The Early Ordovician (Floian) bathyurid trilobite genera *Jeffersonia*, *Cullisonia* and *Bathyurina*

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ADRAIN, J.M., KARIM, T.S. & WESTROP, S.R., 2014:04:25. The Early Ordovician (Floian) bathyurid trilobite genera *Jeffersonia*, *Cullisonia* and *Bathyurina*. *Memoirs of the Association of Australasian Palaeontologists 45*, 305-347. ISSN 0810-8889.

Pioneering work by Christian Poulsen on Early Ordovician Laurentian faunas from Greenland established several genera which have been used often in the literature. Poulsen's original material has not previously been fully revised, and the content and identity of some genera have depended upon interpretations of his tiny photographs. We revise the type material of the type species of *Bathyurina* Poulsen and *Jeffersonia* Poulsen and argue that previous interpretations of their morphology and ideas about potentially related species are not well supported. *Jeffersonia* has been used for a group of species with distinctive pygidial morphology. New photographs of the lectotype pygidium of the type species, *J. exterminata* Poulsen, demonstrate that it lacks this morphology. *Jeffersonia* is restricted to its type species, which is known from a single illustrated pygidium. Other species previously assigned to the genus are transferred to *Cullisonia* Loch. New photographs of the two known cranidia of *B. megalops* show that they are not closely similar to those of *C. timon* (Billings), as has previously been suggested, but rather to those of *Goniotelina* ? *plicolabeonus* Young, from western Utah, which is revised on the basis of new collections and reassigned to *Bathyurina*. New species from the Fillmore Formation of western Utah are: *Bathyurina curtisi* (*Carolinites nevadensis* Zone), *B. sumneri* (*Presbynileus ibexensis* Zone), *B. hooki* (currently unzoned interval above *P. ibexensis* Zone), *B. morrisi* (*Psalikilus spinosum* Zone), and *B*. sp. nov. A (*Psalikilus pikum* Zone).

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Keywords: Trilobita, Bathyuridae, taxonomy, silicified, Utah, Greenland, Laurentia.

CHRISTIAN POULSEN (1927, 1937, 1946) published some of the pioneering systematic work on Early Ordovician shallow subtidal trilobite faunas of Laurentia. His papers were based on material collected by others during various expeditions to northern and eastern Greenland. The fossils used to illustrate new taxa are generally few in number and not well preserved, and Poulsen's illustrations are small and in many cases heavily retouched. Nevertheless, as some of the first modern research carried out, Poulsen was able to name several genera to which multiple species from across Laurentia have subsequently been assigned (e.g., *Cybelopsis* Poulsen 1927, *Jeffersonia* Poulsen 1927, *Bathyurina* Poulsen 1937, *Benthamaspis* Poulsen 1946).

Due to the poor preservation and inadequate illustration of the type species, several of these taxa have become problematic. The type species of *Benthamaspis*, *B. problematica* Poulsen 1946, is based on a single poorly preserved internal mould of a cranidium. The morphology is sufficiently distinct that its phylogenetic affinity to other species since assigned to *Benthamaspis* is clear, but it is otherwise virtually uninterpretable. Others of Poulsen's genera are much more problematical. *Cybelopsis*, for example, has become badly confused. Revision in progress of the syntypes of the type species, *C. speciosa* Poulsen 1927, shows that they include specimens belonging to three separate species and genera (Adrain, work in progress). Poulsen (1927) confused sclerites belonging to species which should now be assigned to *Cybelopsis*, *Strotactinus* Bradley 1925, and *Pseudomera* Holliday 1942, and this confusion has been propagated through much of the literature on the genera.

Here we deal with two other problematic genera, the bathyurids *Jeffersonia* Poulsen 1927, and *Bathyurina* Poulsen 1937, which have been considered probable synonyms following Fortey (1986). The taxa are similar in that their concepts have tended to revolve not around Poulsen's type species, but rather have been based mainly on better known species from elsewhere, whose relationships to the poorly known types species have been asserted, but never adequately demonstrated. We fully revise the type material of both types species for the first time, and consider that the concepts of the genera which have taken hold in the literature are not well supported in light of the morphology of these species.

The goals of this work are: 1) to revise the type material of the type species *Jeffersonia exterminata* Poulsen 1927, and *Bathyurina megalops* Poulsen 1937; 2) to demonstrate that *J. exterminata* is not obviously related to the species that have been assigned to *Jeffersonia* in recent years, and to argue that *Cullisonia* Loch 2007, is the appropriate genus name for this apparent clade; 3) to demonstrate that *B. megalops* is not obviously related to *Bathyurus timon* Billings 1865, the species on which the concept of *Bathyurina* has mostly been based following Fortey (1979, p. 74), and which, by extension, the notion that *Bathyurina* is a junior subjective synonym of *Jeffersonia* has depended (Fortey 1986); 4) to demonstrate that *B. megalops* is directly comparable to and

likely closely related to *Goniotelina* (?) *plicolabeonus* Young 1973, from western Utah; 5) to revise *B. plicolabeona* on the basis of rich new silicified collections; 6) to describe five new species of *Bathyurina* from western Utah, four of which are formally named; and 7) to provide a new diagnosis of *Bathyurina* based on the clade thus identified.

BIOSTRATIGRAPHY

Details of the history of study, localities, maps, stratigraphy, and section logs have been given by Adrain *et al*. (2009) and are not repeated herein. Adrain *et al*. (2009) also introduced a new species-based trilobite zonation for the Tulean and most of the Blackhillsian stages (?latest Tremadocian and Floian) of northern Laurentia (in Ordovician terms). This zonation is followed herein, with one minor amendment. *Goniotelina* (?) *plicolabeonus* was assigned to *Strigigenalis* Whittington & Ross in Whittington 1953, by Adrain *et al*. (2009) and was made the name bearer of the Blackhillsian *Strigigenalis plicolaebona* Zone. With reassignment of the species to *Bathyurina* herein, this becomes the *Bathyurina plicolabeona* Zone.

