The trilobites *Smoothcanyonops* gen. nov. and *Ceeops* gen. nov. from the Early Ordovician (mid-Tremadocian; Stairsian) of the Great Basin, western USA

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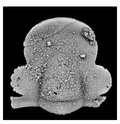

Extensive field-based sampling of the shallow water trilobite faunas of the northern Laurentian palaeo-margin (present day western North America) has yielded an abundance of well preserved, secondarily silicified, faunas spanning the Lower Ordovician. As sampling has accumulated, some very rare species have been revealed. It is unusual to encounter new post-Cambrian trilobites whose family-group affinity is obscure, but two new Stairsian (mid-Tremadocian) genera contain reasonably well known species with effaced morphologies that have no obvious close comparisons among other Ordovician taxa. *Smoothcanyonops* gen. nov. (type species *S. smoothcanyonensis* sp. nov.) includes species with dorsally smooth, considerably effaced morphology, apparently with yoked librigenae. A second assigned species is *S. middlensis* sp. nov. *Ceeops* gen. nov. (type and only species *C. housensis* sp. nov.) is also mostly unsculptured and effaced, but has a greatly anteriorly expanded cranidium, broad librigenae, and very broad cephalic doublure. While their thin cuticles, general lack of sculpture, and weakly expressed dorsal furrows indicate they could be representatives of the same family-group taxon, there are also considerable morphological differences between them. Among other trilobites, they both have some resemblances, particularly in librigenal morphology, to bathyurids. However they are older than the oldest widely agreed species of bathyurids and they lack many bathyurid features. At present their affinity is difficult to assess with any confidence. • Key words: Trilobita, Lower Ordovician, Tremadocian, Laurentia, silicified, taxonomy.

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Post-Cambrian trilobites are classified in a series of reasonably well understood order-level groups (reviewed by Adrain 2013). While there are some families whose ordinal affinity is not obvious (see Adrain 2013, pp. 325–329), it is rare to encounter Ordovician trilobites whose family-group relationships are uncertain. This paper is concerned with two such genera, *Smoothcanyonops* gen. nov. and *Ceeops* gen. nov., both from the mid-Tremadocian Stairsian Stage of the shallow water northern Laurentian palaeo-margin. *Smoothcanyonops* and *Ceeops* have generally effaced morphology that does not closely resemble that of any other trilobites known from the Stairsian, and compares only loosely with some younger taxa in the Laurentian Lower Ordovician (chiefly some bathyurids). The Tremadocian is near the beginning of the stratigraphic range of many of the major post-Cambrian clades and there are some early taxa with less derived morphology whose affinity with newly appeared families is debatable. Adrain and Karim (2019, pp. 202–209), for example, revised the cheiruroidean *Tesselacauda* Ross, 1951, and discussed the historical uncertainty as to whether it represents Cheiruridae Hawle & Corda, 1847, or Pliomeridae Raymond, 1913. It is very rare, however, to find reasonably well known and obviously new genera whose relationships are completely obscure. The goals of this paper are 1) to propose two new, rare, Tremadocian genera from the Fillmore Formation, Great Basin, western USA; 2) to document the morphology of their constituent new species; and 3) to discuss the questions of their potential relationship to each other and to any other group of Ordovician trilobites.

Localities and stratigraphy

An intensive, field-based program sampling the shallow water trilobite faunas of the late Cambrian to early Middle Ordovician northern Laurentian palaeo-margin in what is now the Great Basin, western USA, has been underway since 1996, spurred by the recognition that most of the

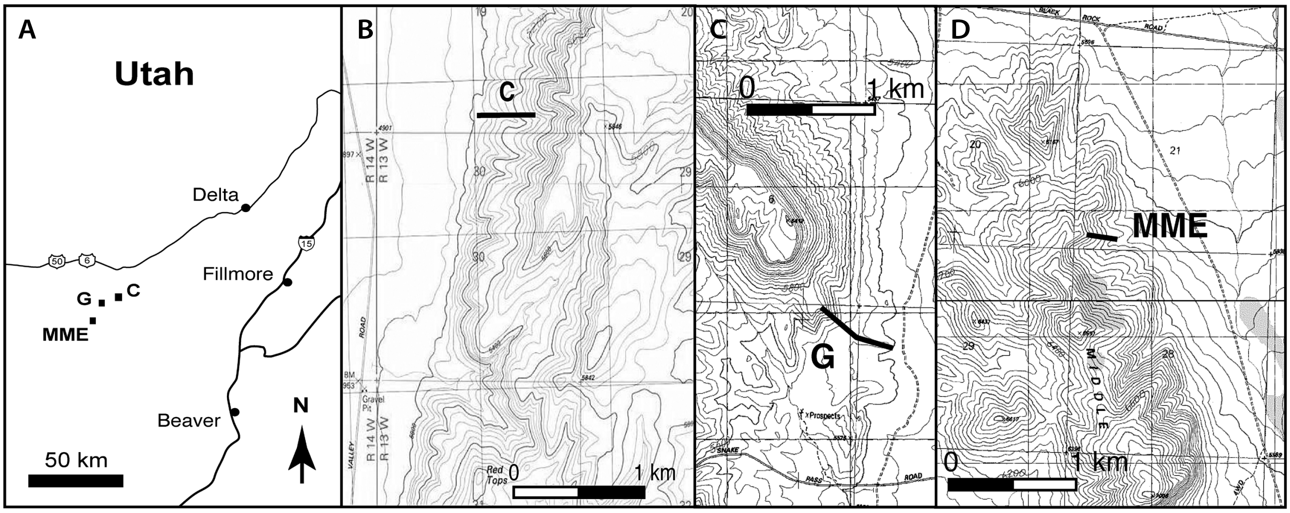


Figure 1. A – index map showing positions of sections from which material is described in Millard County, western Utah. • B – location and line of Section C in the southern House Range, Ibex area. • C – location and line of Section G in the southern Confusion Range, Ibex area. • D – location and line of Section MME at Middle Mountain, Ibex area.

trilobite diversity of the region had yet to be described. The faunas feature extensive and stratigraphically persistent preservation by secondary silicification, spanning the entire Lower Ordovician. Facies are mostly shallow water (above storm wave base), and the region formed part of the northern tropical margin of Laurentia. The rocks are mainly lime mudstones, calcisiltites, and intrarudites, with intervals of microbial buildups.

The history of study of the faunas was reviewed by Adrain *et al.* (2009), and until the present field program began in the late 1990s, it consisted chiefly of two monographs, one on southeastern Idaho faunas by Ross (1951) and one on western Utah faunas by Hintze (1953). A biostratigraphic and chronostratigraphic work published nearly half a century later (Ross *et al.* 1997) used trilobite data almost entirely based on these monographs.

Ross (1949, 1951) introduced a series of lettered (ostensible) assemblage zones which were adopted by Hintze (1953) and widely cited in the late 20th century literature for the Laurentian Lower Ordovician. Ross's (1951) and Hintze's (1953) taxonomic work was good for its time, but it became evident during the current work that they studied relatively few horizons, and the letter-based zones (given names based on genera by Ross *et al.* 1997) were mostly extrapolations over substantial stratigraphic intervals with very little published supporting data. On reinvestigation, they usually turned out to contain multiple intervals with completely different faunas (*i.e.* multiple zones). The letter-based scheme has now been entirely replaced by a species level system based on new sampling, with zonations for the upper Skullrockian (lower Tremadocian) (Adrain *et al.* 2025), Stairsian (mid-Tremadocian) (Adrain *et al.* 2014a), Tulean and Blackhillsian (upper Tremadocian through Floian) (Adrain *et al.* 2009) and Dapingian to lower Darriwilian (Adrain *et al.* 2012). Full details will not be repeated, but localities and stratigraphic intervals dealt with herein are briefly summarised.

Section G

Hintze's (1951, 1953) G Section (Fig. 1A, C), located in the southern Confusion Range on the west side of the Tule Valley, Millard County, western Utah, contains mid-Stairsian to mid-Tulean rocks of the Fillmore Formation. A newly measured and logged line of section was published by Adrain *et al.* (2009, appendix 1). The type horizon of *Smoothcanyonops smoothcanyonensis* gen. nov. sp. nov. is Section G 48.5 m (Fig. 2B). This horizon was assigned to what was then the uppermost Stairsian *Pseudohystricurus obesus* Zone by Adrain *et al.* (2014a). Ongoing work and new sampling, however, has shown that stratigraphic turnover of the upper Stairsian faunas was extremely rapid, and the interval is currently subject to revision. This horizon will be assigned to a new zone in a forthcoming work. New sampling has revealed the presence of additional faunas between it and the Stairsian–Tulean boundary. It is high, but not highest, Stairsian.

Section MME

Section MME (Fig. 1A, D) is not among those studied by Hintze (1951, 1953) but was newly measured in the course of current sampling. A complete section log was published by Adrain *et al.* (2014a, appendix 1). The section is in the northern part of Middle Mountain, which lies to the west of the Tule Valley. It begins in Skullrockian rocks of the uppermost House Formation and spans much of the Stairsian. Section MME 121.9 m (Fig. 2A) is the type horizon of *Smoothcanyonops middlensis* gen nov. sp. nov. This horizon (and MME 121.6 m, which also yielded material of the species) was assigned by Adrain *et al*. (2014a) to the *Pseudoclelandia cornupsittaca* Zone.

Section C

Hintze's (1951, 1953, 1973) C Section (Fig. 1A, B) is located in the southern House Range on the east side of the Tule Valley. It begins near the contact between the House Formation and Fillmore Formation, and contains a complete section of the Stairsian. Section C was remeasured, logged, and intensively sampled in 2024, and a complete section log will be published in a forthcoming work. All of the zones established by Adrain *et al.* (2014a) were located but, as noted earlier, additional previously unsampled diversity in the upper Stairsian necessitated revision and the forthcoming addition of new zones. Section C 69.0 m (Fig. 2C), however, is from lower in the stage, and its faunas represent the *Rossaspis leboni* Zone of Adrain *et al.* (2014a). It is the type horizon of *Ceeops housensis* gen. et sp. nov. Although this zone, associated with a widely distributed buildup interval, is well sampled from both Section MME to the west and from Section HC6 in the Garden City Formation in southeastern Idaho (see Adrain *et al*. 2009, 2014a), *Ceeops housensis* has not been encountered in those sections.

