Phylogenetic analysis and revision of the trilobite subfamily Balnibarbiinae (Olenidae)

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ABSTRACT

The Balnibarbiinae is one of eight subfamilies of the Olenidae, a diverse family of late Cambrian to Ordovician trilobites. Balnibarbiine species occur in a relatively continuous section of deeper-water sediments exposed along the northeastern coastline of Spitsbergen, Svalbard, as well as scattered deeper-water beds in central Nevada. Results of phylogenetic analyses of the subfamily using both parsimony and Bayesian methods are consistent with a previous hypothesis based on phyletic similarity and stratigraphic range. *Cloacaspis* Fortey, 1974, is supported as monophyletic, but the support for *Balnibarbi* Fortey, 1974, is weak, and the genus may be paraphyletic to *Cloacaspis* even with the reassignment of *Balnibarbi ceryx* Fortey, 1974, to *Cloacaspis*. New field collections and discovery of previously undescribed material in museum and survey collections provides the basis for emended descriptions of the genus *Cloacaspis*, as well as *Cloacaspis tesselata* Fortey and Droser, 1999, *Cloacaspis ekphymosa* Fortey, 1974, and *Balnibarbi erugata* Fortey, 1974, and expands the geographic range of the subfamily to Alaska.

INTRODUCTION

The Olenidae is a diverse family of trilobites (408 species in 68 genera; Adrain, 2011) ranging from the Guzhangian to the end of the Ordovician (Adrain, 2013). The Balnibarbiinae is one of eight subfamilies within Olenidae, and is known almost exclusively from deeper-water deposits in Ny Friesland, northeastern Spitsbergen, Svalbard (Fortey, 1974; Kröger et al., 2017). The pre-Carboniferous basement of the Svalbard archipelago consists of several tectonostrati-

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graphically distinct terranes that were stretched along the margin of Laurentia in pre-Caledonian times (Gee and Page, 1994; Gee and Teben'kov, 2004). Other balnibarbiine occurrences are in deeper-water deposits in Nevada and Alaska (Ethington et al., 1995; Fortey and Droser, 1999; this study). Balnibarbiine specimens are much rarer in western Laurentia, however, primarily because deeper-water sediments are rare in the Early to Middle Ordovician rock record preserved there. In contrast, the section at Ny Friesland is one of the most continuous deeper-water sections of Early to Middle Ordovician age anywhere in the world.

The subfamily Balnibarbiinae was first described based on collections made during two expeditions to Ny Friesland, Spitsbergen, in 1967 (Vallance and Fortey, 1968) and 1972 (Fortey and Bruton, 1973; see also Fortey and Bruton, 2013). The abundance of specimens in the Spitsbergen sections made it possible to infer changes in the exoskeletal morphology through stratigraphic time. Based on such observations, Fortey (1974) proposed a phylogeny consisting of three evolutionary lineages. In his conception, the genus *Balnibarbi* Fortey, 1974, comprised two basal evolutionary lineages and was paraphyletic to the third evolutionary lineage, consisting of species of the genus *Cloacaspis* Fortey, 1974. During this time, undescribed olenids were also reported from late Early to early Middle Ordovician deposits in Nevada (McKee et al., 1972), but it was not until the 1990s that these were recognized as having an affinity with Spitsbergen balnibarbiines (Ethington et al., 1995; Fortey and Droser, 1999).

Recently, the author collected new balnibarbiine specimens from both Nevada (2015) and Spitsbergen (2016). The purpose of this study is to use new collections and modern methods to revise the subfamily and test Fortey's (1974) phylogenetic hypothesis.

PHYLOGENETIC ANALYSIS

Materials and Methods

Character design and coding: Forty-five characters are included in the analysis, of which 32 describe the cranidium, four describe the librigenae, and nine describe the pygidium. Characters describing the thorax and hypostome are excluded because these sclerites are unknown for most taxa in the analysis. Characters were coded using reductive coding sensu Strong and Lipscomb (1999). All taxa (including outgroup species, see below) share the following traits: curved and divergent anterior facial suture, deflected S1, and occipital node, where known. These three traits vary in how commonly they occur among olenids (e.g., Monti and Confalonieri, 2019), but because they are constant among the taxa in this analysis, they are excluded from the character matrix. The absence or presence of triangular pleural nodes is also excluded because, while this trait is likely shared by all balnibarbiine species to the exclusion of other olenid species, its presence or absence cannot be coded for the outgroup taxa (for which pygidia are unknown). The data matrix is archived in MorphoBank (http://morphobank. org/permalink/?P3234).

Fortey and Droser (1999) did not describe the pygidium for *Cloacaspis tesselata*. Based on association of specimens, a pygidium found in the U.S. Geological Survey collections is

tentatively assigned to this species (see Systematic Paleontology). The full character matrix includes character states coded from this specimen, but the analysis was also rerun, treating these states as missing.

OUTGROUP SELECTION: Fortey (1974) noted that the glabellae of some *Parabolinella* Brögger, 1882, species resembled those of balnibarbiine species. *Parabolinella prolata* Robison and Pantoja-Alor, 1968, and *Parabolinella tumifrons* Kobayashi, 1936, were selected as outgroup taxa because they have Laurentian occurrences as well as occurrences during the early Skullrockian (i.e., they are older than the ingroup taxa). They are also placed basal to other *Parabolinella* species in recent phylogenetic analyses (Monti and Confalonieri, 2013, 2017). Fortey (1974) also suggested that *Agalatus* (= *Inkouia*, fide Zhang, 1985) was similar to *Balnibarbi* and *Cloacaspis*, but excluded the genus from the Balnibarbiinae because species lacked the diagnostic triangular pleural node. Although this overall similarity makes the genus a candidate outgroup, no *Inkuoia* species were included in the outgroup because it was not possible to code most of the characters from available figures showing specimens assigned to *Inkouia* species (e.g., Lisogor, 1961; Han, 1983).

TREE SEARCHING: Heuristic searching in PAUP*4.0b10 (Swofford, 1998) was used to find the optimal tree according to the maximum parsimony criterion. Inapplicable characters were treated as missing data. Taxa were added by random sequence addition with 100 replicates and branch swapping was performed using the tree bisection reconnection option (TBR). Five characters (1, 9, 14, 19, 33) describing continuous variation were treated as ordered. All characters were weighted equally. Clade support was assessed based on Bremer support values, and bootstrap and jackknife analyses (with 33% deletion of characters), each consisting of 1000 replicates.

For comparison, a Bayesian search was conducted in MrBayes 3.2.6 (Ronquist et al., 2012), employing the Mk model (Lewis, 2001), specifying that only variable characters were sampled, assuming no rate variation across characters, and assigning *Parabolinella prolata* as outgroup. Different analyses were run assuming no character rate variation, and both gamma- and lognormally ($K = 4$) distributed character rate variation (Harrison and Larsson, 2015); 500,000 MCMC repetitions were required for convergence for all analyses.