A large sample from Section H 274.4 m contains species which strongly resemble those from the underlying *Presbynileus ibexensis* Zone, in addition to several clearly new species. Close comparison has shown that many of the species are subtly but clearly distinguished from their older congeners, and it is likely that a distinct zone is represented. Formal treatment is deferred until description of the relevant species is more advanced.

SYSTEMATIC PALAEONTOLOGY

Repositories. Illustrated material is housed in the collections of the Paleontology Repository, University of Iowa, Iowa City (specimen number prefix SUI); the Brigham Young University Museum of Paleontology (prefix BYU); and the Geological Museum, University of Copenhagen (prefix MGUH).

Measurements. For measurement of the distance across sclerites where morphology was preserved only on one side, the distance to the sagittal line from this side was doubled and for measurements made on only a single specimen the figure number is indicated.

Family BATHYURIDAE Walcott 1886

Jeffersonia Poulsen 1927

Type species. By monotypy (see Cullison 1944, p. 70; Boyce 1989, p. 49); *Jeffersonia exterminata* Poulsen 1927, from the Nunatami Formation (Floian), western North Greenland.

Other species. Monotypic.

Diagnosis. Pygidium subsemicircular in outline, with dorsal sculpture of densely distributed subdued small tubercles; axis long, with four defined rings and a long posterior area that may include an additional ring as well as a terminal piece; first and second ring furrows well impressed, third and fourth shallow and weak; axial furrows curve smoothly around posteriorly to fully define rear of axis; pleural bands weakly inflated, not strongly differentiated from general plane of pleural region; only first pleural furrow well impressed, second weakly so and only adaxially, third impressed only faintly near axial furrow, posterior pleural region smooth; broad, concave border terminating at distinct narrow rim along margin.

Remarks. As outlined by Cullison (1944, p. 70), Fortey (1986, p. 18) and Boyce (1989, p. 49), Poulsen was aware of an unpublished manuscript by E.O. Ulrich, in which the genus *Jeffersonia* was to be proposed, based upon a prospective type species from the Jefferson City Formation of Missouri. Ulrich's publication never appeared and bathyurids from Missouri were later described by Cullison (1944). Poulsen listed the genus name as "*Jeffersonia* Ulrich, M S." and described one new species, *J. exterminata*, from Greenland. This species is hence the type species of *Jeffersonia* Poulsen 1927, by monotypy. Although Poulsen indicated that Ulrich should be considered author of the genus, the taxon was not formally diagnosed and as restricted by monotypy is based on a species not considered by Ulrich (and not considered by us to be related to those species from Missouri under study by Ulrich). Hence, authorship is appropriately attributed to Poulsen alone, and not to Ulrich in Poulsen.

Jeffersonia exterminata was based on a single illustrated pygidium (Poulsen 1927, pl. 20, fig. 28) which is selected as the lectotype below and reillustrated for the first time in Figure 1. The morphology of this specimen has only rarely been referred to, and it has largely been taken as a given that Poulsen was correct in considering it closely related to the species from Missouri under study by Ulrich and described by Cullison (1944). Cullison (1944, pp. 70–71) considered that "it must be assumed that Ulrich recognized the pygidium [of *J. exterminata*] as being a species of his manuscript genus *Jeffersonia* although he may not have realized that the publication of the species description would make it the genotype." This is essentially an appeal to authority; although he described nine species from Missouri which he assigned to *Jeffersonia* (two in open nomenclature), Cullison compared none of them with *J. exterminata*. He (Cullison 1944, p. 71) considered either restricting *Jeffersonia* to its type species and erecting a new genus for the Missouri species, or accepting Ulrich's opinion. He chose the latter option, but emphasised that he had not studied *J. exterminata* himself and was relying on Ulrich's judgement. As a result, *Jeffersonia* has historically been interpreted in light of a kind of de facto "type species by committee" of species such as *J. delicatula* Cullison 1944, *J. jennii* Cullison 1944, and *J. producta* Cullison 1944. These species have distinctive pygidia with a vaulted axis occupying a significant portion of the pygidial area and strongly inflated pleural bands of the first three segments, raised well above the surrounding pleural area. It is species with this pygidial morphology which have formed the basis of almost all subsequent interpretations and treatments of *Jeffersonia* (e.g., Boyce 1989; Loch 2007).

Poulsen (1937) introduced *Bathyurina* as a monotypic genus based on a type species, *B. megalops*, known from two cranidia. It attracted little comment in the literature until Fortey (1979) assigned *Bathyurus timon* Billings 1865, to it, based on the supposed similarity of cranidia of this species from the Catoche Formation of Newfoundland with those of *B. megalops*. Pygidia of *Bathyurus timon* are of the distinctive morphology outlined above for Missouri species of "*Jeffersonia*" and, in fact, Fortey (1979, p. 74) reassigned *J. jennii* Cullison to *Bathyurina*. He later (1986, p. 18) came to the opinion that the Missouri species and *B. timon* were congeneric, and that *Bathyurina* was hence a junior subjective synonym of *Jeffersonia*. This opinion was

offered with reservation, given the lack of knowledge of most sclerites of the two Greenland type species, but has been accepted as probable by most subsequent commentators (e.g., Boyce 1989; Adrain & Westrop 2005; Loch 2007).