Systematic palaeontology

Terminology and repository. – Reference is made in descriptions to inflection points in the facial sutures using Greek letters as summarised by Whittington (1997, fig. 3). All type and figured specimens are housed in the Paleontology Repository, School of Earth, Environment, and Sustainability, University of Iowa, with specimen number prefix SUI.

Family Uncertain

Remarks. – There are two main questions about the affinities of *Smoothcanyonops* (Figs 4, 5) and *Ceeops* (Figs 5, 6): i) are they related to one another? and ii) can any potential relatives of either or both be posited among other known Laurentian Early Ordovician taxa?

Smoothcanyonops and *Ceeops* resemble each other in that they almost completely lack sculpture of any kind on dorsal or external surfaces, have dorsally subdued cranidial furrows, have relatively thin cuticles, and completely lack

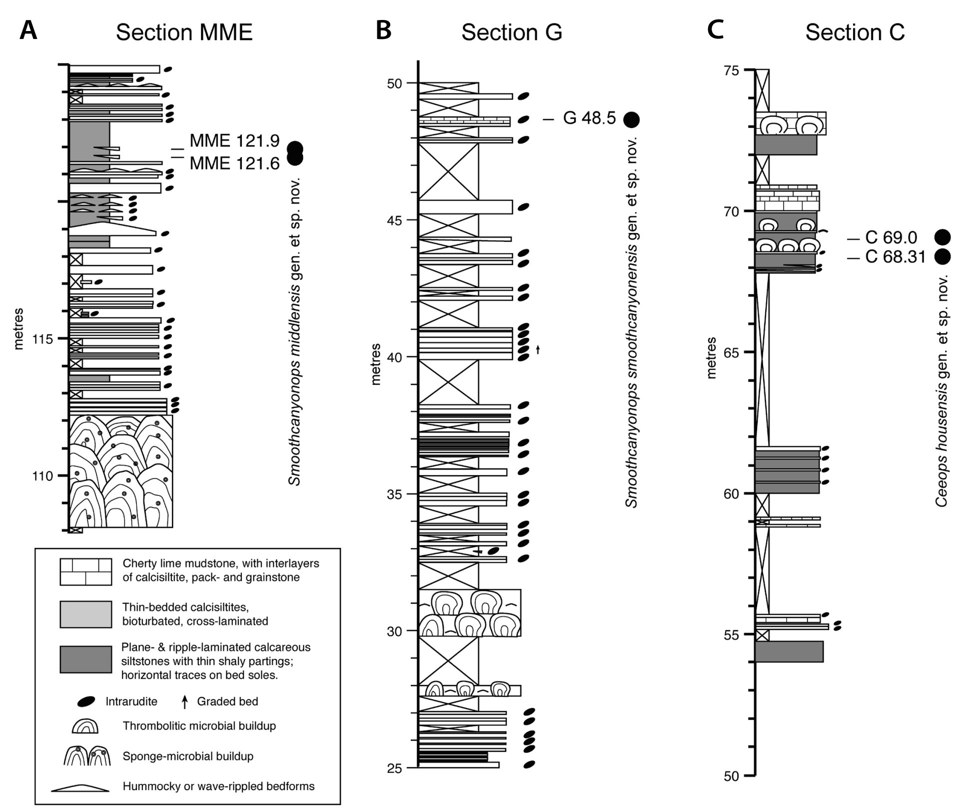


Figure 2. Portions of stratigraphic sections showing horizons from which material is described. • A – Section MME, Middle Mountain; description of the complete section was given by Adrain *et al*. (2014a, appendix 1). • B – Section G, southern Confusion Range; description of the complete section was given by Adrain *et al*. (2009, appendix 1). • C –Section C, southern House Range.

any expression of glabellar lobes or furrows. There are other, better understood, Stairsian taxa with one or more of these features, but none with all of them. Hence, it is possible that the genera are related.

There are also many reasons to doubt close relationship. *Smoothcanyonops* apparently has yoked librigenae, whereas *Ceeops* has an inferred hourglass-shaped rostral plate (see descriptions). Fusion of the connective sutures in one genus would not completely rule out a relationship, but it is rare to have such variation within family-group taxa. Cranidia are also obviously very different, with *Ceeops* having a hugely expanded, laterally protruded, frontal region, much longer anterior border, and far smaller palpebral lobes, as well as more effaced dorsal cranidial furrows. Pygidia are not very comparable, with those of *Smoothcanyonops* semicircular in outline, generally dorsally effaced, with four axial rings, and with broad borders and doublures, whereas those of *C. housensis* are more conventional looking, much shorter relative to their width, with (apparently) three axial rings, a narrower border, and fairly well expressed pleural and interpleural furrows. In the present state of knowledge, it is otherwise impossible to assess the likelihood of affinity between the genera. The question, along with that of their broader affinity (treated next) will require new discoveries or more obviously related taxa to address with any confidence.

The trilobite fauna of the Stairsian stage is taxonomically quite distinct, as it is bracketed by two severe mass extinctions which each nearly completely reset family-group diversity (Adrain *et al*. 2014a). While the faunas were surveyed zone by zone by Adrain *et al*. (2014a), detailed taxonomic work has yet to be published for much of the diversity. Described or revised thus far have been the hillyardinids *Metabowmania* Kobayashi, 1955 (Adrain & Westrop 2007a) and *Bearriverops* Adrain & Westrop, 2007b (initially described as a dimeropygid), the dimeropygid *Pseudohystricurus* Ross, 1951 (Adrain *et al*. 2014b), the cheirurid *Tesselacauda* Ross, 1951 (Adrain & Karim 2019), and the uncertainly classified *Gonioteloides* Kobayashi, 1955 (Adrain & Karim 2021). Nevertheless, all of the sampled diversity has to this point been extensively photographed and is in preparation for publication. With their strong degree of effacement, thin cuticle, and small eyes, neither *Smoothcanyonops* nor *Ceeops* has any convincingly comparable potential relative among other Laurentian Stairsian diversity. Many hillyardinids are at least somewhat effaced (see especially "Hillyardininae gen. nov. 2" of Adrain *et al*. (2014a, fig. 23j, n); see also species assigned to *Hyperbolochilus* Ross, 1951, in the same work) but *Smoothcanyonops* and *Ceeops* are obviously not hillyardinids, as they lack any of that clade's putative synapomorphies (Adrain & Westrop 2007a, p. 230). These include a median furrow in the preglabellar field, a fringe of small spines on the inner edge of the genal spine and posterior librigenal border, and a pygidium with rectangular spines transecting the pleurae at the fulcrum of each segment. Otherwise the only real point of comparison is comparatively effaced species assigned to "Hystricuridae gen. nov. 4" by Adrain *et al.* (2014a; see especially fig. 10i, m). This taxon, however, appears to be part of an as yet unnamed family-group clade including *Paraplethopeltis* Bridge & Cloud, 1947, and *Paenebeltella* Ross, 1951. Its pygidium (Adrain *et al*. 2014a, fig. 10m) is at least superficially similar to that of *Ceeops housensis* (Fig. 6L, N, O). Cranidial differences are profound, with that of "Hystricuridae gen. nov. 4" (Adrain *et al*. 2014a, fig. 10i) having much deeper and well expressed anterior border, preglabellar, axial, occipital, and posterior border furrows, a much shorter anterior border, and much larger palpebral lobes. In addition, the dorsal surface of all sclerites of "Hystricuridae gen. nov. 4" is covered with fine raised line sculpture, while that of *Smoothcanyonops* is entirely smooth and lacking sculpture of any kind whereas *Ceeops* only has faint raised lines on some librigenae. In sum, there are no other Stairsian trilobites for which a plausible case for relationship with either *Smoothcanyonops* or *Ceeops* can be made.

Among taxa from the overlying (upper Tremadocian to lower Floian) Tulean Stage are some that are at least superficially much more comparable. These are members of Bathyuridae Walcott, 1886, and in particular of Adrain's (2025, p. 659) "*Chapmanopyge* group", some of which are illustrated in Figure 7 for comparison. The *Chapmanopyge* group contains the genera *Chapmanopyge* Fortey & Bruton, 2013, *Ibexocephala* Adrain, 2025, *Licnocephala* Ross, 1951, *Punka* Fortey, 1979, and *Uromystrum* Whittington, 1953.

The earliest generally agreed bathyurids occur in Laurentia in the bottom-most faunas of the Tulean (see Adrain *et al*. 2009, fig. 7c, d, g, h). The questions of whether there are any older Laurentian bathyurids, and whether any Stairsian taxa might be assigned, depend on opinions about the affinity of genera such as *Randaynia* Boyce, 1989. Westrop *et al*. (1993) and Adrain & Westrop *in* Landing *et al*. (2012) considered *Randaynia* to be a bathyurid. In stark contrast, Fortey & Bruton (2013) thought that it belonged to an entirely different order (Asaphidae), assigning it to Symphysurinidae Kobayashi, 1955, which they thought belonged to Cyclopygoidea Raymond, 1925. The differing opinions about potential Stairsian bathyurids were summarised by Adrain & Karim (2021, p. 1024).

The most compelling bathyurid comparisons for *Smoothcanyonops* and *Ceeops* are in any case Tulean. Librigenae are the most generally similar. Those of *Ceeops housensis* (Fig. 6A–K) are very similar in overall dimensions and morphology to those of the younger *Punka*? sp. nov. (Fig. 7B) and *Chapmanopyge* sp. nov.