RESULTS

The parsimony-based tree search recovered three most parsimonious trees with tree length of 98. All nodes are resolved in the strict consensus tree (fig. 1) except those leading to the clade comprising *Cloacaspis tesselata*, *Clocacapsis senilis*, and *Cloacapsis ekphymosa*. In the Bayesian analysis, a node uniting *C. senilis* and *C. ekphymosa* is recovered with a posterior probability of 55 regardless of settings for character rate variation (not shown). In both analyses, the two *Cloacapsis ceryx* subspecies are sister to one another, although this node is not as well supported in the parsimony tree as that uniting more-derived *Cloacaspis* species or the node uniting all *Cloacaspis* species, and is recovered in some maximum clade credibility trees but with posterior probability <50. *Balnibarbi pulvurea*
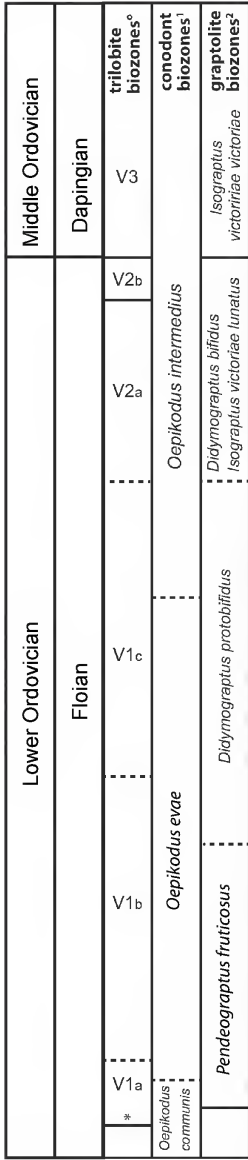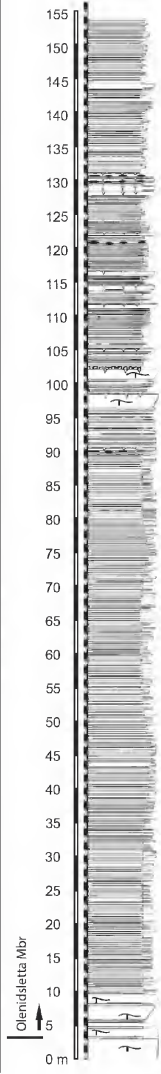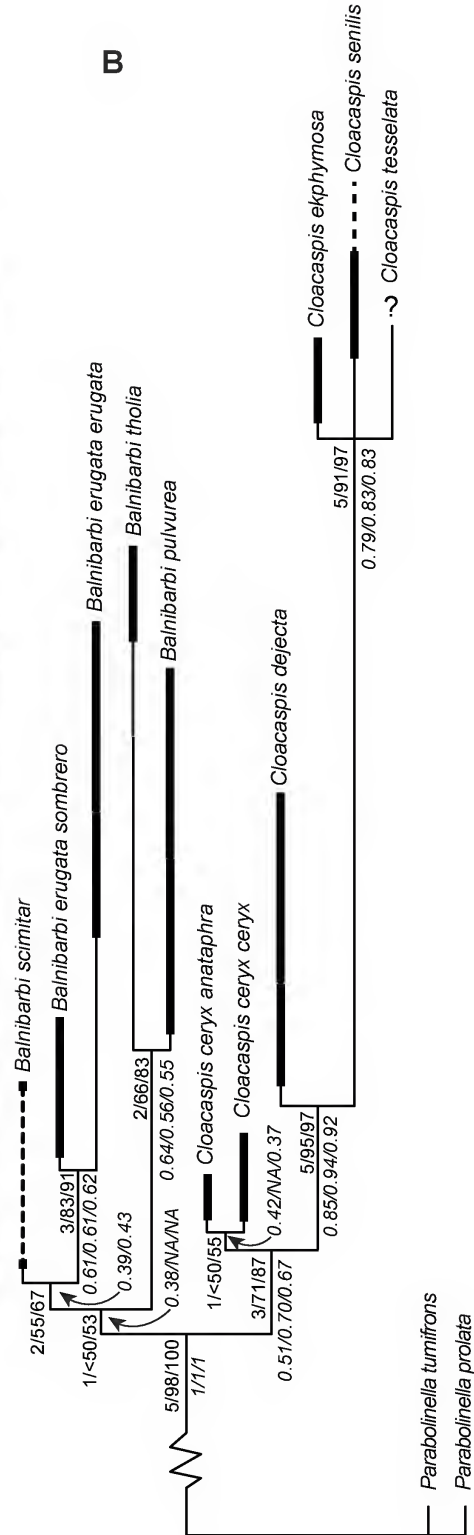
and *Balnibarbi tholia* are recovered as sister taxa, and *Balnibarbi erugata* subspecies are supported as sister taxa in both analyses with moderate support. *Balnibarbi* is weakly supported as monophyletic in the parsimony tree and in the maximum clade credibility tree assuming no rate variation. If log-normal or gamma-shaped rate variation across characters is assumed instead of equal rates, maximum clade credibility trees indicate weak support for a paraphyletic *Balnibarbi*: the branch leading to *B. tholia* and *B. pulvurea* attaches below the node uniting *Cloacaspis*. For all Bayesian analyses, however, nodal support is low (posterior probabilities <50), so these relationships are effectively unresolved at this point. Although it is possible that *Balnibarbi* is actually paraphyletic to *Cloacaspis*, as conceived by Fortey (1974), all species except *C. ceryx* are retained within *Balnibarbi*. Coding pygidial characters as missing for *Cloacaspis tesselata* did not change the tree topologies or node support.

SYSTEMATIC PALEONTOLOGY

Specimens were examined from collections in the Natural History Museum, Oslo (PMO-NF), Sedgwick Museum, University of Cambridge (CAMSM), Cambridge Arctic Shelf Programme (CASP), the U.S. Geological Survey (USGS), the Smithsonian (USNM), and the American Museum of Natural History (AMNH). Because there were differences in section measurements taken between Spitsbergen expeditions (compare Fortey, 1980, with Kröger et al., 2017), stratigraphic ranges in figure 1 are shown scaled to the 2016 sections and include range extensions based on new collections (see below).

FIGURE 1. Results of phylogenetic analysis. **A.** Stratigraphic section of Olenidsletta Member, Profilstranda, Ny Friesland, Spitsbergen. Modified from Kröger et al., 2017. **B.** Strict consensus tree of three most parsimonious trees, scaled to time for graphical representation purposes using the all-branches additive-method (nodes scaled to first occurrence of oldest descendent and an arbitrary constant value is added to all branches in order to remove zero-length branches). Maximum clade credibility tree resulting from Bayesian analysis assuming no rate variation is the same as the strict consensus tree except that the node joining *C. senilis* and *C. ekphymosa* is also recovered with a posterior probability of 55. The only difference in the topology of the maximum clade credibility tree if rates are assumed to be gamma- or log-normally distributed is that the branch leading to *B. tholia* and *B. pulvurea* attaches below the node uniting *Cloacaspis*, which is also more strongly supported (posterior probability = 70); 50% majority-rule consensus trees are unable to resolve *Balnibarbi* as a monophyletic clade (all nodes with posterior probabilities <50 collapse). Values to left of nodes show Bremer support values/bootstrap frequencies/jackknife frequencies. Italicized values to right of nodes show posterior probabilities for analyses assuming no rate variation/gamma-distributed rate variation/log-normally distributed rate variation; NA indicates that the node shown was not supported in the maximum clade credibility tree for that analysis. Stratigraphic ranges based on Fortey (1980), Fortey and Droser (1999), and new collections that extend the range of *Cloacaspis ceryx anataphra* and *Balnibarbi scimitar*. *Cloacaspis tesselata* is Rangerian and likely just younger than *C. senilis*.

CLASS TRILOBITA WALSH, 1771

ORDER OLENIDA ADRAIN, 2011

FAMILY OLENIDAE BURMEISTER, 1843

SUBFAMILY BALNIBARBIINAE FORTEY, 1974

Balnibarbi Fortey, 1974

TYPE SPECIES: *Balnibarbi pulvurea* Fortey, 1974.

DIAGNOSIS: As in Fortey, 1974: 21.

INCLUDED SPECIES: *Balnibarbi pulvurea* Fortey, 1974; *Balnibarbi erugata erugata* Fortey, 1974; *Balnibarbi erugata sombrero* (Fortey, 1974); *Balnibarbi scimitar* Fortey, 1974; *Balnibarbi tholia* Fortey, 1974.