Remarkably, neither of the type species has been photographically revised since they were first published, with the sole exception of Fortey's (1979, pl. 25, fig. 11) illustration of a cropped anterior view of one of the cranidia assigned to *B. megalops*. The case of the genus identity and content of *Jeffersonia* and for the recognition of *Bathyurina* as its junior synonym, boils down to two claims of morphological similarity and close relationship: 1) that the single pygidium of *J. exterminata* is very similar in morphology to those of species from elsewhere generally assigned to *Jeffersonia*; and 2) that the cranidia from the Catoche Formation assigned to *B. timon* by Fortey (1979) are very similar in morphology to those of *B. megalops*. As noted above, Cullison simply accepted the first claim by recourse to Ulrich's authority. Fortey (1986, p. 18), however, explicitly defended the assertion of close morphological agreement and relationship: "Others, for example, *J. crassimarginata* (Cullison 1944, pl. 35, fig. 15), have pygidia closely similar to the type species of *Jeffersonia* from Greenland." Fortey & Bruton (2013, p. 38) argued "the pygidium of *B. timon* is closely similar to that of *Jeffersonia exterminata*, being elongate with three well-defined convex pleural segments, a distinct border and lacking a terminal spine." Fortey (1979, p. 78) supported the second claim with the contention that "The cranidium of *B. timon* is very like that of the type species, *B. megalops* (Poulsen 1937, Pl. 6, fig. 14, 15) in the form of the glabella and the size of the palpebral lobes." He noted, however, that holotype of *B. megalops* has "a short, almost vertical pre-glabellar field, which is not present on *B. timon*." He also noted that a pygidium similar to those of *B. timon* was illustrated by Poulsen (1937, pl. 8, fig. 4).

In modern photographs of Poulsen's (1927, 1937) type material (Figs 1, 4), it does not appear that either of these claims can be sustained. The pygidium of *J. exterminata* (Fig. 1) is strikingly different from those of species now generally assigned to *Jeffersonia*. The axis is not nearly as dorsally vaulted, the axial rings are not inflated, the posterior of the axis does not come to a slightly swollen and bulbous termination, and in particular the pleural bands are not strongly inflated and raised above the surrounding pleural region but rather are barely inflated at all and are almost obscure posterior to the first segment. As noted above, Fortey (1986, p. 18) explicitly compared the pygidium of *J. crassimarginata* Cullison with that of *J. exterminata*. The Missouri pygidium has been reillustrated by Fortey & Bruton (2013, fig. 12L, M). Its lack of a bulbous pygidial termination and general proportions are at least broadly comparable with the pygidium of *J. exterminata*. However, it very clearly shows the strongly inflated and elevated pleural bands of segments 1–3 typical of "*Jeffersonia*" and completely absent from the pygidium of *J. exterminata*. We consider that Cullison likely chose the wrong option: much confusion would have been avoided had he restricted *Jeffersonia* to its type species and introduced a new name for the Missouri species he was describing.

Hence, we consider that *Jeffersonia* should be restricted to the inadequately known *J. exterminata*, as recommended by Whittington (1953, p. 662). The morphology of the pygidium of this species (Fig. 1) does not seem comparable in detail to that of any other bathyurid species. It is unlikely that its affinities can be determined with any confidence until other sclerites become known. With this action, a genus is required for the putative clade previously assigned to *Jeffersonia*. A new taxon is not required, however, because Loch (2007) introduced the monotypic *Cullisonia* for the species *Jeffersonia producta* Cullison. Loch (2007, p. 29–30) recognised that the species was related to other species assigned to *Jeffersonia*, but chose to erect a new genus because of the derived pygidial morphology involving a triangular outline with a border which lengthens and widens posteriorly, among other features. Despite this unusual morphology, the pygidium of *J. producta* (Loch 2007, pl. 8, fig. 3) displays all of the features characteristic of the group, including inflated axial rings, an inflated, bulbous axial termination, and inflated pleural bands raised well above the surrounding pleura. If the generally agreed concept of *Jeffersonia* were accepted, it seems almost certain that *Cullisonia* is a monotypic genus which does little but create paraphyly in "*Jeffersonia*" and as such it should likely be considered a junior subjective synonym. With the restriction of *Jeffersonia* to its type species, however, *Cullisonia* becomes the available name for the overall putative clade previously assigned to *Jeffersonia*. Membership of this genus is outlined below. We regard the pygidium (Poulsen 1937, pl. 8, fig. 4) noted by Fortey (1986) as possibly belonging to *B. megalops* as belonging to a species of *Cullisonia*, similar to or possibly even conspecific with *Cullisonia* sp. nov. A, described below.

If Fortey's (1979) claim that cranidia of *Bathyurina megalops* and *Cullisonia timon* are so similar that the species are congeneric is correct, then *Bathyurina* would be the senior name and *Cullisonia* its junior subjective synonym. Revision of Poulsen's type cranidia of *B. megalops*, however, (Fig. 4), strongly suggests that no close comparison or relationship with *C. timon* exists, and that *B. megalops* is instead directly comparable with a species from northern Laurentia, *Goniotelina* (?) *plicolabeonus* Young 1973 (see Fig. 3), from the Fillmore Formation of western Utah. Both of the cranidia of *B. megalops* have the anterior border broken off, but the anterior border furrow clearly describes a nearly even arc, exactly as in *B. plicolabeona*. In fact, cranidia of the species are strikingly similar, differing only in minor proportion. The glabella of *B. megalops* is broader anteriorly and its palpebral lobes are larger. The cranidia otherwise agree almost exactly in every detail, including the presence of small depressions on the glabella flanking the contact with the obliquely set, nearly effaced eye ridge (Fig. 3A, B) and the presence of a very fine transverse ridge set within SO (Fig. 3C, D). Cranidia of *C. timon*, on the other hand (Fortey 1979, pl. 25, figs 1, 2, 4, 6), agree instead with those of other species of *Cullisonia* in having an anteriorly protruded glabella which overhangs the anterior border, and (as noted by Fortey 1979) in lacking a preglabellar field. Hence, we regard *Bathyurina* as a valid genus, and in light of the overall morphology revealed by the silicified species from western Utah, not obviously closely related to *Cullisonia*.