(Fig. 7C). All share a generally effaced external surface, a very narrow visual surface, strongly laterally convex anterior facial sutures, posterior facial sutures of limited extent, weak to obscure lateral and posterior border furrows, an anterior projection with broad doublure, a blade-like edge to the lateral margin, and flattened, triangular, genal spines with a broad base. Those of *Smoothcanyonops smoothcanyonensis* resemble those of other species of *Chapmanopyge* (Fig. 7F), which are narrower, with considerably reduced fields. Even considering the librigenae in isolation from the rest of the trilobites, however, there are significant differences. Those of *Smoothcanyonops* appear to have been yoked, a condition unknown in Bathyuridae, all of which have a rostral plate or in some rare cases a rostellum. All bathyurid librigenae for which information is available have a Panderian notch in their librigenal doublure near the posterior facial suture (*e.g.* Adrain *et al*. 2011, fig. 1). While this region is not completely preserved in available librigenae of *Smoothcanyonops* (Figs 3H, S; 4I) there is no evidence of a notch, and a Panderian notch is definitively absent from *Ceeops* (Fig. 6F, K). Librigenae of members of the *Chapmanopyge* group also universally have some form of raised line sculpture around the base of the genal spine or along the lateral margin. The librigenae in Figure 7 were chosen for comparison specifically because they represent species with relatively subdued sculpture, which compare more closely to the externally smooth *Smoothcanyonops* and *Ceeops*. Even these, however, show raised lines on the external surface along the lateral margin (most easily seen in Fig. 7B). While a few specimens of *Ceeops housensis* show faint raised line sculpture (particularly Fig. 6A; see description), most are smooth and there is no sculpture whatsoever on the external librigenal surface of either species of *Smoothcanyonops*.

Once cranidia and pygidia are considered, the notion of relationship becomes much more difficult to sustain. In particular, *Chapmanopyge* group bathyurids (Fig. 7A, D) have large, very anteriorly extended glabellae with a very short preglabellar field, and huge palpebral lobes whose curved outline describes more than a semicircle and which nearly directly abut the glabella with little interocular fixigenae. Pygidia are also scarcely comparable, as those of members of the *Chapmanopyge* group tend to be wide and fan-shaped,with very wide borders and doublures (Fig. 7E, G). They closely resemble those of neither *Smoothcanyonops* nor *Ceeops*.

Hence, it seems likely that the reasonably compelling similarities between the shape and dimensions of the librigenae of all of the taxa concerned are superficial. Cranidia and pygidia show few features that would indicate relationship, and the librigenae of *Smoothcanyonops* and *Ceeops* are missing some librigenal features that are universal in the *Chapmanopyge* group. At the moment, then, the family relationship of *Smoothcanyonops* and *Ceeops* is obscure.

Genus *Smoothcanyonops* gen. nov.

Type species. – *Smoothcanyonops smoothcanyonensis* sp. nov, from the Fillmore Formation (mid-Tremadocian; upper Stairsian), western Utah, USA.

Other species. – *Smoothcanyonops middlensis* sp. nov., Fillmore Formation (mid-Tremadocian; Stairsian; *Pseudoclelandia cornupsittaca* Zone), western Utah, USA.

Etymology. – From Smooth Canyon, which is near to the type locality of the type species, and the Greek noun *ops*, eye. Gender is masculine.

Diagnosis. – All dorsal/external surfaces smooth and entirely lacking in sculpture; anterior border long (sag., exsag.), anterior border furrow very shallow dorsally; long preglabellar field present; palpebal lobes large, separated from glabella by broad interocular fixigenae; glabella weakly inflated, narrower anteriorly, fully circumscribed by axial and preglabellar furrows; glabellar furrows and lobes not expressed; LO relatively long, lacking median node; posterior projection short (exsag.) and strap-like; librigenae apparently yoked; eye long; lateral and posterior border furrows almost entirely effaced; lateral border and doublure very broad; long triangular genal spine with broad base, tapering to a pointed tip; pygidium sub-semicircular in outline; axis relatively short with four axial rings; ring furrows nearly effaced; pleural and interpleural furrows dorsally obscure; border and doublure broad.

Remarks. – Both species of *Smoothcanyonops* are extraordinarily rare at their respective horizons, and only the dissolution of several hundreds of kilograms of limestone through the years led to the accumulation of enough specimens for formal description. There is no question of matching of sclerites – strong morphological correspondence, morphology so unusual that the taxon‘s affinity is obscure, and the absence of any other species with which any of the sclerite types might be associated in either occurrence confirm the sclerite association beyond doubt.

***Smoothcanyonops smoothcanyonensis* sp. nov.**
Figure 3

1953 *Licnocephala* ? sp. – Hintze, p. 192, pl. 8, fig. 7a, b.

Holotype. – Cranidium, SUI 149007 (Fig. 3A, E, I, N).

Type horizon and locality. – Section G 48.5 m, Fillmore Formation (mid-Tremadocian; unnamed new upper Stairsian zone above the *Pseudoclelandia cornupsittaca* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

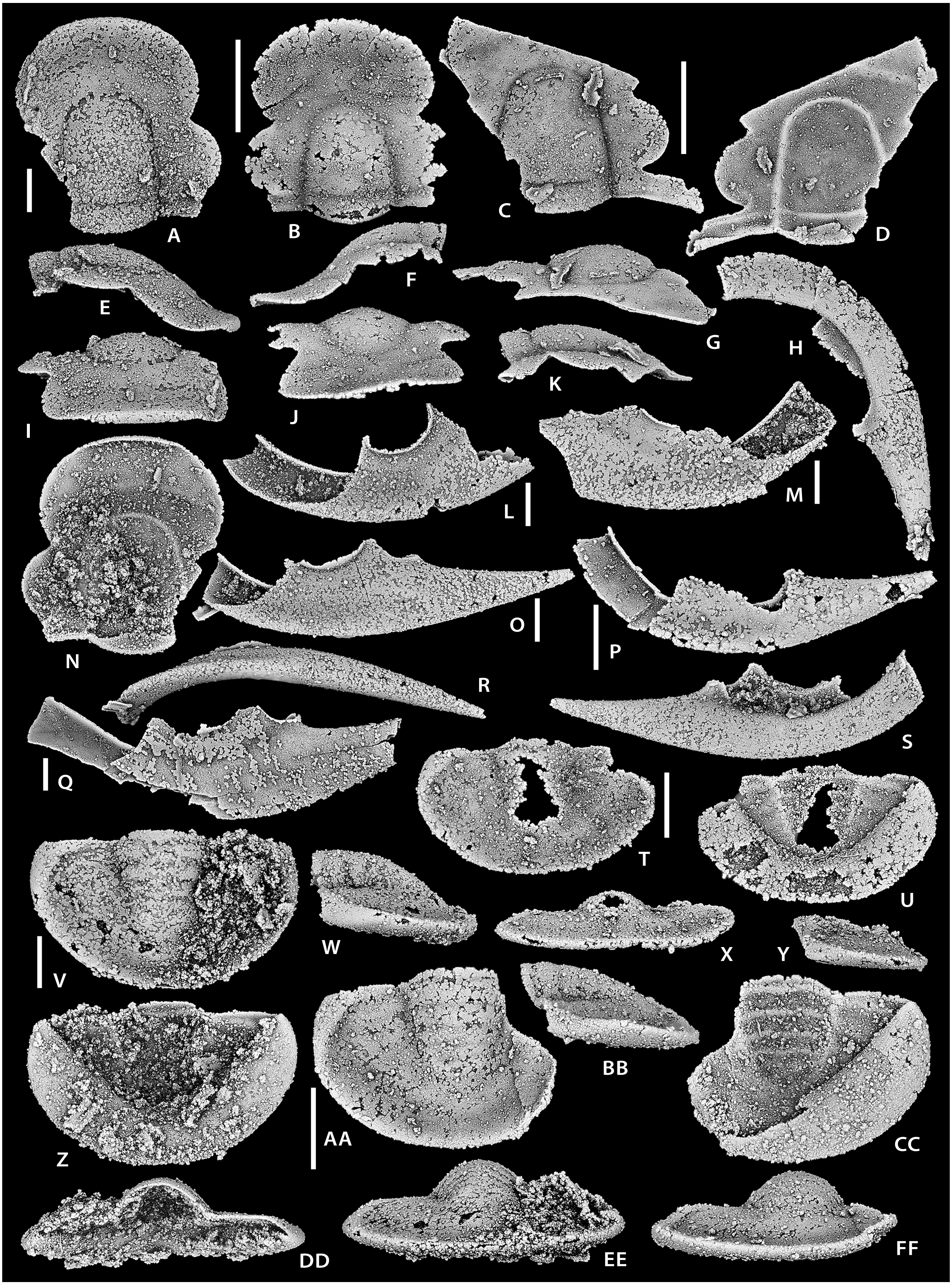
Other material. – Assigned specimens SUI 149008–149014, 152228–152230, from the same horizon as the holotype.

Etymology. – From Smooth Canyon.

Diagnosis. – Cephalic doublure (and hence anterior cranidial and lateral librigenal borders) very broad; anterior border furrow impressed ventrally as a distinct ridge; librigenal field very narrow; pygidial doublure very broad.