Balnibarbi erugata Fortey, 1974

Figure 2

TYPE SUBSPECIES: *Balnibarbi erugata erugata* Fortey, 1974.

TYPE LOCALITY: Profilstranda, Olenidsletta Member, Valhallfonna Formation, Ny Friesland, Spitsbergen, Svalbard.

SUBSPECIES: *Balnibarbi erugata erugata* Fortey, 1974, *Balnibarbi erugata sombrero* (Fortey, 1974).

EMENDED DIAGNOSIS: *Balnibarbi* species with long (sag.) anterior border rounded on midline. Anterior border with 25–30 pits; pits expressed only on internal mold. Glabella rounded anteriorly; preglabellar field broad. Palpebral lobes long, with anterior end forward of 2p and posterior end at occipital furrow. Moderately large pygidium with four axial rings.

DISCUSSION: In both subspecies, distinct pits are visible only on the internal mold of the anterior border furrow (fig. 2E, F). In this case (where the pit is not expressed on the dorsal surface), this trait may be better described as a series of "protuberances" on the ventral surface that form pits on the internal mold. These protuberances meet nodes on the doublure of the librigena beneath the anterior border of the cranidium (see Fortey, 1974: pl. 5, fig. 10). On other *Balnibarbi* species, the structures are visible on the anterior border (e.g., *Balnibarbi pulvurea*, see Fortey, 1974: pl. 1, fig. 4), and more in keeping with the idea of a "pit."

The holotype of *Balnibarbi erugata erugata* is almost completely exfoliated (fig. 2A), but specimens that otherwise fit the diagnosis (including some listed by Fortey, 1974) show very fine granulation across the glabella (fig. 2D), in the posterior border furrow (fig. 2C), and more rarely preserved on the frontal area (fig. 2B). Terrace lines are evident on the border of the holotype (fig. 2A) and some better-preserved specimens (fig. 2B). Fortey (1974) differentiated *Balnibarbi erugata* and *Balnibarbi sombrero* based on the length (sag.) of the preglabellar field relative to the glabella. The type and figured specimens of *B. sombrero* do have a larger preglabellar field (fig. 3), and there is no granulation visible on the external surface where preserved. However, some specimens that have fine granulation
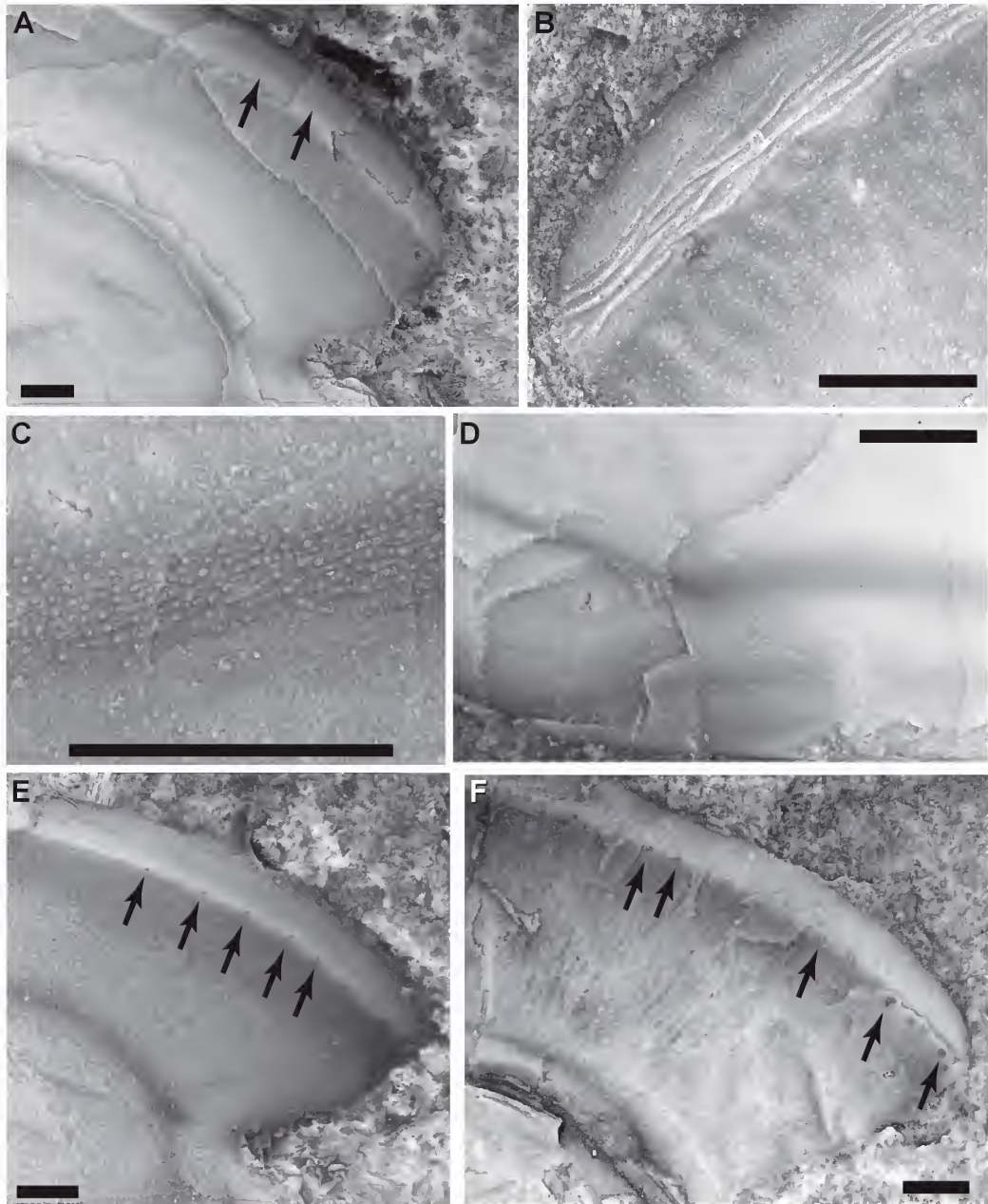
FIGURE 2. *Balnibarbi erugata* Fortey, 1974, close-ups. **A.** *Balnibarbi erugata erugata*, holotype cranidium, PMO-NF-3016. Note exfoliation of frontal area and glabella. Arrow points to terrace lines on anterior border that are expressed on both the external surface and internal mold. **B.** Anterior border of *Balnibarbi erugata erugata*, CAMSM F3976, showing faint caeca and very fine granulation on frontal area near anterior border furrow and terrace lines on border. **C.** Posterior border furrow on *Balnibarbi erugata erugata*, CAMSM F3976, showing very fine granulation. **D.** Occipital ring of *Balnibarbi erugata erugata*, PMO-NF-695, showing very fine granulation on glabella. **E.** *Balnibarbi erugata erugata* PMO-NF-772. Arrows point to select pits in anterior border furrow; specimen is exfoliated. **F.** *Balnibarbi erugata sombrero*, PMO-NF-2054. Arrows point to select pits in anterior border furrow on exfoliated surface. Scale bars = 1 mm.

also have large preglabellar fields (e.g., PMO-NF-227.730). In addition, fine granulation is easily eroded away on exposed surfaces (see fig. 4F). No new specimens of *Balnibarbi erugata sombrero* were recovered during the 2016 expedition to Spitsbergen, nor were any *Balnibarbi erugata erugata* specimens collected from trilobite zone V1b, thus the known stratigraphic ranges are still nonoverlapping. This separation in stratigraphic time may have contributed to Fortey's decision to rank each at the species level. However, the two subspecies differ morphologically in the same way that subspecies of *Cloacaspis ceryx* do (expression of granulation and morphometric differences in the frontal area). Thus, *B. sombrero* was lowered to subspecies status; the name *erugata* takes precedence following ICZN Article 24.2.