Fortey & Bruton (2013, p. 44) assigned specimens from the Kirtonryggen Formation of Ny Friesland, Spitsbergen to *J. timon*, but these are of markedly different morphology than those, including the holotype, from the Catoche Formation of Newfoundland. One pygidium (Fortey & Bruton 2013, fig. 13B, C) is from 25 m below the only other one whose provenance is known and is obviously not conspecific with the other figured pygidia. Its terminal piece is much more strongly inflated, the axis and pleural bands are relatively wider, and the border does not taper as strongly posteriorly.

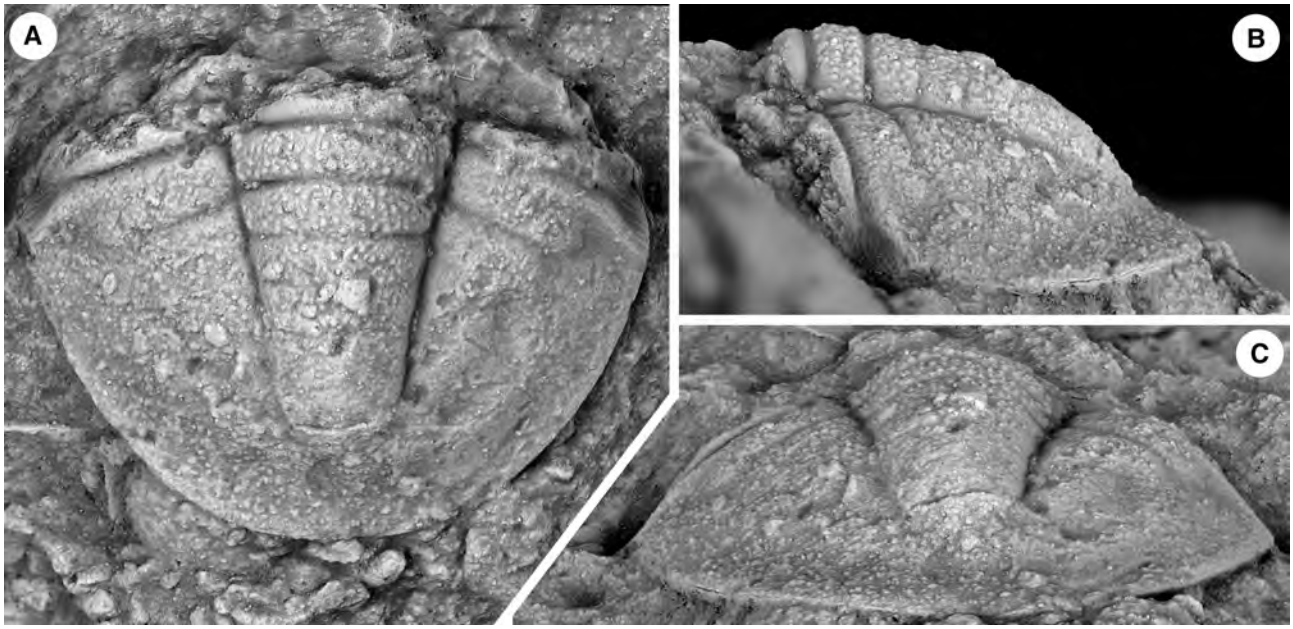


Figure 1. ***Jeffersonia exterminata*** Poulsen 1927, from the "Ostracod Limestone", Nunatami Formation, western North Greenland. **A–C**, pygidium, lectotype, MGUH 2407, dorsal, left lateral, and posterior views, x10 (original of Poulsen 1927, pl. 20, fig. 28).

Fortey & Bruton (2013, p. 46) recognised in their text that the specimen was distinct and explained "it is included as *J.* cf. *timon* and a likely cranidium associated." However the explanation of figure 13 lists all of the material as *J. timon* without distinction, and the cranidium thought possibly to belong with the "*J.* cf. *timon*" pygidium is not identified. One of the two illustrated cranidia (Fortey & Bruton 2013, fig. 13D–F) is from the same horizon (105 m) and is presumably what was meant. This cranidium has morphology typical of other members of the putative clade, with a steeply declined anterior region and inflated glabella overhanging the anterior border in dorsal view. The remaining specimens thought to represent *J. timon* (Fortey & Bruton 2013, fig. 13 A, G–M) include one cranidium and three pygidia. The cranidium and two of the pygidia are of unknown stratigraphic position. The basis for their association with one another was not discussed. The pygidia are plausibly conspecific, but they do not represent *J. timon*. They differ from the two illustrated Catoche Formation pygidia (Fortey 1979, pl. 25, figs 3, 5, 8, 10) in the possession of considerably wider, more inflated, and bulbous terminal pieces. In the Catoche specimens, the fourth pygidial axial ring is not fully merged with the terminal piece, and the ring furrow is gently impressed laterally. In the Spitsbergen specimens, the fourth ring is indistinguishable from the terminal piece. The border is of nearly even width anteriorly and posteriorly in the Catoche specimens, but broader anteriorly in the Spitsbergen specimens. The assigned cranidium (Fortey & Bruton 2013, fig. 13A), of unknown provenance and illustrated only in dorsal view, does not resemble the two illustrated cranidia from the Catoche (Fortey 1979, pl. 25, figs 1, 2, 4, 6). The Catoche specimens have a nearly parallel-sided glabella that is strongly inflated anteriorly and overhangs the anterior border, in common with other members of "*Jeffersonia*". The Spitsbergen specimen has an anteriorly expanded glabella, and the anterior border is plainly visible in dorsal view (though photographic orientation may not be consistent). The posterior fixigena of the Catoche specimens appears to be of limited exent (though is it mostly obscured by shadows) while that of the Spitsbergen specimen is broad and independently inflated. The basis for its association with the three pygidia is unclear, but none of the specimens represent "*J.*" *timon*, and there is no evidence the Newfoundland species occurs in Spitsbergen.

