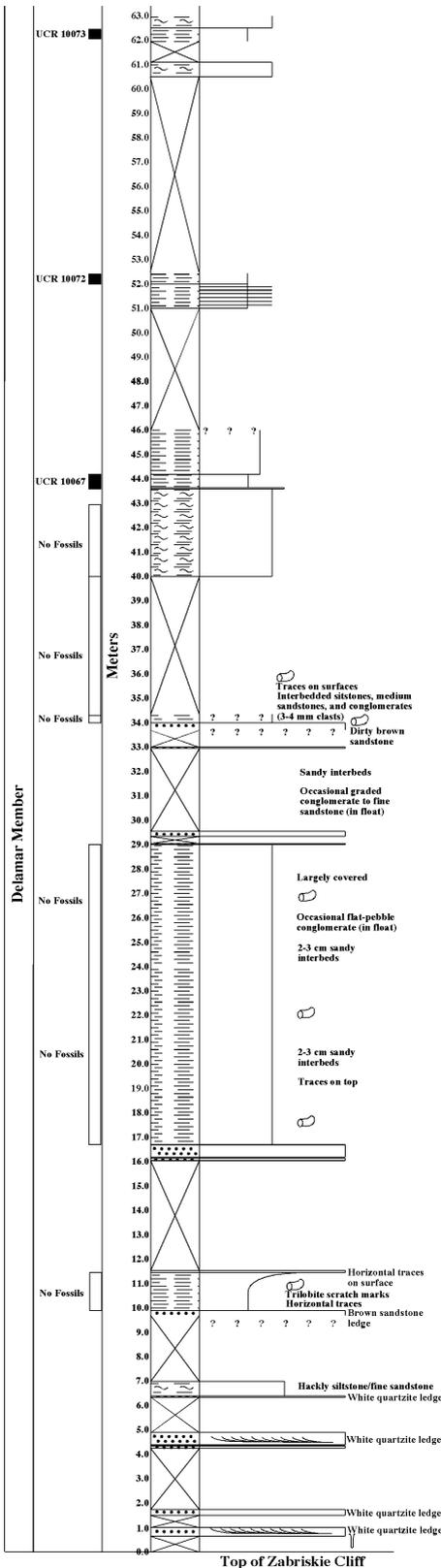
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**APPENDIX**

The lithostratigraphy and trilobite occurrences within each of the five partially overlapping measured sections (Fig. 1B) used to construct the composite biostratigraphic range chart (Fig. 2) are detailed below (also Figs 13-17). The stratigraphic distance above or below useful marker horizons (e.g., the ‘*Insolens Beds*’; see text) is given for each collection.

**Section A (Fig. 13)**

37°45.138’ N, 114°33.558’ W. Section measured from top of Zabriskie Quartzite cliff. The lowest portion of the section (0-40 m) youngs in a downslope direction on a hillside and was difficult to accurately measure (although repeated measurements were taken to check for consistency). The section covers approximately the lower two-thirds of Delamar Member.

UCR 10067: 44 m above top of Zabriskie Quartzite cliff, 18 m below ‘*Insolens Beds*’.

- Mesonacis fremonti*
- Olenellus clarki*
- Olenellus* sp. indet.
- Olenelloid sp. indet.

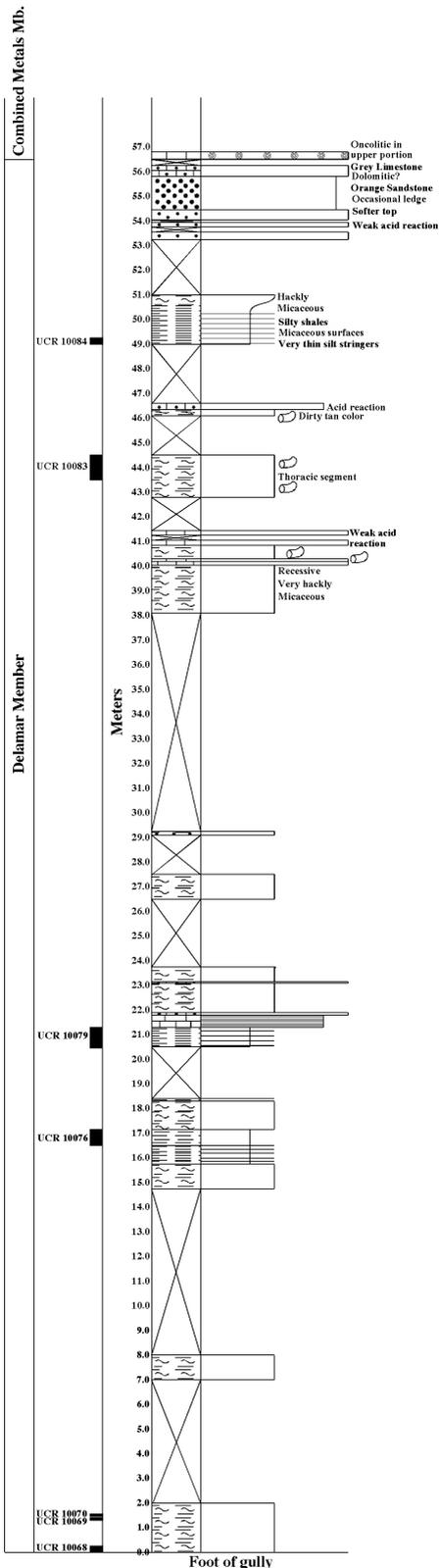
UCR 10072: 52 m above top of Zabriskie Quartzite cliff, 10 m below ‘*Insolens Beds*’.