Balnibarbi erugata erugata Fortey, 1974

Figure 2A–D, E

Balnibarbi erugata Fortey, 1974: 31, pl. 5, fig. 1-10.

HOLOTYPE: Cranidium, PMO NF 3016 (figured in Fortey, 1974: pl. 5, fig. 1-3).

TYPE LOCALITY: Profilstranda, Olenidsletta Member, Valhallfonna Formation, Ny Friesland, Spitsbergen, Svalbard.

STRATIGRAPHIC RANGE: Throughout trilobite zone V1c and the very beginning of V2a (Fortey, 1980). These zones coincide with the upper *Oepikodus evae* and lower *Oepikodus intermedius* conodont zones, and the *Didymographtus protobifidus* graptolite zone within the upper Floian (fig. 1; see also Kröger et al., 2017).

DIAGNOSIS: *Balnibarbi erugata* subspecies with relatively short (sag.) preglabellar field (<0.35 length of glabella) and fine granulation present on glabella, axial, palpebral, and posterior border furrows, and on frontal area adjacent to anterior border furrow.

Balnibarbi erugata sombrero (Fortey, 1974)

Figure 2F

Balnibarbi sombrero Fortey, 1974: 32, pl. 6, fig. 1-4.

HOLOTYPE: Cranidium, PMO NF 835 (figured in Fortey, 1974: pl. 6, fig. 1-2).

TYPE LOCALITY: Profilstranda, Olenidsletta Member, Valhallfonna Formation, Ny Friesland, Spitsbergen, Svalbard.

STRATIGRAPHIC RANGE: Middle of trilobite zone V1b (Fortey, 1980). This zone coincides with the lower *Oepikodus evae* conodont zone and *Pendeograptus fruticosus* graptolite zone within the upper Floian (fig. 1; see also Kröger et al., 2017).

DIAGNOSIS: *Balnibarbi erugata* species with relatively long (sag.) preglabellar field (>0.35 length of glabella) and smooth exoskeletal surface. Known only from cranidia.
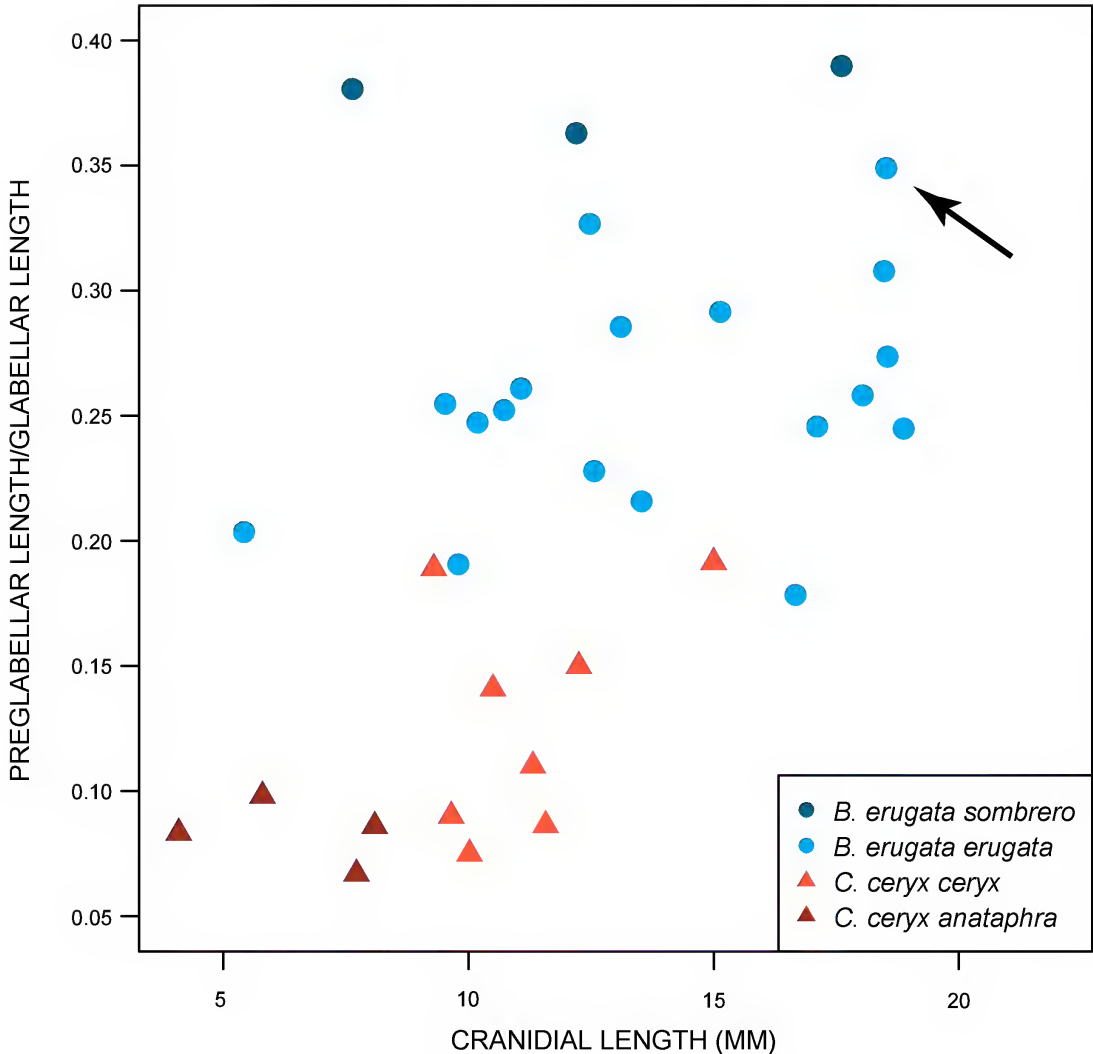
FIGURE 3. Size of preglabellar field relative to glabella in subspecies of *Balnibarbi erugata* and *Cloacaspis ceryx*. Arrow points to PMO-NF-227.730. Differences in relative length of preglabellar field are not correlated with overall size of the cranidium, and are thus not due to allometry. However, while subspecies of *Balnibarbi erugata* overlap in cranidial length, all measured specimens of *C. ceryx anataphra* are smaller than those of *C. ceryx ceryx*. Since these subspecies also differ in expression of surface granulation, it is possible that expression of granulation is related to size.

Balnibarbi scimitar, Fortey, 1974

Balnibarbi scimitar Fortey, 1974: 33, pl. 7, fig. 1-10.

HOLOTYPE: Cranidium, PMO NF 2785 (figured in Fortey, 1974: pl. 7, figs. 1, 3, 8).

TYPE LOCALITY: Melt stream D on Olenidsletta, Olenidsletta Member, Valhallfonna Formation, Ny Friesland, Spitsbergen, Svalbard.

STRATIGRAPHIC RANGE: The type material for this species was sampled from a single bed estimated to be no more than 6 m from the base of the Olenidsletta member (Fortey, 1974), which would put the occurrence in trilobite zone V1a (Fortey, 1980; coincident with conodont zone *Oepikodus communis*; see Kröger et al., 2017). New specimens were recovered in 2016 from the Profilstranda section from a bed 30 m above the base of the Olenidsletta member which extends the stratigraphic range into trilobite zone V1b (fig. 1).

DIAGNOSIS: As in Fortey, 1974: 33.

Cloacaspis Fortey, 1974

TYPE SPECIES: *Cloacaspis senilis* Fortey, 1974.