Jeffersonia exterminata Poulsen 1927 (Fig. 1)

1927 *Jeffersonia exterminata*; Poulsen, p. 303, pl. 20, fig. 28.
1953 *Jeffersonia exterminata* Poulsen; Whittington, p. 662.
1986 *Jeffersonia exterminata* Poulsen; Fortey, p. 18.
1992 *Jeffersonia exterminata* Poulsen; Fortey, p. 118.
1996 *Jeffersonia exterminata* Poulsen; Fortey & Droser, p. 83.
1998 *Jeffersonia exterminata* Poulsen; Zhou *et al*., p. 276.
2000 *Jeffersonia exterminata* Poulsen; Boyce *et al*., p. 123.
2003 *Jeffersonia exterminata* Poulsen; Jell & Adrain, p. 389.
2005 *Jeffersonia exterminata* Poulsen; Adrain & Westrop, p. 1543.
2007 *Jeffersonia exterminata* Poulsen; Loch, p. 37.

Lectotype. Selected here; pygidium, MGUH 2407 (Poulsen 1927, pl. 28, fig. 28; Fig. 1), "Ostracod Limestone", Nunatami Formation, western North Greenland. Although Poulsen (1927, p. 303, pl. 20, fig. 28) illustrated only a single specimen, it is not the holotype by monotypy, as he indicated the species was based on "...a couple of tails."

Diagnosis. See generic diagnosis.

Remarks. See generic remarks.

Cullisonia Loch 2007

Type species. Jeffersonia producta Cullison 1944, from the Jefferson City Formation, Missouri.

Other species. Jeffersonia angustimarginata Boyce 1989, Catoche Formation, Newfoundland; *J. delicatula* Cullison

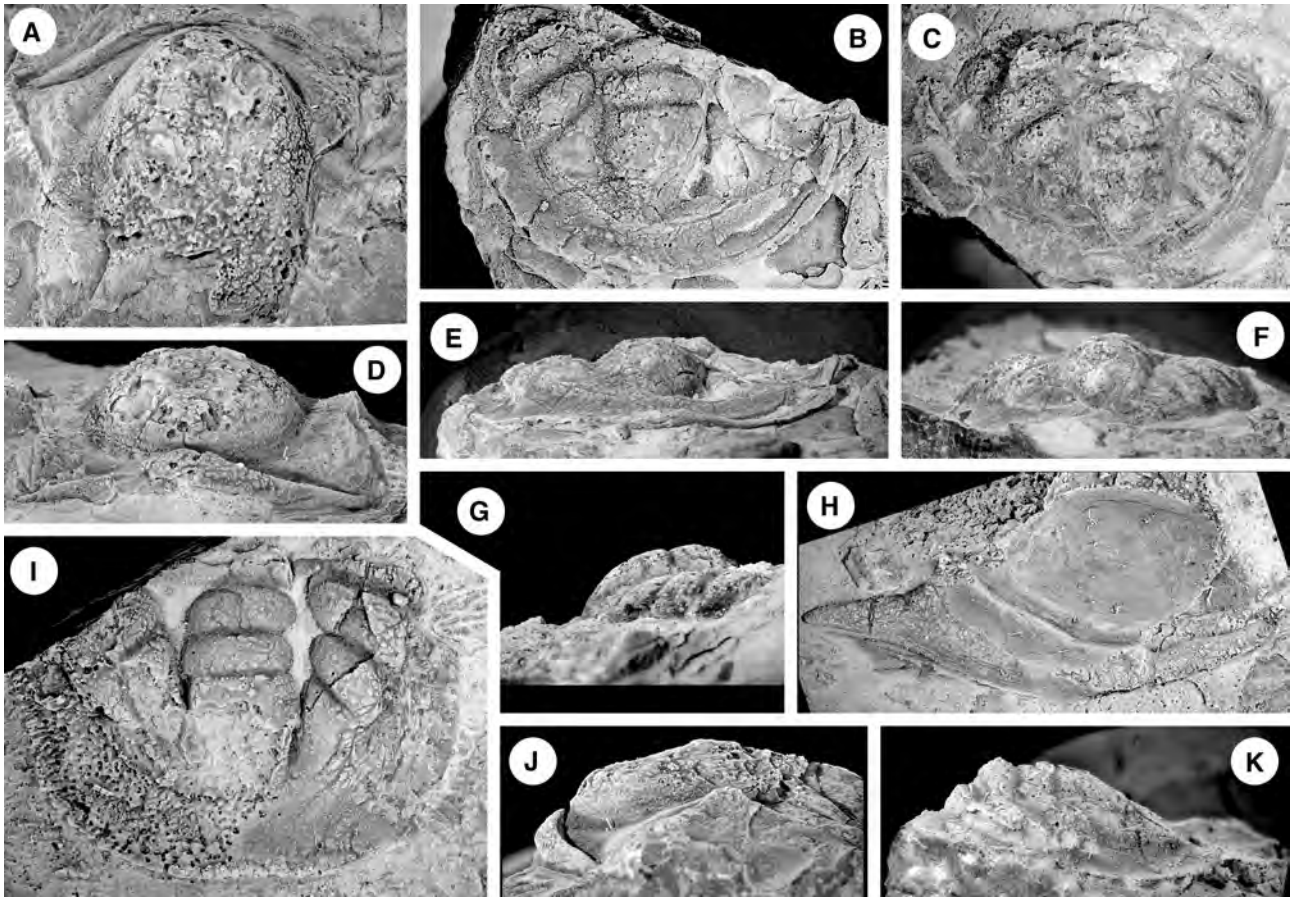


Figure 2. ***Cullisonia*** **sp. nov. A,** from the Baumann Fiord Formation (Floian), Scoresby Bay, eastern Ellesmere Island, Nunavut, Canada. **A**, **D**, **J**, cranidium, OU BT 68, dorsal, anterior, and left lateral views, x2.5 (original of Poulsen 1946, pl. 23, fig. 6). **B**, **E**, **K**, pygidium, OU BT 70, dorsal, posterior, and left lateral views, x2.5 (original of Poulsen 1946, pl. 23, fig. 8). **C**, **F**, **G**, pygidium, OU BT 193, dorsal, posterior, and right lateral views, x2.5 (original of Poulsen 1946 pl. 23, fig. 10). **H**, left librigena, OU BT 69, internal view, x2.5 (original of Poulsen 1946, pl. 23, fig. 7). **I**, pygidium, OU BT 71, dorsal view, x3 (original of Poulsen 1946, pl. 23, fig. 9).