Description. – Where features (palpebral lobe and posterior projection) are preserved on only one side of a specimen, ratios were calculated by doubling the distance to the sagittal midline. Ratios throughout the paper are reported as means and ranges – the species are so rare that in many cases multiple specimens cannot be measured, in which case a single percentage is given. Cranidium with width across maximum divergence of anterior facial sutures (β) 86% (84–88%) sagittal length and 85% (83–87%) width across midlength of palpebral lobes (δ); anterior margin anteriorly arcuate, more transverse in median part, strongly and evenly curved adaxially; position where facial suture cuts margin (α) not easily discerned dorsally, with no break in curvature of the cranidial outline; entire cranidium lacking dorsal sculpture of any kind; anterior border difficult to delineate in dorsal view, as anterior border furrow is largely effaced, but the border furrow and hence the length of the border is clear in ventral view (Fig. 3N); anterior border with sagittal length 23% cranidial sagittal length, smooth, dorsal surface slightly dorsally concave (Fig. 3E, F), sloping from contact with preglabellar field at effaced anterior border furrow relatively steeply down, but shallower anteriorly until about subparallel to the plane of the palpebral lobes, anteriormost sector slightly expanded into a subdued subcylindrical rim, forming a narrow, curved anterior edge lacking sculpture in anterior view (Fig. 3I); anterior border furrow dorsally obscure (Fig. 3A, B) to faintly impressed (Fig. 3C, intact left side), preglabellar field and frontal areas largely confluent with border; anterior facial sutures originating at α, positioned to cut the cranidial margin almost exactly in front of the anterior end of the axial furrow (Fig. 3N), describing nearly even, parenthesis-shaped lateral arc (Fig. 3A, C); palpebral lobe with γ set more adaxially than ε, width (tr.) 14% width across δ; lobes held essentially horizontally in lateral (Fig. 3E, F) and anterior (Fig. 3G, I, J) view, top surface dorsally convex, sloping down from inner edge toward lateral margin (Fig. 3I, J), positioned only slightly higher than interocular fixigena and well below top of glabella in either lateral or anterior view; frontal area, interocular fixigena, and palpebral lobe confluent with one another, smooth, with very slight dorsal inflation; palpebral furrow expressed only ventrally at posteriormost part of lobe (Fig. 3D) as small ridge curving strongly around ε; interocular fixigena with width (tr.) 11% width across δ, sloped downward very gently from contact with base of palpebral lobe toward axial furrow (Fig. 3G, H, J); glabella with sagittal length (excluding LO) 48% (45–51%) cranidial sagittal length, maximum width (at base) 92% glabellar sagittal length; axial furrows narrow, moderately deep, gently anteriorly convergent, very slightly bowed laterally in posterior half (best seen ventrally in Fig. 3D), forming fairly sharp break in course at contact with preglabellar furrow; preglabellar furrow similar in depth to axial furrows, describing gentle anteriorly directed arc, slightly less curved in median region; glabella with no sign of delineated glabellar lobes or furrows, even ventrally, completely lacking in surface sculpture, very weakly dorsally inflated; SO not as long (sag., exsag.) as axial furrows are wide (tr.), slightly shallower than axial furrows, more or less transverse but with slight posterior curvature; LO with sagittal length 13% cranidial sagittal length, slightly longer sagittally than exsagittally, posterior margin with stronger posterior curvature than SO, lacking any sculpture including median node; posterior fixigena consisting only of a very short (exsag.) strip immediately in front of posterior border furrow, best seen ventrally (Fig. 3D); width across posterior projections is maximum width of cranidium, extended well laterally past lateral edge of palpebral lobe, but direct comparison to sagittal length is not possible on any specimen due to incomplete preservation, running posterolaterally at about 30 degrees from transverse line, relatively short (exsag.), anterior and posterior margins straight and subparallel for most of width, posterior facial suture curved around distal extremity and posterior

Figure 3. *Smoothcanyonops smoothcanyonensis* gen. et sp. nov, from Section G 48.5 m, Fillmore Formation (mid-Tremadocian; upper Stairsian), southern Confusion Range, Ibex area, Millard County, western Utah, USA. A, E, I, N – holotype cranidium, SUI 149007, dorsal, right lateral, anterior, and ventral views. B, F, J – cranidium, SUI 149008, dorsal, left lateral, and anterior views. C, D, G, K – cranidium, SUI 149009, dorsal, ventral, anterior, and right lateral views. H, P – left librigena, SUI 149010, ventral and external views. L – left librigena, SUI 149011, external view. M – right librigena, SUI 149012, external view. O, R, S – left librigena, SUI 149013, external, ventrolateral, and internal views. Q – left librigena, SUI 149014, external view. T, U, X, Y – pygidium, SUI 152228, dorsal, ventral, posterior, and left lateral views. V, W, Z, DD, EE – pygidium, SUI 152229, dorsal, left lateral, ventral, anterior, and posterior views. AA–CC, FF – pygidium, SUI 152230, dorsal, left lateral, ventral, and posterior views. Scale bars = 1 mm.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border with slight posterior, triangular, extension at tip (Fig. 3C); ventrally, no eye ridge or fossula visible; no doublure underlying anterior border, suture cuts across immediately beneath anterior margin; doublure below LO forming elliptical articulating surface, slightly ventrally concave, with no obvious raised line sculpture; short (exsag.) wedge-shaped doublure, longest (exsag.) distally, developed under distal half of posterior projection.

Librigenae mostly likely yoked and fused with rostral plate, as most intact anterior projections (both 3L and 3P, H), when positioned in juxtaposition with cranidia, cross the sagittal line before the point of apparent breakage; field, lateral border, and dorsal aspect of genal spine merged into single uninterrupted surface; small and narrow (tr.) field slightly distinguished from broader lateral border by subtle change in slope (Fig. 3L, M), but otherwise posterior and lateral border furrows completely dorsally effaced; broad lateral border with slight dorsal concavity (Fig. 3L); visual surface not preserved on any specimen, but relatively large and long (exsag.), separated from field by narrow, shallow furrow; course of anterior section of facial suture as described for cranidium; anterior projection broad and long, with considerable ventral convexity, anterior margin cut by suture immediately at edge, posterior margin with strongly upturned "wall" along inner edge of doublure, anterior projections apparently yoked and medially contiguous, no sign of any trace of connective suture; lateral margin formed into slightly inflated, blade-like edge (Fig. 3O, R, S), narrow anteriorly in ventrolateral view (Fig. 3R) but wider posteriorly at base of genal spine, lacking any dorsal or ventrolateral raised line sculpture; lateral margin describing weak lateral arc from α to opposite base of genal spine, lateral margin of spine nearly straight; posterior facial suture not complete on any single specimen, but course as described for cranidial posterior projection; posterior edge of posterior border forming only tiny area in front of base of genal spine (Fig. 3O, Q); genal spine with very broad base and triangular outline, dorsoventrally flattened (Fig. 3R), adaxial edge with slight posterior curvature; edges posteriorly convergent to evidently sharp tip; genal spine long (exsag.), with estimated length from base to tip 79% exsagittal length from β to base; doublure very broad with moderate ventral convexity, nearly smooth but with faint sculpture of moderately spaced raised lines subparallel with one another and the lateral margin (Fig. 3H, S); doublure underlying adaxial base of genal spine and posterior border with ventrally concave depression (Fig. 3H, S), no Panderian notch visible (Fig. 3H), but preservation of the region is generally poor among available specimens.

Rostral plate, hypostome, and thorax not recovered.

Pygidium with sagittal length 61% (59–63%) maximum width; maximum (anterior) width of axis 34% maximum pygidial width; sagittal length of axis 65% (63–66%) pygidial sagittal length; fulcrum set 79% of distance abaxially from sagittal plane; articulating half ring very short (sag., exsag.), longer sagittally, lacking any sculpture; anterior margin of pleura transversely straight (Fig. 3T, V, AA); axial furrows shallow, mainly represented as a significant break in slope between the flat proximal pleura and the inflated axis, gently posteriorly convergent, very shallow posteriorly but meeting medially to fully circumscribe axis, posterior shape a shallow "U"; axial rings very weakly inflated, of similar length sagittally and exsagittally; ring furrows short (sag., exsag.), transverse, and very shallow; the specimen with the best preserved axis, both dorsally and ventrally (Fig. 3AA, CC) shows that there are four axial rings, with a crescent-shaped terminal piece; pleural regions adaxial to fulcrum dorsally flat, lacking sculpture, with very faint impressions of pleural and interpleural furrows, which are better expressed ventrally (Fig. 3U, CC) though still faint; anterolateral corner of pygidium developed into a relatively short (exsag) and posteriorly narrow (tr.) articulating facet with moderate rim-like inflation and lacking sculpture; border furrow not impressed, marked as a change in slope and concavity between flat adaxial pleura and slightly dorsally concave border; pygidial outline with nearly anteroposteriorly aligned region along fulcrum by anterolateral corner, more posterior margin describing a portion of a semicircle, with even posterior curvature; border very broad, inner edge abutting rear of axis, much of thickness forming a shallow dorsal trough (see especially Fig. 3AA), region immediately adjacent to margin forming slightly thickened rim, most evident in posterior aspect (Fig. 3X, EE, FF), entirely without sculpture; doublure broad, matching border, with moderate ventral convexity, inner edge turned dorsally, sculpture of very faint subparallel raised lines similar to that of librigena.

Remarks. – *Smoothcanyonops smoothcanyonensis* is compared with *S. middlensis* under discussion of the latter species.

***Smoothcanyonops middlensis* sp. nov.**
Figure 4

Holotype. – Cranidium, SUI 152231 (Fig. 4A, B, D, G, L).

Type horizon and locality. – Section MME 121.9 m, Fillmore Formation (mid-Tremadocian; Stairsian; *Pseudoclelandia cornupsittaca* Zone), Middle Mountain, Ibex area, Millard County, western Utah, USA.

Other material. – SUI 152232–SUI 15234, from the same horizon as the holotype and from Section MME 121.6 m.