EMENDED DIAGNOSIS: Balnibarbiine trilobites with facial sutures moderately divergent in front of eyes. Pits present on internal mold of anterior border furrow, and may also expressed on the dorsal surface. Frontal area relatively short (sag.), ranging from 10%–20% of the total cranidial sagittal length. Glabella with four pairs of glabellar furrows of balnibarbiinae type: 1P extends posterolaterally from axial furrow before turning abruptly posteriorly; 2P straight, extending posterolaterally from axial furrow, or curving slightly posteriorly; 3P straight, short, transverse, not reaching axial furrow; 4P straight, short, slightly oblique, not reaching axial furrow. 3P and 4P tend to be longer than in other balnibarbiine genera (*Balnibarbi* species), and 4P is more weakly expressed than other furrows. Postocular fixed cheeks triangular. Posterior border of free cheek curves forward to long genal spine. Pygidium small, with two to three axial rings. Posterior border of pygidium may bear short spines.

INCLUDED SPECIES: *Cloacaspis senilis* Fortey, 1974; *Cloacaspis ceryx* (Fortey, 1974); *Cloacaspis dejecta* Fortey, 1974; *Cloacaspis ekphymosa* Fortey, 1974; *Cloacaspis tesselata* Fortey and Droser, 1999.

Cloacaspis ekphymosa Fortey, 1974

Figure 4A

Triarthrus sp. Ross, 1965: 18, pl. 8, fig. 4.
Cloacaspis ekphymosa Fortey, 1974: 41, pl. 11, figs. 12, 14–18.

HOLOTYPE: Cranidium, SMA 84075 (figured in Fortey, 1974: pl. 11, fig. 12).

TYPE LOCALITY: Profilstranda, Olenidsletta Member, Valhallfonna Formation, Ny Friesland, Spitsbergen, Svalbard.

OTHER GEOGRAPHIC OCCURRENCES: Lost River Area, Seward Peninsula, Alaska (see Ross, 1965).

STRATIGRAPHIC RANGE: Fortey (1974, 1980) recovered this species from 105 m to 120 m in the section of Fortey (1980), stratigraphically below the congeneric *Cloacaspis senilis,* which was recovered from 120 m to 145 m above the base of the Olenidsletta Member. This species was recovered in 2016 cooccurring with *Cloacaspis senilis* at 139 m above the base of the
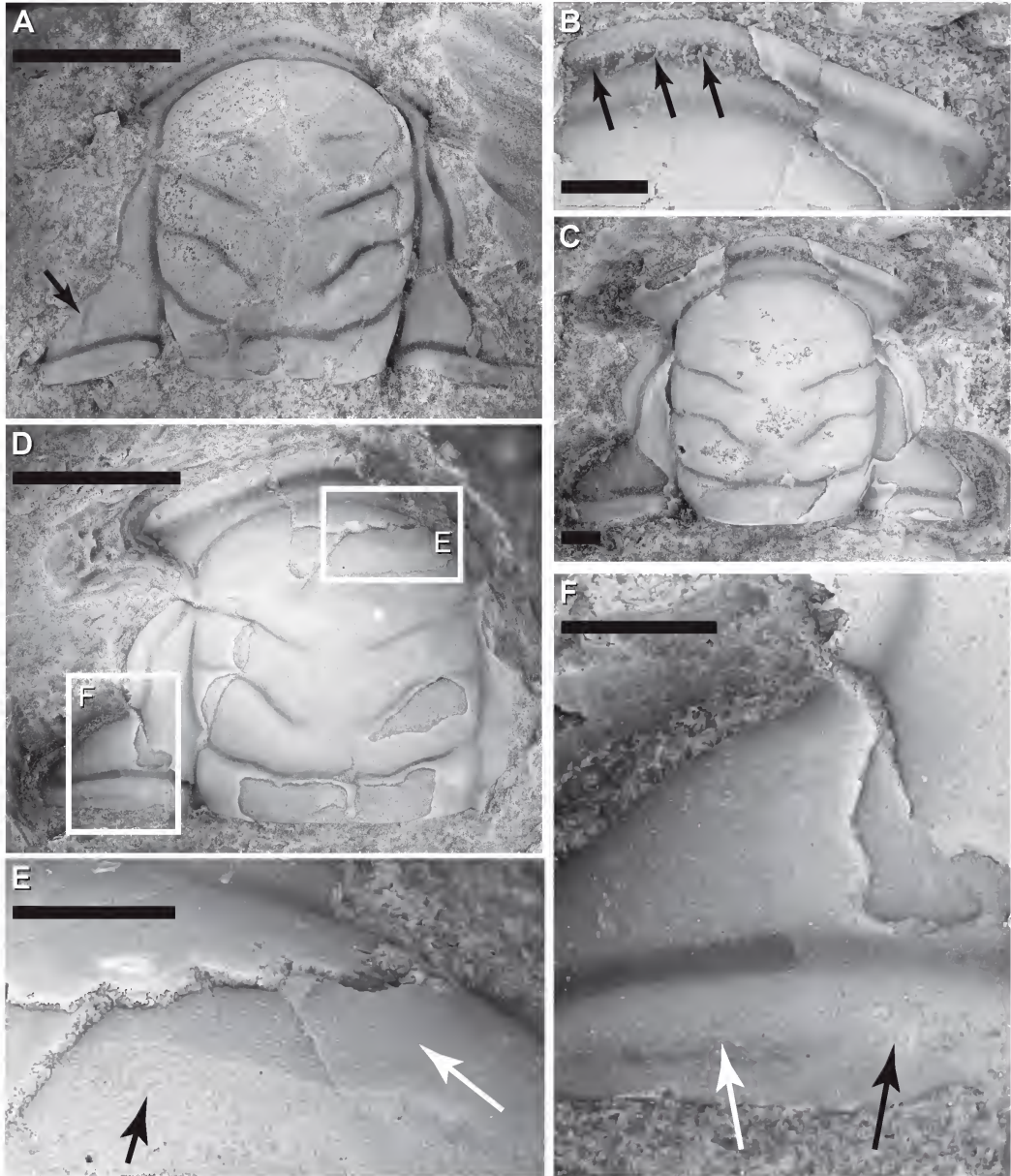
FIGURE 4. *Cloacaspis* spp. **A.** *Cloacaspis ekphymosa* Fortey, 1974, USNM 144232. Collected from the Lost River Area on Seward Peninsula, Alaska, and previously identified as *Triarthrus* sp. (Ross, 1965). Arrow pointing to postpalpebral furrow. **B.** Anterior border of *Cloacaspis ceryx anataphra* (Fortey, 1974), AMNH-FI-101655. Black arrows pointing to faint anterior border pits on internal mold. **C.** *Cloacaspis ceryx anataphra* (Fortey, 1974), AMNH-FI-101655. Collected from PO-18 of the Olenidsletta Member of the Valhallfonna Formation (Kröger et al., 2017). **D)** *Cloacaspis ceryx ceryx* (Fortey, 1974), AMNH-FI-101657. Close-up of **E,** anterior glabellar lobe and **F,** posterior wing, showing presence of fine granulation of recently prepared surface (white arrow) and lack of granulation on exposed and slightly eroded surface (black arrow). Collected from bed PO-18 of the Olenidsletta Member of the Valhallfonna Formation (Kröger et al., 2017). Scale bars = 1 mm except A and D, where scale bar = 5 mm.

Olenidsletta Member at the Profilstranda section (Kröger et al., 2017; see also fig. 1), which is estimated to be at about 119 m within the stratigraphic section of Fortey (1980). It is thus not clear whether this should be considered an extension of the stratigraphic range of *Cloacaspis senilis* or of *Cloacaspis ekphymosa*, but does indicate that the species overlapped just after the first appearance of the former and just before the last appearance of the latter.

DIAGNOSIS: As in Fortey, 1974: 41–42.