1944, Jefferson City Formation, Missouri; *J. jennii* Cullison 1944, Cotter Formation, Missouri; *J. striagena* Fortey & Bruton 2013, Kirtonryggen Formation, Spitsbergen; *Bathyurus timon* Billings 1865, Cathoche Formation, Newfoundland; *J. ulrichi* Loch 2007, Kindblade Formation, Oklahoma; *J. viator* Fortey & Bruton 2013, Kirtonryggen Formation, Spitsbergen; *Bathyurina* sp. indet. of Fortey (1979), Catoche Formation, Newfoundland; "*Jeffersonia timon*" of Fortey (1992), Durness Group, Scotland; "*Jeffersonia timon*" of Fortey & Bruton (2013), Kirtonryggen Formation, Spitsbergen; *Jeffersonia* sp. cf. *J. timon* of Desbiens *et al*. (1996), Beauharnois Formation, Quebec; *Jeffersonia* cf. *timon* of Fortey & Bruton (2013, p. 46), Kirtonryggen Formation, Spitsbergen; *Jeffersonia* sp. of Adrain & Westrop (2005), Baumann Fiord Formation, Nunavut (=*Cullisonia* sp. nov. A herein); *Jeffersonia* sp. 1 of Loch (2007), Kindblade Formation, Oklahoma; *Jeffersonia* sp. 2 of Loch (2007), Kindblade Formation, Oklahoma; *Jeffersonia* sp. 3 of Loch (2007), Kindblade Formation, Oklahoma.

Diagnosis. Cranidium with parallel-sided glabella; glabella vaulted anteriorly and overhanging anterior border; preglabellar field very short. Pygidium with vaulted axis occupying a significant portion of the pygidial area and strongly inflated pleural bands of the first three segments, raised well above the surrounding pleural region; terminal piece usually laterally inflated and bulbous.

Remarks. The concept of *Cullisonia* arrived at herein was outlined above in the discussion of *Jeffersonia*. *Jeffersonia granosa* Cullison 1944, from Jefferson City Formation, Missouri, does not appear to belong to the genus. Material from the Kindblade Formation, Oklahoma, was assigned to the species by Loch (2007, p. 34, pl. 11, figs 1-11), and the species was assigned to *Jeffersonia* (now *Cullisonia*) . Its affinity will be discussed in a forthcoming work. *Jeffersonia bridgei* Heller 1956, is a Stairsian species unrelated to *Cullisonia*. Its classification will also be addressed in a forthcoming work. "*Jeffersonia* sp. A" of Hintze (1953, p. 174, pl. 10, figs 7–10) is a species of *Peltabellia* Whittington 1953, and will be revised in a forthcoming work. "*Jeffersonia* ? sp. B" of Hintze (1953, p. 175, pl. 9, figs 8, 11, 12) was described as *Psalikilopsis newmani* Adrain, McAdams, Westrop & Karim 2011.

Cullisonia sp. nov. A (Fig. 2)

?1937 Genus et sp. ind. (cf. *Bathyurus*); Poulsen, p. 58, pl. 8, fig. 4.
1946 Genus et sp. indet. II; Poulsen, p. 329, pl. 23, figs 6–10.
1979 "Genus et sp. indet. II (bathyurid?)"; assigned to