- Bristolia harringtoni*
- Bristolia* sp. indet.
- Mesonacis fremonti*
- Mesonacis* sp. A
- Olenellus clarki*
- Olenelloid sp. indet.

UCR 10073: 62 m above top of Zabriskie Quartzite cliff, the ‘*Insolens Beds*’.

- Bristolia bristolensis*
- Bristolia insolens*
- Bristolia* sp. indet.
- Mesonacis fremonti*
- Olenellus nevadensis*
- Paranephrolenellus klondikensis*
- Olenelloid sp. indet.

Fig. 13. Lithostratigraphic details of measured section A at Klondike Gap, Chief Range, Lincoln County, Nevada. See Fig. 1 for location of section. See Fig. 16 for key to symbols and lithologies. Black bars to the left of the metre scale indicate provenance of stratigraphically constrained fossil collections housed in the Geology Museum, University of California, Riverside (UCR); empty bars indicate intervals of failed searches for body fossils. Trilobite assemblages for each collection are listed in the Appendix.



**Section B** (Fig. 14)

37°44.733' N, 114°33.293' W. Section measured from top surface of prominent bedding plane exposed in foot of gully. The section covers approximately the upper two-thirds of the Delamar Member and the base of Combined Metals Member.

UCR 10068: Foot of gully, 0 m in section, 56.5 m below base of Combined Metals Member, 17 m below 'Insolens Beds'.

*Mesonacis fremonti*

*Olenellus clarki*

Olenelloid sp. indet.

UCR 10069: 1.4 m above base of section, 55.1 m below base of Combined Metals Member, 15.6 m below 'Insolens Beds'.

*Mesonacis fremonti*

Olenelloid sp. indet.

UCR 10070: 1.5 m above base of section, 55 m below base of Combined Metals Member, 15.5 m below 'Insolens Beds'.

*Mesonacis fremonti*

*Olenellus clarki?*

*Olenellus* sp. indet.

UCR 10076: 17 m above base of section, 39.5 m below base of Combined Metals Member, the 'Insolens Beds'.

*Bristolia bristolensis*

*Paranephrolenellus klondikensis*

UCR 10079: 21 m above base of section, 35.5 m below base of Combined Metals Member, 4 m above 'Insolens Beds'.

*Bristolia* sp. indet.

*Mesonacis fremonti*

*Olenellus nevadensis*

*Olenellus* sp. indet.

*Paranephrolenellus inflatus*

Olenelloid sp. indet.

UCR 10083: 44 m above base of section, 12.5 m below base of Combined Metals Member, 27 m above 'Insolens Beds'.

*Peachella* sp. indet.

Olenelloid sp. indet.

UCR 10084: 49 m above base of section, 7.5 m below base of Combined Metals Member, 32 m above 'Insolens Beds'.

*Bolbolenellus euryparia?*

*Mesonacis fremonti?*

Fig. 14. Lithostratigraphic details of measured section B at Klondike Gap, Chief Range, Lincoln County, Nevada. See Fig. 1 for location of section. See Fig. 16 for key to symbols and lithologies. Black bars to the left of the metre scale indicate provenance of stratigraphically constrained fossil collections housed in the Geology Museum, University of California, Riverside (UCR). Trilobite faunal assemblages for each collection are listed in the Appendix.