DISCUSSION: Fortey (1974: 14) suggested that the "*Triarthrus*" cranidium figured by Ross (1965: pl. 8, fig. 4) was more likely *Cloacaspis.* Examination of this specimen confirms this, and the presence of the postpalpebral furrow indicates that the specimen belongs to *Cloacaspis ekphymosa* Fortey, 1974, although the extensive exfoliation does not allow for the confirmation of granulate surface sculpture (fig. 4A). This identification extends the geographic range of this species and genus to Alaska.

Cloacaspis ceryx (Fortey, 1974)

Figure 4B–F

Balnibarbi ceryx Fortey, 1974: 29.

HOLOTYPE: Cranidium, SMA 84034 (figured in Fortey, 1974: pl. 8, fig. 1).

TYPE LOCALITY: Profilstranda, Olenidsletta Member, Valhallfonna Formation, Ny Friesland, Spitsbergen, Svalbard.

EMENDED DIAGNOSIS: *Cloacaspis* species with greater (sag., exsag.) preglabellar length than other species of the genus; anterior border comes to a point on midline. Moderately sized pygidium with three axial rings.

DISCUSSION: Fortey (1974) distinguished *Cloacaspis ceryx ceryx* and *Cloacaspis ceryx anataphra* by the latter having a shorter (sag.) preglabellar field relative to the glabella, no visible pits in the anterior border furrow, and a smooth exoskeletal surface. Examination of new and old specimens suggests that the mean preglabellar/glabella ratio is on average shorter in *C. ceryx anataphra*, but there is overlap in variation in this variable. In addition, while pits are not visible in the anterior border furrow, they are present and visible on the internal mold (fig. 4B, C). On the few specimens where it was possible to estimate the number of anterior pits, the number is slightly smaller (25–30) compared to *C. ceryx ceryx* (>30). Although granulation is very fine on *C. ceryx ceryx* and its preservation is very sensitive to any erosion of the surface (fig. 4D–F), it does appear that some specimens truly lack surface granulation. Based on this evidence, the two taxa are retained as subspecies, but the species complex is reassigned to the genus *Cloacaspis* based on the results of the phylogenetic analysis. The species complex is united with other *Cloacaspis* species by having advanced genal spines (char. 34), relatively large palpebral lobes (char. 19), and forward curvature of the palpebral lobe (char. 20). However, *Cloacaspis ceryx* shares some characters with some *Balnibarbi* species, including greater divergence of the anterior dorsal suture (char. 9), relatively wide palpebral lobes (char. 21), relatively short 3P (char. 25) larger number of axial rings (char. 37), and medial indent on posterior margin of pygidium (char. 44). The latter three characters are also shared with *Cloacaspis dejecta*.

Cloacaspis ceryx ceryx (Fortey, 1974)

Figure 4D–F

Balnibarbi ceryx ceryx Fortey, 1974: 28, pl. 8, fig. 1-6, pl. 9, figs. 1, 3, 4.

HOLOTYPE: Cranidium, SMA 84034 (figured in Fortey, 1974: pl. 8, fig. 1).

TYPE LOCALITY: Profilstranda, Olenidsletta Member, Valhallfonna Formation, Ny Friesland, Spitsbergen, Svalbard.

STRATIGRAPHIC RANGE: Lower V1b trilobite zone (Fortey, 1980), which coincides with the lower *Oepikodus evae* conodont zone and *Pendograptus fruticosus* zone within the upper Floian (fig. 1; see also Kröger et al., 2017).

DIAGNOSIS: *Cloacaspis ceryx* species with relatively long (sag.) preglabellar field (0.08 – 0.19 length of glabella) and finely granular exoskeletal surface.

Cloacaspis ceryx anataphra (Fortey, 1974)

Figure 4B, C

Balnibarbi ceryx anataphra Fortey, 1974: 30, pl. 9, fig. 5-7.

HOLOTYPE: Cranidium, PMO NF 651 (figured in Fortey, 1974: pl. 9, fig. 5).

TYPE LOCALITY: Profilstranda, Olenidsletta Member, Valhallfonna Formation, Ny Friesland, Spitsbergen, Svalbard.

STRATIGRAPHIC RANGE: Fortey (1974) reported this subspecies from a single horizon about 8 m above the base of the Olenidsletta Member, which is estimated to be around 12.5 m in the 2016 stratigraphic section. Additional specimens were recovered in 2016 from 17–19 m in section, which extends the stratigraphic range of this subspecies, but the total range remains within the early half of the stratigraphic range of the other subspecies, *Cloacaspis ceryx ceryx* (fig. 1).

DIAGNOSIS: *Cloacaspis ceryx* species with relatively narrow preglabellar field (0.06–0.10 length of glabella) and smooth exoskeletal surface.

Cloacaspis tesselata Fortey and Droser, 1999

Figures 5–7

Clocaspis tesselata Fortey and Droser, 1999: 187, fig. 3.1–3.5.

HOLOTYPE: Cranidium, USNM 495868 (figured in Fortey and Droser, 1999: fig. 3.4).

TYPE LOCALITY: "Olenid bed," Antelope Valley Formation, Little Rawhide Mountain, Hot Creek Range, Nye County, Nevada.

OTHER OCCURRENCES: Antelope Valley Limestone, June Canyon Sequence, Ike's Canyon, Nevada.

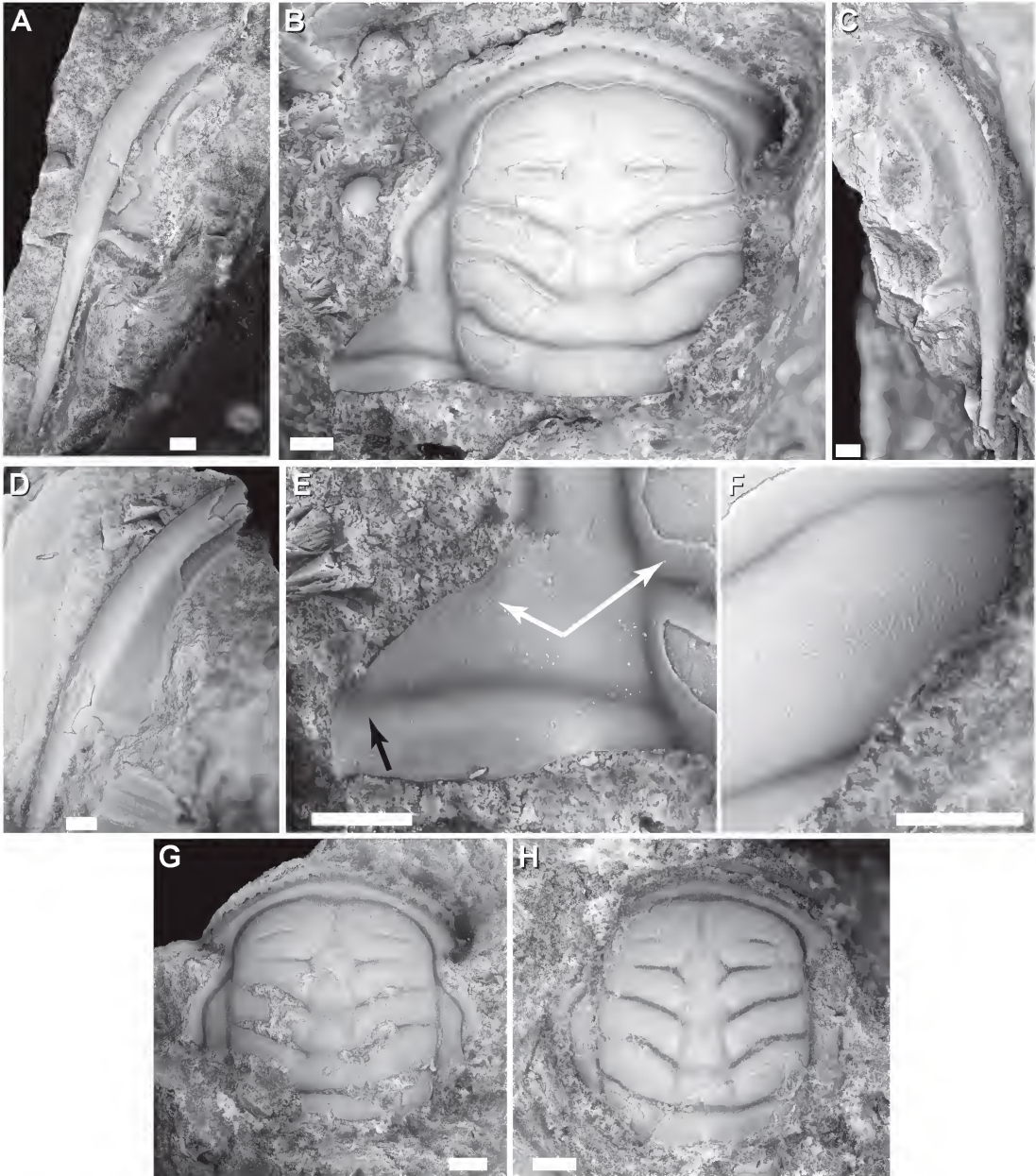STRATIGRAPHIC RANGE: Lower Dapingian. See discussion for more detail.