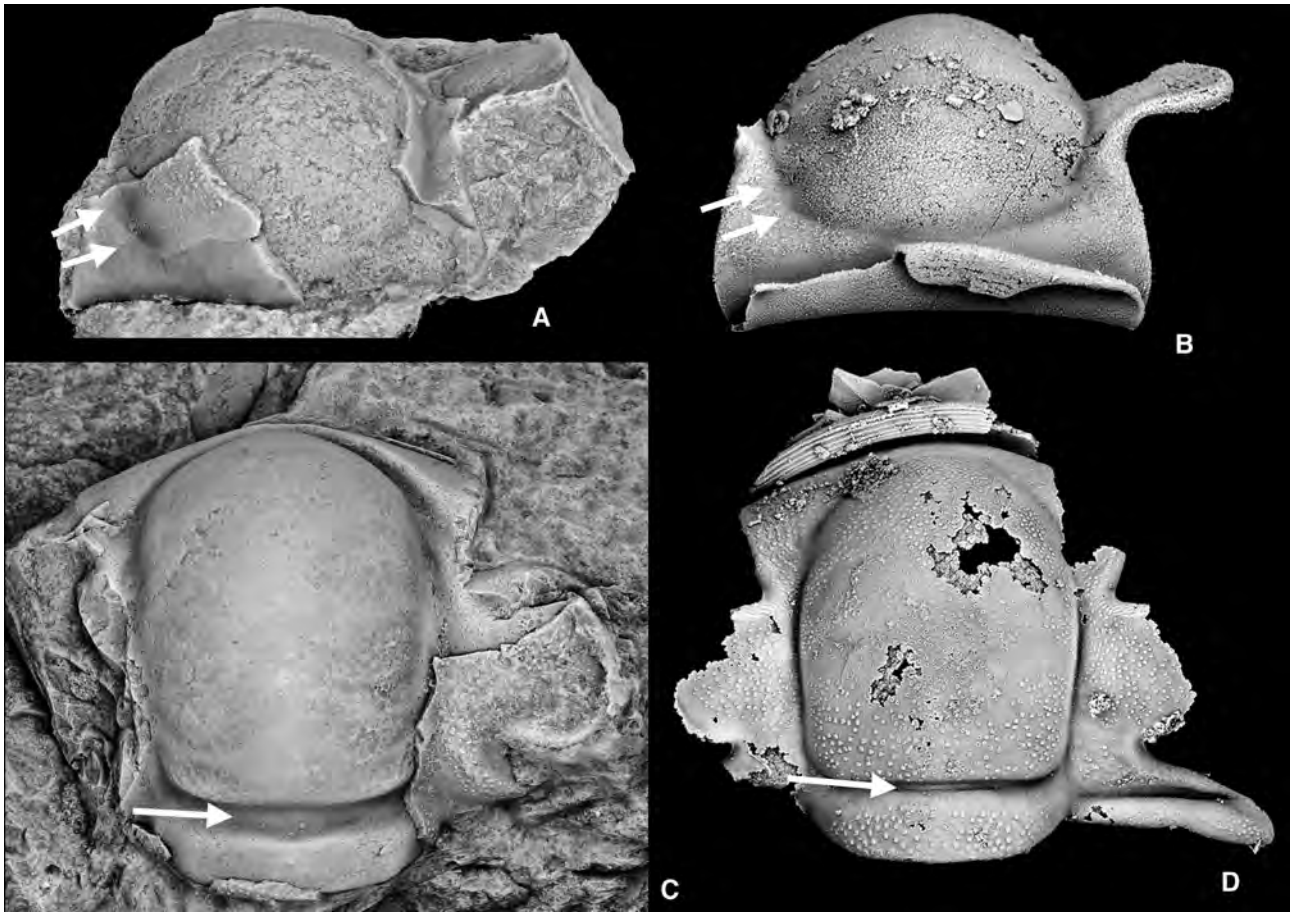


Figure 3. Comparison of cranidia of *Bathyurina megalops* Poulsen 1937 and *B. plicolabeona* (Young 1973). **A**, **C**. ***Bathyurina megalops*** Poulsen 1937, from the Cape Weber Formation, eastern Greenland (see Fig. 4 for full locality and other details). **A**, cranidium, MGUH 3700 (see Fig. 4B, D, F, G), anterior view, x6. **C**, cranidium, holotype, MGUH 3699 (see Fig. 4A, C, E, H), dorsal view, x3. **B**, **D**. ***Bathyurina plicolabeona*** (Young 1973), from the Fillmore Formation, western Utah (see Fig. 5 for full locality and other details). **B**, cranidium, SUI 124833 (see Fig. 5K, M, O), anterior view, x8. **D**, cranidium, SUI 124830 (see Fig. 5A, D, F, J), dorsal view, x5. Arrows on A and B compare nearly identical depressions flanking contact of nearly effaced eye ridge with glabella. Arrows on C and D indicate shared presence of a narrow transverse ridge within SO.

Bathyurina; Fortey, p. 74.

2005 *Jeffersonia* sp.; Adrain & Westrop, p. 1543, fig. 10n–10p.

Material. Specimens originally illustrated by Poulsen (1946, pl. 23): OU BT 68–71, 193, from the Baumann Fiord Formation (Floian), Scoresby Bay, eastern Ellesmere Island, Nunavut, Canada.

Remarks. Fortey (1979, p. 74) correctly interpreted specimens from eastern Ellesmere Island illustrated in open nomenclature by Poulsen (1946, pl. 23, figs 6–10) as representing a species of "*Jeffersonia*" (=*Cullisonia* as understood herein). Adrain & Westrop (2005) illustrated one associated cranidium and pygidium from the Baumann Fiord Formation, near the base of the Bache Peninsula and to the south along the coast from the Scoresby Bay locality from which Poulsen's specimens were collected, as *Jeffersonia* sp. Although neither set of specimens is very well preserved, new photographs of Poulsen's material show that there are no apparent differences between them. Poulsen's specimens were hence likely also collected from the middle carbonate unit of the Baumann Fiord Formation. By the inadequate standards of most of the systematic trilobite literature the species is represented by a reasonable number of specimens, but preservation is too poor for formal naming, although the species is apparently distinct. The species seems most similar to *C. timon* from the Catoche Formation, Newfoundland (Fortey 1979, pl. 25, figs 1–10), but appears to differ, to the extent comparison is possible, in the possession of a generally broader pygidial border, particularly medially, and a considerably longer and stouter genal spine.

Bathyurina Poulsen 1937

Type species. *Bathyurina megalops* Poulsen 1937, from the Cape Weber Formation, eastern Greenland.

Other species. *Bathyurina curtisi* sp. nov., Fillmore Formation, Utah; *B. hooki* sp. nov., Fillmore Formation, Utah; *B. morrisi* sp. nov., Fillmore Formation, Utah; *Goniotelina* (?) *plicolabeonus* Young 1973, Fillmore Formation, Utah; *B. sumneri* sp. nov., Fillmore Formation, Utah; *Bathyurina* sp. nov. A (herein), Fillmore Formation, Utah.