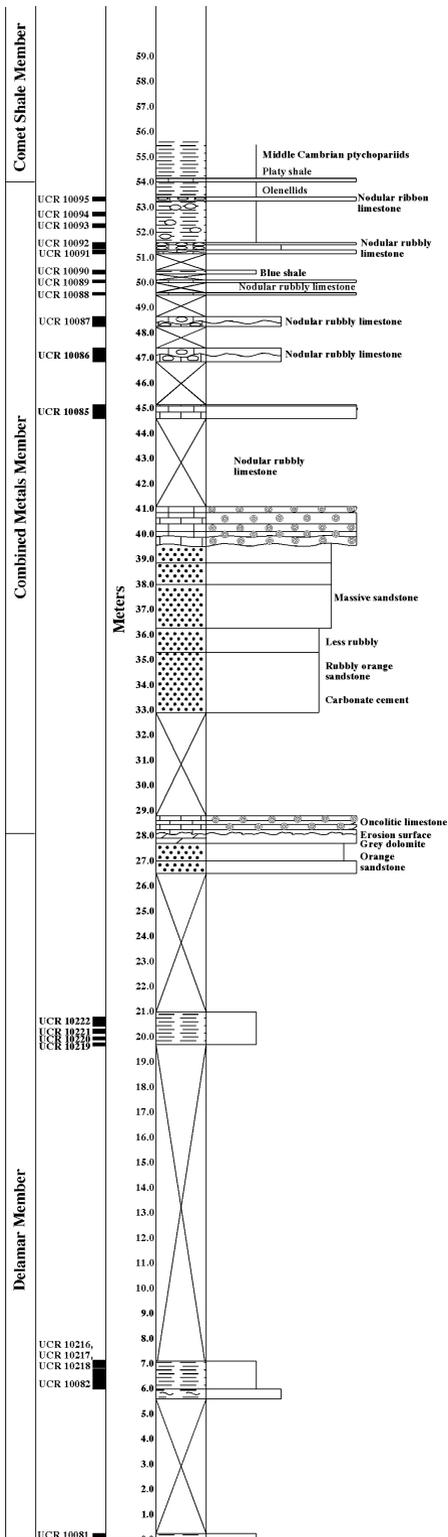
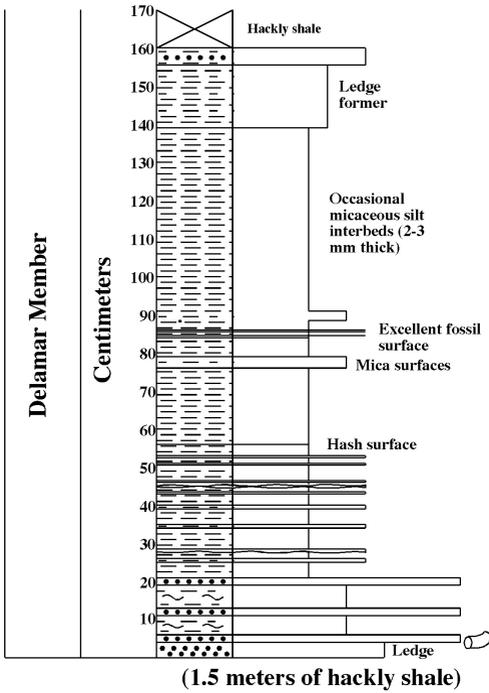


Fig. 15. Lithostratigraphic details of measured section C at Klondike Gap, Chief Range, Lincoln County, Nevada. See Fig. 1 for location of section. See Fig. 16 for key to symbols and lithologies. Black bars to the left of the metre scale indicate provenance of stratigraphically constrained fossil collections housed in the Geology Museum, University of California, Riverside (UCR). Trilobite faunal assemblages for each collection are listed in the Appendix.