FIGURE 5. *Cloacaspis tesselata* Fortey and Droser, 1999, specimens from Little Rawhide Mountain, Nevada. **A.** Librigena, AMNH-FI-115819. Specimen oriented relative to cranidium shown in B. **B.** Cranidium, AMNH-FI-115818. **C.** Librigena, AMNH-FI-115820. **D.** Paratype librigena, USNM 495690. Close-ups of B: **E,** posterior wing showing anastomizing lines along dorsal suture and glabella (white arrows) and curvature of distal part of posterior furrow (black arrow); and **F,** glabellar lobe L1, showing anastomizing lines and very fine granulation. **G.** Cranidium, AMNH-FI-115807. **H.** Cranidium, AMNH-FI-115808. All specimens except paratype collected by author in 2015. Scale bar = 1 mm.
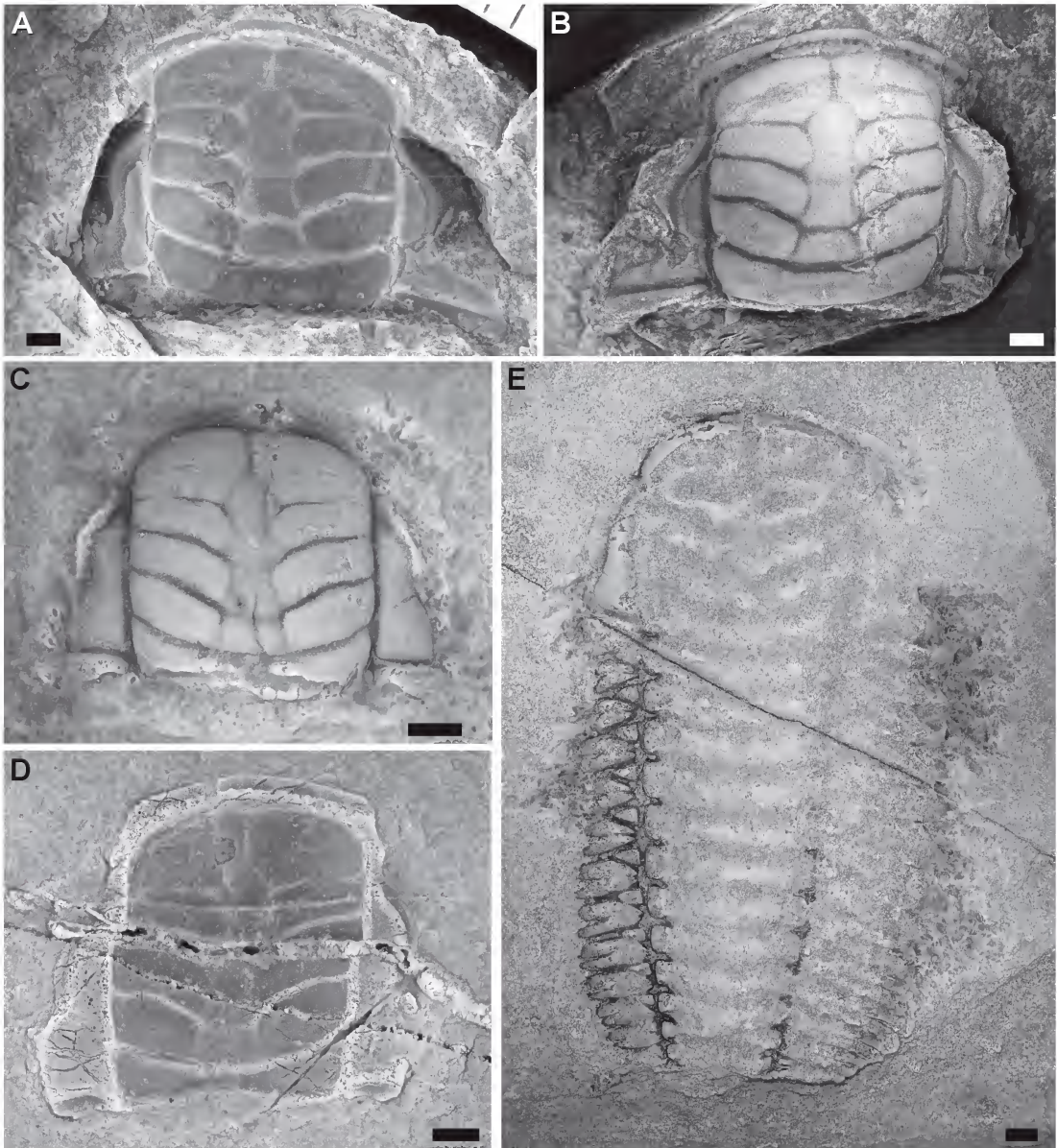
FIGURE 6. *Cloacaspis tesselata* Fortey and Droser, 1999, specimens from Ike's Canyon, Nevada. **A.** External mold of cranidium, USNM 720100. From USGS-D2219. **B.** Latex mold of cranidium, AMNH-FI-115823, cast from USNM 720100 (see A). **C.** Cranidium, AMNH-FI-115825. Found in Columbia University collections. **D.** Cranidium, AMNH-FI-115824. Found in Columbia University collections. **E.** Cranidium and thorax, USNM 720101. From USGS D2282-CO. Scale bar = 1 mm.
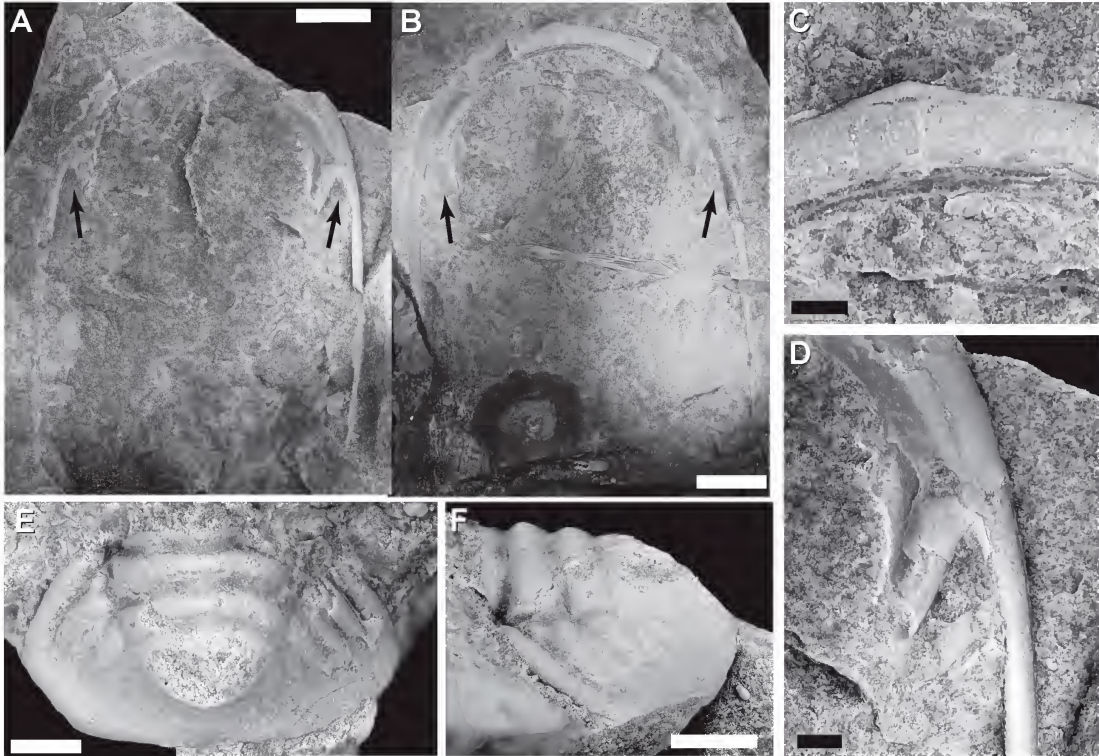
FIGURE 7. *Cloacaspis tesselata?* Fortey and Droser, 1999, specimens from Ike's Canyon, Nevada. **A.** Dorsal view of fused librigena, USNM 720102 (part). From USGS-D2217. **B.** Ventral view of fused librigena, USNM 720102 (counterpart). **C.** Close-up of anterior part of librigena USNM 720102 (counterpart), showing fusion and triangular projection. **D.** Close-up of advanced genal spine on librigena USNM 720102 (part). **E.** Pygidium, USNM 720103. From USGS D2217. **F.** Lateral view of pygidium, USNM 720103. Scale bar = 1 mm, except for A and B, where scale bar = 5 mm.