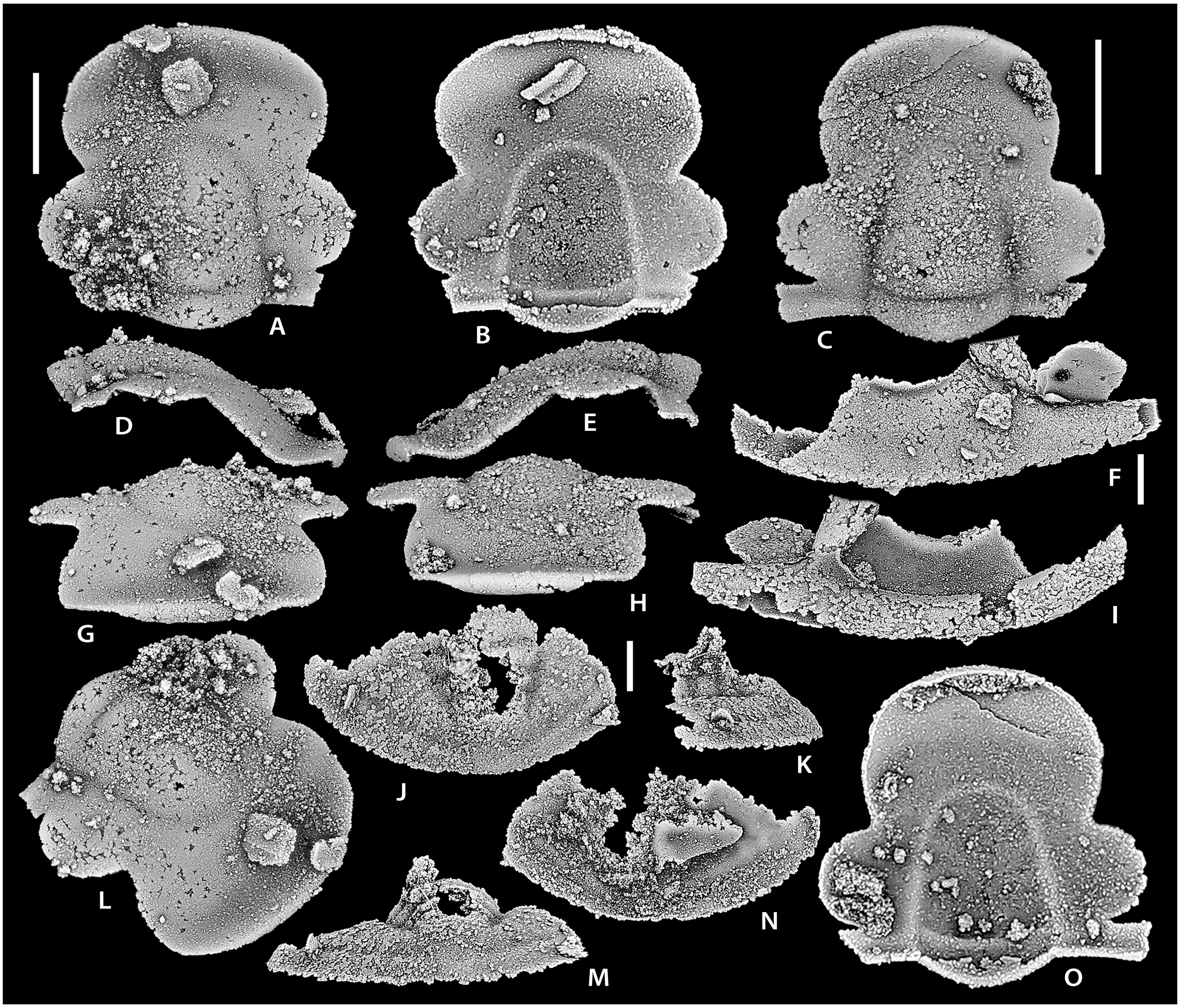

Figure 4. *Smoothcanyonops middlensis* gen. et sp. nov., from Section MME 121.6–121.9 m, Fillmore Formation (mid-Tremadocian; upper Stairsian; *Pseudoclelandia cornupsittaca* Zone), Middle Mountain, Ibex area, Millard County, western Utah, USA. A, B, D, G, L – holotype cranidium, SUI 152231, dorsal, ventral, right lateral, anterior, and oblique views (MME 121.9 m). C, E, H, O – cranidium, SUI 152232, dorsal, left lateral, anterior, and ventral views (MME 121.9 m). F, I – left librigena, SUI 152233, external view (MME 121.6 m). J, K, M, N – pygidium, SUI 152234, dorsal, left lateral, posterior, and ventral views (MME 121.6 m). Scale bars = 1 mm.

Etymology. – From Middle Mountain.

Diagnosis. – Anterior border relatively short (sag.; exsag.); anterior border furrow marked by break in slope, but not otherwise delineated, even ventrally; anterior sections of facial sutures with subparallel, anteroposteriorly aligned course in front of β; librigenal field relatively broad; librigenal doublure relatively narrow; pygidial doublure relatively narrow.

Description. – *Smoothcanyonops middlensis* is similar enough to *S. smoothcanyonensis* that description is best accomplished via differential comparison listing all perceived morphological differences. Anterior facial suture with more anteroposteriorly aligned course in front of β versus laterally bowed over entire course; anterior border shorter (sag.; exsag.); anterior border furrow not impressed either dorsally or ventrally, versus clearly expressed as a ventral ridge; preglabellar furrow not as well expressed dorsally, shallower than axial furrows versus about equally well expressed; glabella narrower anteriorly, preglabellar furrow more strongly anteriorly arcuate.

Librigenal doublure much narrower (*cf*. Fig. 4I with Fig. 3S), field concomitantly much wider; base of genal spine much narrower and tube-like, portion of the proximal spine that is preserved tapered less rapidly posteriorly.

Rostral plate, hypostome, and thorax not recovered.

Pygidial border much narrower, about half as wide as in *S. smoothcanyonensis* at any respective anteroposterior position.

Remarks. – Although known from only four sclerites, there is enough represented (cranidia, librigena, pygidium) to get an adequate sense of the morphology of the species and in particular to document its clear differentiation from the younger type species. Given the extreme rarity of *Smoothcanyonops*, it seems reasonable to formally name *S. middlensis* rather than to consign it to open nomenclature.

Smoothcanyonops middlensis is very similar to *S. smoothcanyonensis*, and superficial comparison might not immediately suggest that they are different species. They are, however, clearly differentiated in a number of features of each of the available sclerite types. The main difference is that *S. middlensis* has considerably narrower borders and doublure, and this is reflected in the respective length of the cranidial anterior border, the width of the librigenal lateral border and doublure, and the pygidial doublure. The much narrower doublure means that the librigenal field of *S. middlensis* is about twice as wide as that of *S. smoothcanyonensis*, despite the sclerites being of very similar overall dimensions. The cranidium shows obvious differences in the shape of the anterior facial suture, with an antero-posteriorly oriented segment in front of β in *S. middlensis* versus continuously laterally arcuate. Although the preglabellar furrows are equally well expressed as ventral ridges in either species (Figs 3D, 4B), that of *S. middlensis* is considerably shallower and more faint dorsally. The general area of the glabella relative to the cranidium is smaller in *S. middlensis* and the axial furrows converge more strongly anteriorly so that the front of the glabella is narrower. The genal spine of *S. middlensis* has a much narrower base and is more subcylindrical versus subtriangular. While comparisons of much of the pygidial morphology are hampered by the poor state of preservation of the only available example of *S. middlensis* (Fig. 4J, K, M, N), the shape of its border is unequivocal, and matches the situation seen in the cephalic border, as it is much narrower than the pygidial border of *S. smoothcanyonensis*.

Genus *Ceeops* gen. nov.

Type species. – *Ceeops housensis* sp. nov, from the Fillmore Formation (mid-Tremadocian; Stairsian; *Rossaspis leboni* Zone), western Utah, USA.

Other species. – Monotypic.

Etymology. – From Section C and the Greek noun *ops*, eye. Gender is masculine.

Diagnosis. – Most dorsal surfaces smooth and lacking sculpture, with the exception of some raised lines on some of the librigenae; cranidium with frontal regions anterior to the anterior edge of the palpebral lobe and front of glabella greatly laterally expanded; anterior sections of facial suture strongly anteriorly divergent between γ and β; anterior border very long; anterior border furrow shallow, mostly a break in slope dorsally; preglabellar field present but relatively short; palpebral lobe relatively small and narrow, base set near glabella with narrow interocular fixigena; axial and preglabellar furrows narrow and shallow, but fully discernible dorsally, axial furrows curving into preglabellar furrow with no obvious inflection point; glabella weakly inflated, glabellar lobes and furrows not expressed; LO long (sag.); posterior projection with posterior border furrow not expressed, turned strongly posteriorly; librigena with small eye, relatively wide trapezoidal field, and extremely wide lateral border and doublure; genal spine with very broad base, flattened, triangular in outline; hourglass shaped rostral plate inferred to be present; pygidium short (sag.) and wide (tr.), axis with at least three axial rings, doublure relatively narrow (especially as compared with cephalon).

Remarks. – The question of affinity with *Smoothcanyonops* and other taxa was addressed earlier.

***Ceeops housensis* sp. nov.**
Figures 5, 6

Holotype. – Cranidium, SUI 152235 (Fig. 5A, D, G, J, M).

Type horizon and locality. – Section C 69.0 m, Fillmore Formation (mid-Tremadocian; Stairsian; *Rossaspis leboni* Zone), southern House Range, Ibex area, Millard County, western Utah, USA.

Other material. – Assigned specimens SUI 152236–152249, from the same horizon as the holotype and Section C 68.3–68.6 m.

Etymology. – From the House Range.

Diagnosis. – As for genus.