- Bristolia harringtoni*  
*Bristolia* sp. indet.  
*Mesonacis fremonti*  
*Olenellus clarki?*  
*Olenellus nevadensis*  
*Olenellus* aff. *nevadensis*  
*Paranephrolenellus inflatus*  
*Olenellid* sp. indet.  
*Olenelloid* sp. indet.
- UCR 10081: Shale outcrop at base of bitter brush, 0 m in section, 28 m below base of Combined Metals Member.  
*Bristolia* sp. indet.  
*Mesonacis fremonti*  
*Olenellus nevadensis?*  
*Peachella iddingsi*  
*Olenelloid* sp. indet.
- UCR 10082: 6.8 m above base of section, 21.2 m below base of Combined Metals Member.  
*Mesonacis fremonti?*  
*Olenellus nevadensis*  
*Paranephrolenellus besti*  
*Paranephrolenellus* sp. indet.  
*Olenellid* sp. indet.  
*Olenelloid* sp. indet.
- UCR 10216: 7 m above base of section, 21 m below base of Combined Metals Member.  
*Bristolia* cf. *fragilis*  
*Bristolia* sp. indet.  
*Mesonacis fremonti*  
*Olenellus nevadensis*  
*Olenellus* sp. indet.  
*Paranephrolenellus besti*  
*Olenelloid* sp. indet.
- UCR 10217: 7.1 m above base of section, 20.9 m below base of Combined Metals Member.  
*Mesonacis fremonti?*
- UCR 10218: 6.8-7.1 m above base of section, 21.2-20.9 m below base of Combined Metals Member.  
*Mesonacis fremonti*  
*Olenellus nevadensis*  
*Olenellus* sp. indet.  
*Paranephrolenellus besti*  
*Peachella iddingsi*  
*Olenelloid* sp. indet.
- UCR 10219: 19.66-19.77 m above base of section, 8.34-8.23 m below base of Combined Metals Member.  
*Bristolia fragilis*  
*Olenellus* cf. *terminatus*  
*Olenellus* sp. indet.  
*Olenelloid* sp. indet.
- UCR 10220: 19.9-20.06 m above base of section, 8.1-7.94 m below base of Combined Metals Member.  
*Bristolia fragilis*  
*Bristolia* sp. indet.  
*Olenellus* cf. *terminatus*  
*Olenellus* sp. indet.
- Olenelloid* sp. indet.  
UCR 10221: 20.16-20.34 m above base of section, 7.84-7.66 m below base of Combined Metals Member.  
*Olenellus* cf. *terminatus*  
*Olenellus* sp. indet.  
UCR 10222: 20.46-20.8 m above base of section, 7.54-7.2 m below base of Combined Metals Member.  
*Olenellus* cf. *terminatus*  
*Olenellus* aff. *fowleri*
- UCR 10085, UCR 10086, and UCR 10087: Limestone ledges 17 m, 19 m, and 20.5 m above base of Combined Metals Member, respectively. Currently being processed for silicified faunas.
- UCR 10088: Bioclastic grainstone/wackestone ledge 49.5 m above base of section, 21.5 m above base of Combined Metals Member. Crackout material.  
Trilobite fragments
- UCR 10089: Bioclastic grainstone/wackestone ledge 50 m above base of section, 22 m above base of Combined Metals Member. Crackout material.  
*Zacanthopsis* sp.  
Trilobite thoracic segments
- UCR 10090: Blue-colored, rubbly weathering, nodular shale, 0.3 m above UCR 10089, 22.3 m above base of Combined Metals Member. Currently being processed for silicified fauna.
- UCR 10091 and UCR 10092: Limestone ledges 23.2 m and 23.6 m above base of Combined Metals Member, respectively. Currently being processed for silicified faunas.
- UCR 10093: 24.13 m above base of Combined Metals Member.  
*Olenellid* sp. indet.  
*Zacanthopsis* sp.
- UCR 10094: Carbonate nodules within shale 24.83 m above base of Combined Metals Member. Currently being processed for silicified fauna.
- UCR 10095: Limestone ledge 53.3 m above base of section, 25.3 m above base of Combined Metals Member. Currently being processed for silicified fauna.
- Section D** (Fig. 16)  
37°45.065' N, 114°33.366' W. Detailed section measured through the '*Insolens* Beds' of the Delamar Member. The base of the section is at top of a 1.5 m interval of hackly, bioturbated siltstone and shale. This entire section is correlative with collections UCR 10073, UCR 10075, and UCR 10076 of other sections.
- UCR 10074: 0.2-1.39 m above base of section.  
*Bristolia bristolensis*  
*Bristolia insolens*  
*Bristolia* sp. indet.  
*Mesonacis fremonti*  
*Olenellus nevadensis*



- Sandy limestone
- Ribbon limestone
- Dolomite
- Limestone
- Shale
- Bioturbated siltstone
- Covered interval
- Sandstone
- Vertical burrow
- Horizontal burrow
- Oncoids
- Carbonate nodules
- Cross-bedding

Fig. 16. Lithostratigraphic details of measured section D at Klondike Gap, Chief Range, Lincoln County, Nevada. See Fig. 1 for location of section. Trilobite faunal assemblages for collections made from this section are listed in the Appendix.

*Paranephrolenellus klondikensis*  
 Olenelloid sp. indet.  
 UCR 10078: 3-4 m above top of 'Insolens Beds', 4.6-5.6 m above base of section.  
*Bristolia* aff. *fragilis* A?  
*Olenellus* sp. indet.