DIAGNOSIS: As in Fortey and Droser, 1999: 187.

EMENDED DESCRIPTION: Posterior area of fixigenae broadly triangular in shape, steeply downsloping. The posterior border is elevated to form an articulating socket close to the occipital ring, as was described for *Cloacaspis ceryx ceryx* (Fortey, 1974) and is apparent in other *Cloacaspis* species (Fortey, 1974). Fine anastomizing lines distributed across entire glabella, not just frontal glabellar lobe; fine anastomizing lines on genal field bordering posterior dorsal suture (fig. 5D, E). Very fine granulation apparent on glabella (fig. 5F). Occipital lobe has very small medial tubercle. Librigenae fused at midline, with advanced genal spine, such that posterior border curves toward it. Triangular projection of anterior border at midline. Raised ridge follows outline of eye, more prominent anteriorly (fig. 5A, C, E). Tentatively assigned pygidium 1.6 times as wide as long, with two axial rings and rounded terminal piece. Anterolateral margin curves posteriorly from axis, posterior border smoothly curving. Pleural field slopping ventrally, with two strongly expressed pleural furrows, two moderately strongly expressed interpleural furrows, and weakly visible triangular pleural nodes. No border furrow. Surface sculpture unknown (fig. 7E, F).

DISCUSSION: *Cloacaspis tesselata* was first described from the Antelope Valley Limestone exposed at Little Rawhide Mountain, Nevada. Specimens are rare at this locality, having been sparsely collected from a single 30 cm black limestone bed by Fortey and Droser in the mid- to late-1990s, and by the author in 2015. A similar olenid had been reported from the Antelope Valley Limestone in Ike's Canyon in the Toquima Range, Nye County, Nevada (McKee et al., 1972; McKee, 1976; Ethington et al., 1995). The author found one scrappy olenid specimen (AMNH-FI-101458, not figured) over four days of fieldwork in Ike's Canyon in 2015; however, additional specimens were found in the Columbia University collections now housed at the American Museum of Natural History (AMNH-FI-115824-825) and in the U.S. Geological Survey collections (USGS D2217-CO, D2219-CO, D2220-CO, D2280-CO, D2282-CO). Where the glabellar furrows are adequately preserved, all cranidia have the distinctive bifurcating glabellar furrows diagnostic of *Cloacaspis tesselata*; thus, it seems likely that other *Cloacaspis*-like sclerites found in these collections also belong to *Cloacaspis tesselata*. Specimens include complete fused librigena and a single pygidium (figs. 5, 6, 7), thereby making it possible to expand on the description.

None of the paratype cranidia of *Cloacaspis tesselata* (USNM 495686–88) have the posterior area of the fixigenae preserved. However, two new specimens, one collected from Little Rawhide Mountain (fig. 5B) and one found in the USGS collections, show the entire dorsal suture including the posterior area of the fixigenae (fig. 6A-B). Comparisons of these cranidia with new librigenal specimens (figs. 5A, C, 7A, B, D) show that there is an advanced genal spine, in contrast to Fortey and Droser's (1999) description. It is also possible to see the distal end of the posterior border furrow start to gently curve up on the posterior wing of the cranidium (fig. 5A, C). The librigena assigned by Fortey and Droser (1999) appears to belong to *Cloacaspis tesselata* as well, but the posterior margin is not preserved well enough to see the genal angle (fig. 5D). Other librigenae from the USGS collections (fig. 7A–C) also show advanced genal spines (fig. 7D). Of the specimens examined, the acuteness of the angle in the Ike's Canyon specimens is greater than that of the specimens recovered from Little Rawhide Mountain (compare fig. 5A with fig. 7A, B, and D), but it is possible that some of this variation is taphonomic, as the specimens from Ike's Canyon are flattened relative to the specimens from Little Rawhide Mountain. Some librigenae recovered from Ike's Canyon are fused (fig. 7A, B), as seen in other *Cloacaspis* species (and other olenid trilobites), but there is also a triangular projection at the anterior midline of the fused librigenae (fig. 7C) that has not been reported before. Fortey and Droser (1999) did not identify any pygidia, and only one specimen was found among the USGS or AMNH collections (fig. 7E) that could belong to *Cloacaspis tesselata* based on similarities to those described for *Cloacaspis dejecta* (Fortey, 1974: pl. 12, figs. 1, 4). The specimen is almost entirely exfoliated, so any surface sculpture remains unknown, though it is possible that there is fine granulation on the bit of exoskeleton on the right pleural region. One partially complete olenid specimen was found in USGS collection D2282-CO. Triangular pleural nodes are preserved on the thorax, indicating that it belongs to Balnibarbiinae. The glabellar furrows are poorly preserved, but the shape of the cranidium is consistent with *Cloacaspis* species, including *Cloacaspis tesselata*. The specimen shows a minimum of 11 thoracic segments (fig. 6E).

At Little Rawhide Mountain, the "olenid" bed is at the base of the North American Whiterockian Stage, which puts it around the Floian-Dapingian boundary at the base of the Middle Ordovician. The occurrences at Ike's Canyon are not as well constrained. USGS collections D2217-CO and D2219-CO were sampled from the *Orthidiella* zone (McKee et al., 1972), however, which is correlative with Zone L of Ross (1951), the *Psephosthenaspis* Zone of Fortey and Droser (1996; see also Adrain et al., 2012, for trilobite zonation) and the Rangerian zone as defined by Ross et al. (1997). This places the Ike's Canyon occurrences within the Dapingian.

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