Description. – Percentages are based on the large holotype cranidium. Cranidium considerably effaced, lacking any dorsal sculpture; maximum width (across β, maximum divergence of anterior facial sutures) 98% sagittal length; width across midlength of palpebral lobes (δ) 72% width across β; anterior sections of facial sutures strongly anteriorly divergent in front of γ, laterally bowed, more gently curved around β, and strongly anteriorly convergent in front of β; anterior margin of cranidium

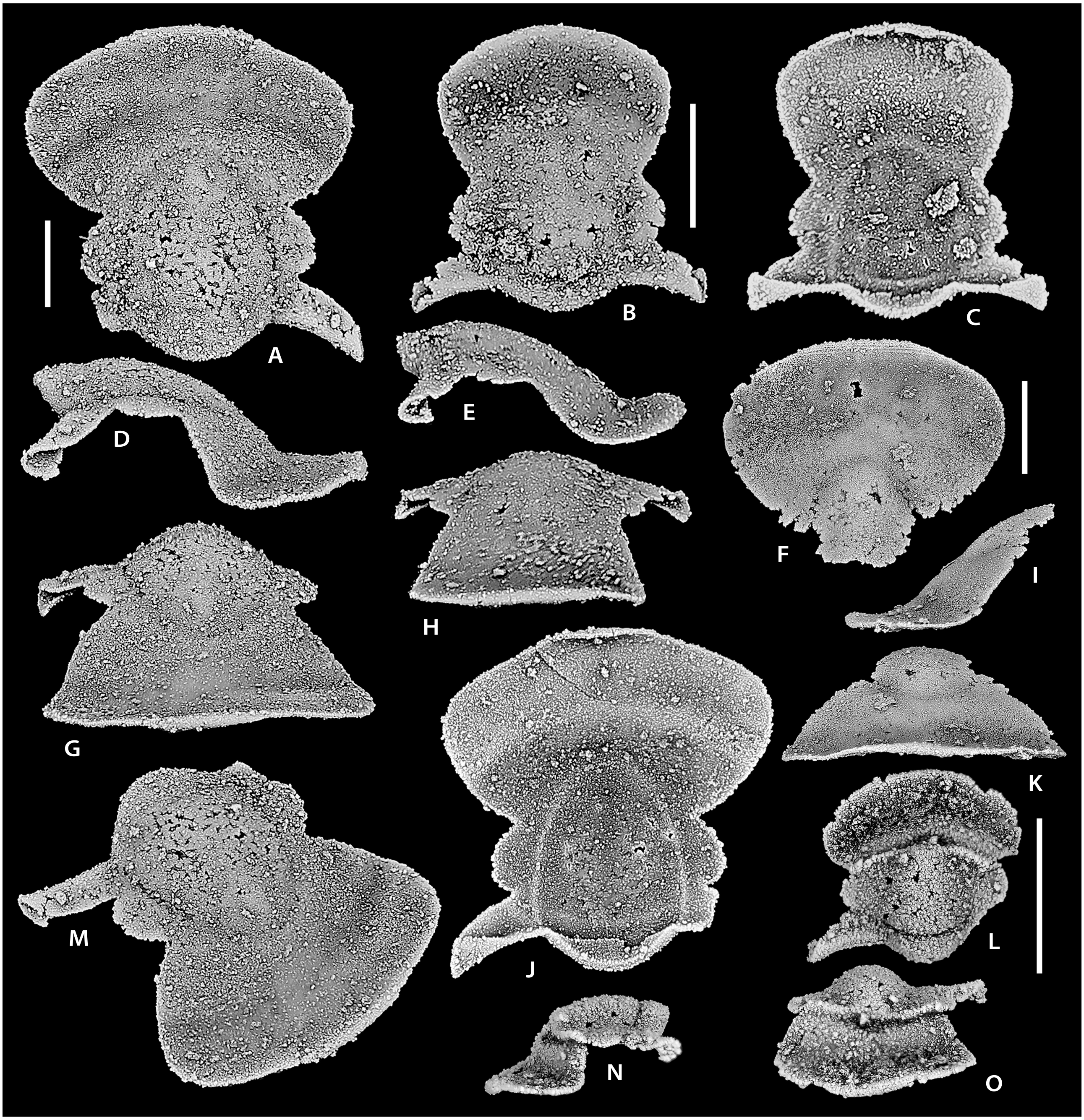

Figure 5. *Ceeops housensis* gen. et sp. nov., from Section C 69.0 m, Fillmore Formation (mid-Tremadocian; Stairsian; *Rossaspis leboni* Zone), southern House Range, Ibex area, Millard County, western Utah, USA. A, D, G, J, M – holotype cranidium, SUI 152235, dorsal, right lateral, anterior, ventral, and oblique views. B, C, E, H – cranidium, SUI 152236, dorsal, ventral, right lateral, and anterior views. F, I, K – cranidium, SUI 152237, dorsal, left lateral, and anterior views. L, N, O – cranidium, SUI 152238, dorsal, left lateral, and anterior views. Scale bars = 1 mm.

is almost entirely composed of the facial sutures, with α spaced closely together to form narrow median area with anterior cephalic rim (matched ventrally by doublure, Fig. 5J) that is subcylindrical in anterior profile (Fig. 5G); anterior border very long (sag.), appearing somewhat shorter exsagittally because it is cut anteriorly by the facial suture and part of the border lies on the librigenal anterior projection, sagittal length 26% cranidial sagittal length; anterior border essentially flat, lacking dorsal sculpture with the exception of very fine subparallel raised lines near the median rimmed anterior margin (best seen in Fig. 5F), very slightly dorsally concave in sagittal profile (Fig. 5E, I); anterior border furrow marked mainly by distinct break in slope between border and front areas/preglabellar field, on largest specimen appearing dorsally as a very shallow trough, gently and evenly anteriorly arcuate, approximately subparallel with anterior cranidial margin; preglabellar field with sagittal length 12% that of cranidium, with slight dorsal inflation in sagittal profile, sloped steeply from front of glabella toward anterior border, forming an angle of about 135° with the border; frontal areas smooth and with similar slight dorsal inflation as preglabellar field; palpebral lobes with exsagittal length 22% cranidial sagittal length, narrow, with width 11% width across δ, dorsally smooth, sloped slightly ventrolaterally in anterior profile (Fig. 5G, H), γ set slightly adaxial to ε, lateral margin with slightly stronger lateral curvature posteriorly versus anteriorly; front area, interocular fixigena, and posterior fixigena intergrade with no significant changes in slope or interrupting features, all completely dorsally smooth; palpebral furrow not expressed dorsally or ventrally; glabella excluding LO with maximum width (opposite rear of palpebral lobes) 95% sagittal length; axial furrows shallow and very narrow, better expressed ventrally (Fig. 5J) than dorsally (Fig. 5A), weakly laterally bowed, slightly anteriorly divergent in front of contact with SO, reaching maximum point of divergence opposite rear of palpebral lobes, increasingly anteriorly convergent in front of this point, running with no break in curvature or inflection point into preglabellar furrow; preglabellar furrow of similar length (exsag.; sag.) to width (tr.) of axial furrow, and of similar depth, strongly curved around front of glabella to form shallow inverted "V" shape; glabella with little independent dorsal inflation in sagittal profile, following curvature of LO and preglabellar field (Fig. 5D); no glabellar lobes or furrows visible, dorsally or ventrally, and glabella completely lacking dorsal sculpture; posterior projection extended laterally just past abaxial margin of anterior facial suture, length (exsag.) similar along most of width, about 14% cranidial sagittal length, projection turned strongly posterolaterally and curved posteriorly; posterior facial suture cutting distally across tip of furrow to posterolateral point; curvature of posterior facial suture across width of projection stronger than curvature of posterior margin; posterior border furrow not visible either dorsally or ventrally, and posterior border scarcely developed, confluent with posterior fixigena; SO very shallow and weakly defined dorsally, somewhat stronger ventrally, slightly posteriorly arcuate, similarly impressed sagittally and exsagittally; LO long, sagittal length 15% that of cranidium, tapered in length exsagittally, at lateralmost point near axial furrows only 9% as long as sagittal cranidial length, with slight independent dorsal inflation in sagittal profile (Fig. 5D), lacking any dorsal sculpture, posterior margin strongly bowed posteriorly; relatively large doublural articulating surface beneath LO (Fig. 5J), slightly ventrally concave, lacking obvious sculpture; triangular doublure underlying posterior projection, longest (exsag.) near tip, lacking sculpture; tiny piece of very short (sag.; exsag.) doublure underlying median part of anterior margin between closely spaced α.

Librigena with maximum width (behind eye) 40% (38–41%) length from intersection of inner edge of anterior projection doublure with anterior section of facial suture to tip of genal spine; visual surface small, width 10% maximum librigenal width and length (exsag.) 16% length from intersection of inner edge of anterior projection doublure with anterior section of facial suture to tip of genal spine; visual surface laterally curved, separated from field by very narrow, shallow furrow; posterior section of facial suture cutting posterior border just abaxial to lateral extent of visual surface; lateral border, field, posterior border, and dorsal aspect of genal spine nearly confluent and subplanar; some specimens (Fig. 6B, D, G) appear to completely lack sculpture on the subplanar surface but one (Fig. 6A) has faint U-shaped raised lines along the genal spine and near the posterior part of the lateral border; fine and faint raised lines may be present, subparallel to the margin, present on dorsal border portion of anterior projection (see especially Fig. 6H; faint subparallel lines may be present near the adaxial margin of the genal spine (Fig. 6A, G); posterior and lateral border furrows visible but extremely shallow and nearly effaced in some specimens (Fig. 6D, H), completely obscure in others (Fig. 6A, G); where present lateral border with moderate lateral curvature, posterior border with limited course; lateral border flat, with gentle dorsal concavity, terminating in a sharp, blade-like, lateral margin; margin with strong lateral curvature from front of anterior projection to base of genal spine; anterior projection with very broad, ventrally somewhat complex, doublure, apparently not extending to cranidial sagittal midline, inner edge of doublure turned strongly dorsally to form "walled" rim, presumptively intact connective suture (Fig. 6D) adaxially bowed; base of genal spine very broad, completely confluent with lateral border, blade-like edge of lateral border continued more than half way down ventrolateral aspect of spine (Fig. 6C, E), adaxial edge of spine more inflated and rounded, spine with moderate posterior curvature, inner edge more curved than outer edge; genal spine long, straight line distance from intersection of inner edge of anterior project and anterior facial suture to ω 53% straight line distance from ω to tip of spine; doublure very broad, with gentle ventral convexity, sculpture of subparallel raised lines over entire width, more closely spaced near inner edge, more prominent in small specimen (Fig. 6K) than large (Fig. 6F); no Panderian opening present; underside of genal spine smooth, lacking in raised line sculpture.