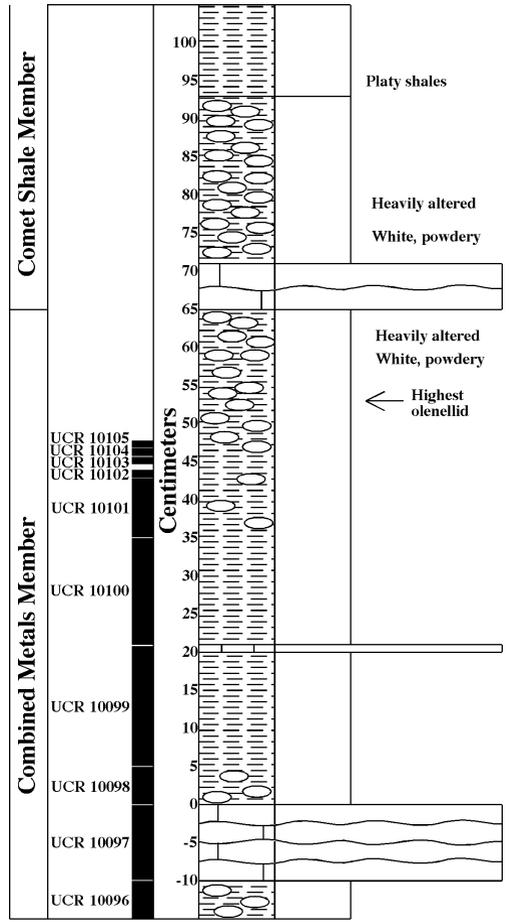


Fig. 17. Lithostratigraphic details of measured section E at Klondike Gap, Chief Range, Lincoln County, Nevada. See Fig. 1 for location of section. See Fig. 16 for key to symbols and lithologies. Black bars to the left of the centimetre scale indicate provenance of stratigraphically constrained fossil collections housed in the Geology Museum, University of California, Riverside (UCR). Trilobite faunal assemblages for each collection are listed in the Appendix.

**Section E (Fig. 17)**  
 37°45.045' N, 114°33.261' W. Detailed section measured through the uppermost metre of the Combined Metals Member (Dyeran) and basal Comet Shale Member (Delamaran). The base of the section is at the top of a 10 cm limestone ledge, 65 cm below the limestone ledge marking the base of the Delamaran.

UCR 10096: Shale and carbonate nodules 0.2-0.1 m below base of section, immediately underlying limestone ledge, 0.85-0.75 m below base of Delamaran.  
*Nephrolenellus* sp. indet.  
*Olenellus gilberti*?  
 Olenellid sp. indet.

- UCR 10097: Limestone ledge 0.1-0.0 m below base of section, 0.75-0.65 m below base of Delamaran. Currently being processed for silicified fauna.
- UCR 10098: Carbonate nodules 0.0-0.05 m above base of section, 0.65-0.6 m below base of Delamaran. Currently being processed for silicified fauna.
- UCR 10099: 0.05-0.21 m above base of section, 0.6-0.44 m below base of Delamaran.  
*Nephrolenellus geniculatus*  
*Olenellus chiefensis*  
*Olenellus gilberti*  
*Olenellus terminatus*  
 Oryctocephalid sp.
- UCR 10100: 0.21-0.35 m above base of section, 0.44-0.3 m below base of Delamaran.  
*Bolbolenellus brevispinus?*  
*Nephrolenellus geniculatus*  
*Olenellus chiefensis*  
*Olenellus fowleri*  
*Olenellus gilberti*  
*Olenellus terminatus*
- UCR 10101: 0.35-0.43 m above base of section, 0.3-0.22 m below base of Delamaran.  
*Bolbolenellus brevispinus*  
*Nephrolenellus geniculatus*
- Olenellus chiefensis?*  
*Olenellus fowleri?*  
*Olenellus gilberti*
- UCR 10102: 0.43-0.44 m above base of section, 0.22-0.21 m below base of Delamaran.  
*Nephrolenellus geniculatus*  
*Olenellus gilberti*  
*Olenellus terminatus?*
- UCR 10103: 0.45 m above base of section, 0.2 m below base of Delamaran.  
*Bolbolenellus brevispinus*  
*Nephrolenellus geniculatus*  
*Olenellus chiefensis*  
*Olenellus gilberti*  
*Olenellus terminatus?*
- UCR 10104: 0.46 m above base of section, 0.19 m below base of Delamaran.  
*Nephrolenellus geniculatus*  
*Olenellus chiefensis*  
*Olenellus fowleri*  
*Olenellus gilberti*  
*Olenellus terminatus*
- UCR 10105: 0.47 m above base of section, 0.18 m below base of Delamaran.  
*Olenellus gilberti*