Rostral plate not recovered, but the morphology of the largest librigena (Fig. 6D–F), which seems to have a nearly intact connective suture, would indicate

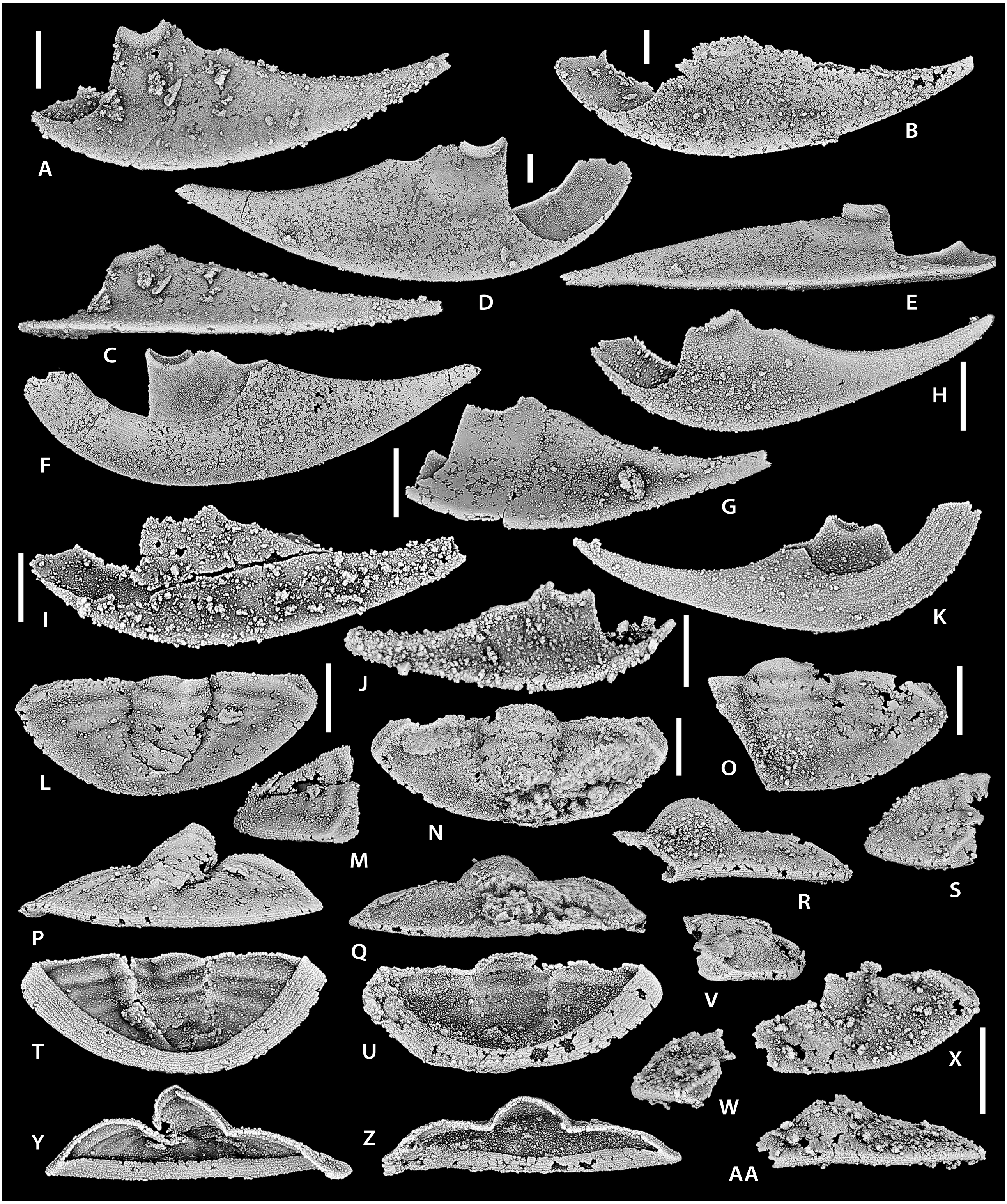

Figure 6. *Ceeops housensis* gen. et sp. nov., from Section C 69.0 m (except G, from 68.3–68.6 m), Fillmore Formation (mid-Tremadocian; Stairsian; *Rossaspis leboni* Zone), southern House Range, Ibex area, Millard County, western Utah, USA. A, C – left librigena, SUI 152239, external and ventrolateral views. B – left librigena, SUI 152240, external view. D–F – right librigena, SUI 152241, external, ventrolateral, and internal views. G – left librigena, SUI 152242, external view. H, K – left librigena, SUI 152243, external and internal views. I – left librigena, SUI 152244, external view. J – right librigena, SUI 152245, external view. L, M, P, T, Y – pygidium, SUI 152246, dorsal, right lateral, posterior, ventral, and anterior views. N, Q, U, V, Z – pygidium, SUI 152247, dorsal, posterior, ventral, left lateral, and anterior views. O, R, S – pygidium, SUI 152248, dorsal, posterior, and right lateral views. W, X, AA – pygidium, SUI 152249, right lateral, dorsal, and posterior views. Scale bars = 1 mm, except J = 0.5 mm.

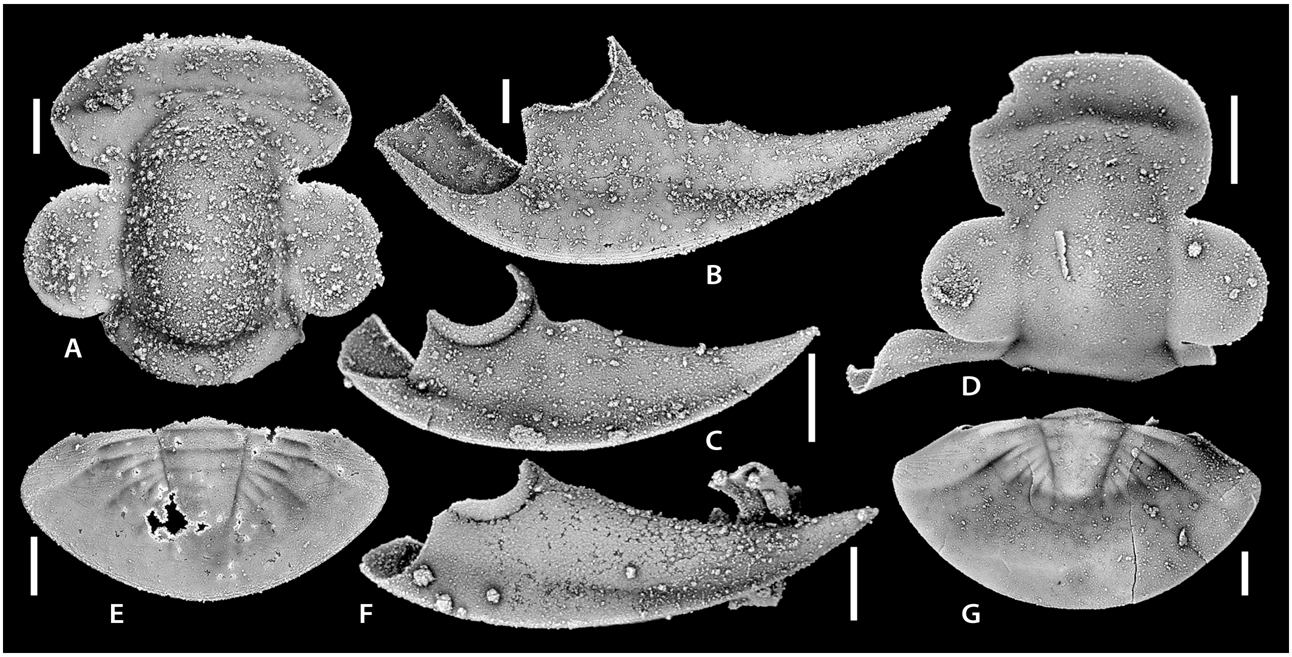

Figure 7. Younger (Tulean; upper Tremadocian) taxa that in some respects at least superficially resemble *Smoothcanyonops* and *Ceeops*. • A, B, E – *Punka*? sp. nov, from Section D 155.9 m, Fillmore Formation (upper Tremadocian; Tulean; upper *Protopliomerella contracta* Zone), southern House Range, Ibex area, Millard County, western Utah, USA. A – cranidium, SUI 152412, dorsal view. B – left librigena, SUI 152413, external view. E – pygidium, SUI 152414, dorsal view. • C, D, G – *Chapmanopyge* sp. nov, from Section HC6 221.5 m, Garden City Formation (upper Tremadocian; Tulean; high *Protopliomerella contracta* Zone), west crest of Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho, USA. C – left librigena, SUI 152415, external view. D – cranidium, SUI 152416, dorsal view. G – pygidium, SUI 152417, dorsal view. • F – *Chapmanopyge* sp., from Section HC5 186.5 m, Garden City Formation (upper Tremadocian; Tulean; *Hintzeia celsaora* Zone), east side of Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho, USA, left librigena, SUI 152418, external view. Scale bars = 1 mm.

an hourglass-shaped plate. This is consistent with the presence of doublure beneath the median region of the cranidial anterior border.

Hypostome and thorax not recovered.

Pygidium with sagittal length 41% (40–42%) maximum width (across rear of articulating facets); axis with sagittal length 78% (77–81%) pygidial sagittal length and maximum width (across first axial ring) 28% (27–29%) pygidial maximum width; articulating half ring quite large, dorsally smooth; anterior margin of pleura transversely straight to fulcrum; fulcrum set about 60% of distance from axis, distal part of pleurae sloped down at fulcrum about 40° from plane formed by proximal part of pleurae; posterior margin posteriorly arcuate, more transverse and less arcuate in median region; axial, ring, pleural, and interpleural furrows all quite broad but very shallow, interpleural furrows narrower than others; axis and pleural regions lacking dorsal sculpture; axis moderately inflated, axial furrows gently posteriorly convergent, curved more strongly posteriorly to circumscribe a broad and blunt terminus to the axis; apparently three axial rings, but the posterior region is not well preserved or is obscured in the available specimens, and the presence of a fourth posterior ring is difficult to rule out; three sets of pleural and interpleural furrows impressed, degree of effacement increased posteriorly; pleural and interpleural furrows almost completely effaced distal to fulcrum; anterolateral corner formed into short (exsag.) trapezoidal articulating facet, turned posteriorly, rear marked by narrow raised ridge; border broad and somewhat flattened, border furrow extremely shallow, mostly a break in slope; posterior margin with fine subparallel raised lines on posterior aspect (Fig. 6P, R); doublure quite broad, broadest anteriorly and tapering in extent posterior, sagittal length about 60% maximum anterior width, with sculpture of dense subparallel raised lines across entire width, finer and more closely spaced posteromedially, and partially anastomosing anteriorly; inner edge of doublure sharp and lacking rim, entire doublure set at strong angle dorsally to plane described by based of pygidial margin (Fig. 6Y, Z).

Remarks. – *Ceeops housensis* is quite rare at horizon C 69.0 m, but more abundant than either species of *Smoothcanyonops* are at their respective localities. Most of the species it occurs with are common in the *Rossaspis leboni* Zone (see Adrain *et al*. 2014a, fig. 8) and occur in most sections and horizons of the zone. *Ceeops housensis*, however, has never been found at any other locality. As with the species of *Smoothcanyonops*, *C. housensis* has very distinctive morphology and there is no doubt about the correct association of sclerites.

Larger cranidia (Fig. 5A, F) show greatly expanded frontal regions but a smaller specimen (Fig. 5B) has the anterior facial sutures much less anteriorly divergent and only barely extended laterally beyond the outer edge of the palpebral lobes. More data would be welcome, but this suggests ontogenetic expansion of the anterior region from more conventional dimensions earlier in life history. A tiny cranidium (Fig. 5L, N, O) does seem to have quite divergent anterior facial sutures. The specimen is obviously deformed, however, as the ridge traversing it, joining the front edges of the palpebral lobes and cutting across the anterior glabella, is certainly preservational, representing anteroposterior buckling and foreshortening of the cranidium, probably during post-depositional diagenesis. This likely means that the anterior region has also been shortened and the path of the sutures likely deformed.

Whereas yoked librigenae seem to be present in *Smoothcanyonops*, the *Ceeops housensis* librigena of Fig. 6D–F seems to show an anterior projection that ends not in an obvious break, but in an arcuate (if not perfectly preserved) connective suture. If this is correct, then placing and scaling the specimen in juxtaposition with the holotype cranidium (Fig. 5A) suggests the presence of a relatively broad (tr.), hourglass-shaped rostral plate.

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References

Adrain, J.M. 2013. A synopsis of Ordovician trilobite distribution and diversity, 297–336. *In* Harper, D.A.T. & Servais, T. (eds) *Early Palaeozoic Biogeography and Palaeogeography. Geological Society London, Memoir 38.* DOI 10.1144/M38.20

Adrain, J.M. 2025. The Early Ordovician bathyurid trilobites *Licnocephala* and *Ibexocephala*. *Journal of Paleontology 98*, 658–685. DOI 10.1017/jpa.2024.10

Adrain, J.M. & Karim, T.S. 2019. Revision of the Early Ordovician (late Tremadocian; Stairsian) cheirurid trilobite *Tesselacauda* Ross, with species from the Great Basin, western USA. *Zootaxa 4661*, 201–255. DOI 10.11646/zootaxa.4661.2.1

Adrain, J.M. & Karim, T.S. 2021. Systematics of the Early Ordovician (late Tremadocian; Stairsian) trilobite *Gonioteloides* Kobayashi, with species from the Great Basin, western USA. *Journal of Paleontology 95*, 1022–1047. DOI 10.1017/jpa.2021.37

Adrain, J.M. & Westrop, S.R. 2007a. The hystricurid trilobite *Metabowmania* in the Lower Ordovician (Ibexian; Stairsian) of the Great Basin, Utah and Idaho, USA. *Memoirs of the Association of Australasian Palaeontologists 34*, 227–242.

Adrain, J.M. & Westrop, S.R. 2007b. *Bearriverops*, a new Lower Ordovician trilobite genus from the Great Basin, western USA, and classification of the family Dimeropygidae. *Canadian Journal of Earth Sciences 44*, 337–366. DOI 10.1139/e06-103

Adrain, J.M., McAdams, N.E.B. & Westrop, S.R. 2009. Trilobite biostratigraphy and revised bases of the Tulean and Blackhillsian Stages of the Ibexian Series, Lower Ordovician, western United States. *Memoirs of the Association of Australasian Palaeontologists 37*, 541–610.

Adrain, J.M., McAdams, N.E.B., Westrop, S.R. & Karim, T.S. 2011. Systematics and affinity of the Lower Ordovician (Tulean; lower Floian) trilobite *Psalikilopsis*. *Memoirs of the Association of Australasian Palaeontologists 42*, 369–416.

Adrain, J.M., McAdams, N.E.B. & Karim, T.S. 2012. The Middle Ordovician bathyurid trilobite *Pseudoolenoides*, with a revised trilobite biostratigraphy of the Dapingian and lower Darriwilian of western Laurentia. *Zootaxa 3467*, 1–97. DOI 10.11646/zootaxa.3467.1.1

Adrain, J.M., Karim, T.S., Westrop, S.R. & Landing, E. 2014a. Trilobite biostratigraphy of the Stairsian Stage (upper Tremadocian) of the Ibexian Series, Lower Ordovician, western United States. *Memoirs of the Association of Australasian Palaeontologists 45*, 167–214.

Adrain, J.M., Karim, T.S. & Westrop, S.R. 2014b. The Early Ordovician (late Tremadocian; Stairsian) dimeropygid trilobite *Pseudohystricurus* Ross. *Memoirs of the Association of Australasian Palaeontologists 45*, 215–232.

Adrain, J.M., Westrop, S.R., Landing, E., Karim, T.S., Losso, S.R., Ng, R.Y., Bradley, A.B. & Pérez-Peris, F. 2025. Trilobite biostratigraphy of the upper Skullrockian Stage (Lower Ordovician; lower Tremadocian) on the northern Laurentian margin, western United States. *Australasian Palaeontological Memoirs 57*, 397–432.

Boyce, W.D. 1989. Early Ordovician trilobite faunas of the Boat Harbour and Catoche Formations (St. George Group) in the Boat Harbour-Cape Norman area, Great Northern Peninsula, western Newfoundland. *Newfoundland Department of Mines and Energy, Geological Survey Branch, Report 89-2*, 1–169.

Bridge, J. & Cloud, P.E., Jr. 1947. New gastropods and trilobites critical in the correlation of Lower Ordovician rocks. *American Journal of Science 245*, 545–559. DOI 10.2475/ajs.245.9.545

Fortey, R.A. 1979. Early Ordovician trilobites from the Catoche Formation (St. George Group), western Newfoundland. *Geological Survey of Canada Bulletin 321*, 61–114. DOI 10.4095/106173

Fortey, R.A. & Bruton, D.L. 2013. Lower Ordovician trilobites of the Kirtonryggen Formation, Spitsbergen. *Fossils and Strata 59*, 1–116. DOI 10.1002/9781118850657.ch1

Hawle, I. & Corda, A.J.C. 1847. *Prodrom einer Monographie der böhmischen Trilobiten*. 176 pp. J.G. Calve, Prague.

Hintze, L.F. 1951. Lower Ordovician detailed stratigraphic sections for western Utah. *Utah Geological and Mineralogical Survey Bulletin 39*, 1–99.

Hintze, L.F. 1953. Lower Ordovician trilobites from western Utah and eastern Nevada. Utah Geological and Mineralogical Survey Bulletin *48*, 1–249. [for 1952]

Hintze, L.F. 1973. Lower and Middle Ordovician stratigraphic sections in the Ibex area, Millard County, Utah. *Brigham Young University Geology Studies 20*, 3–36.

Kobayashi, T. 1955. The Ordovician fossils of the McKay Group in British Columbia western Canada, with a note on the early Ordovician palaeogeography. *Journal of the Faculty of Science, Tokyo University, Section 2 9*, 355–493.

Landing, E., Adrain, J.M., Westrop, S.R. & Kröger, B. 2012. Tribes Hill–Rochdale formations in east Laurentia: proxies for Early Ordovician (Tremadocian) eustasy on a tropical passive margin (New York and west Vermont). *Geological Magazine 149*, 93–123. DOI 10.1017/S0016756811000598

Raymond, P.E. 1913. Subclass Trilobita, 607–638. *In* Eastman, C.R. (ed.) *Text-book of paleontology (2nd edition), Volume 1*. MacMillan, New York.

Raymond, P.E. 1925. Some trilobites of the lower Middle Ordovician of eastern North America. *Bulletin of the Museum of Comparative Zoology, Harvard University 67*, 1–180.

Ross, R.J., Jr. 1949. Stratigraphy and trilobite faunal zones of the Garden City Formation, northeastern Utah. *American Journal of Science 247*, 472–491. DOI 10.2475/ajs.247.7.472

Ross, R.J., Jr. 1951. Stratigraphy of the Garden City Formation in northeastern Utah, and its trilobite faunas. *Peabody Museum of Natural History, Yale University, Bulletin 6*, 1–161.

Ross, R.J., Jr., Hintze, L.F., Ethington, R.L., Miller, J.F., Taylor, M.E. & Repetski, J.E. 1997. The Ibexian, lowermost series in the North American Ordovician. *United States Geological Survey Professional Paper 1579*, 1–50.

Walcott, C.D. 1886. Second contribution to the studies on the Cambrian faunas of North America. *United States Geological Survey Bulletin* 30, 1–369. DOI 10.5962/bhl.title.38399

Westrop, S.R., Knox, L.A. & Landing, E. 1993. Lower Ordovician (Ibexian) trilobites from the Tribes Hill Formation, central Mohawk Valley, New York State. *Canadian Journal of Earth Sciences 30*, 1618–1633. DOI 10.1139/e93-140

Whittington, H.B. 1953. North American Bathyuridae and Leiostegiidae (Trilobita). *Journal of Paleontology 27*, 647–678.

Whittington, H.B. 1997. Morphology of the exoskeleton, 1–74. *In* Kaesler, R.L. (ed.) *Treatise on invertebrate paleontology. Part O. Arthropoda 1, Trilobita. Revised.* Geological Society of America and University of Kansas Press, Lawrence, Kansas.