Diagnosis. Anterior border more or less evenly arcuate in plan view, short, with sculpture of subparallel raised lines, turned back against preglabellar field so that part of anterior-

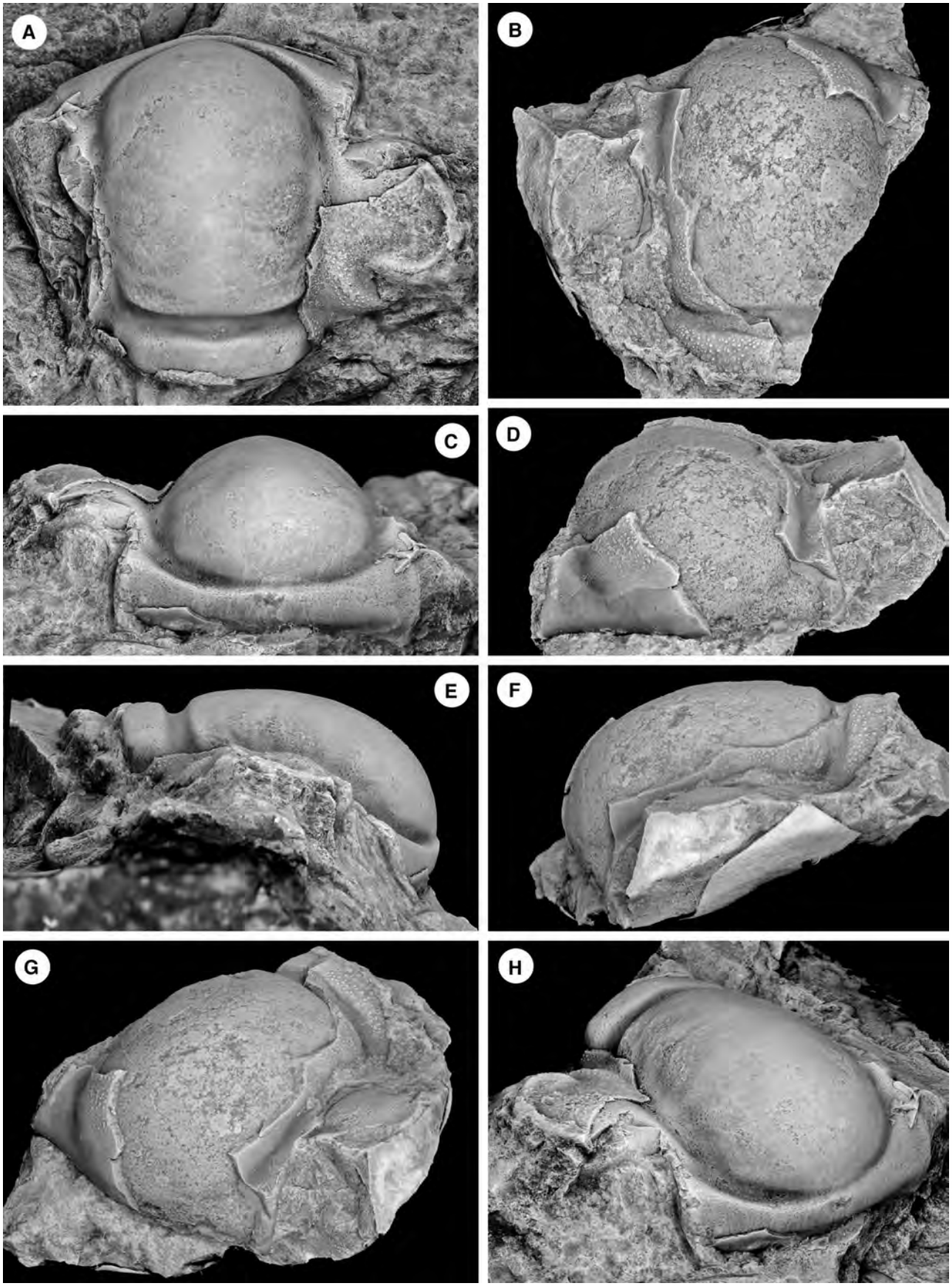


Figure 4. ***Bathyurina megalops*** Poulsen 1937, Cape Weber Formation (Floian), Mt. Gunvor, Strindberg Land, eastern Greenland. **A**, **C**, **E**, **H**, cranidium, holotype, MGUH 3699, dorsal, anterior, right lateral, and oblique views, x3 (original of Poulsen 1937, pl. 6, fig. 14, pl. 7, fig. 1). **B**, **D**, **F**, **G**, cranidium, MGUH 3700, dorsal, anterior, left lateral, and oblique views, x6 (original of Poulsen 1937, pl. 6, fig. 15).

facing field is obscured and anterior border furrow is a deep trench; glabella with distinct anterolateral angle, protruded anteromedially in several species to overlie anterior border; genal spine in large specimens either very short and blunt or entirely lost; pygidia with doublure distinctly ventrally concave, lacking strong anterior ventral rim.

Remarks. The basis for recognising *B. megalops* as closely related to *B. plicolabeona* was discussed under *Jeffersonia* above. As recognised herein, *Bathyurina* is a distinctive putative clade likely part of the "*Acidiphorus* Group" of McAdams & Adrain (2007). As is a recurrent theme with taxa in the richly fossiliferous northern Laurentian sections, inclusion of a species with presumably plesiomorphic morphology, *B. morrisi* sp. nov., excludes from the diagnosis some of the more strikingly derived characters of younger species (compare, for example, with the inclusion in *Psalikilopsis* of the early species *P. newmani* Adrain, McAdams, Westrop & Karim 2011, which is from the same lower Tulean horizon as *B. morrisi*).

Bathyurina plicolabeona was assigned to *Strigigenalis* Whittington & Ross in Whittington 1953, by Adrain *et al*. (2009). Species of *Strigigenalis* are similar to those of *Bathyurina* in the possession of cranidia with arcuate, non-nasute anterior borders, and it is possible the genera will prove to be closely related. *Bathyurina plicolabeona*, in particular, bears a strong, at least superficial, similarity to the type species of *Strigigenalis*, *S. cassinensis* Whittington 1953 (see Brett & Westrop 1996, fig. 17.1-17.9). In plan view the cranidia are generally similar, with a relatively long preglabellar field exposed in front of the glabella. Pygidia of *S. cassinensis* have the border posteriorly extended to a broad triangular point. Large pygidia of *B. plicolabeona* (Fig. 8) also have the border extended posteriorly, albeit in somewhat different fashion than in *S. cassinensis*. Consideration of other morphological details, however, strongly suggests that most of these similarities are convergent. Many species of *Strigigenalis*, including *S. cassinensis*, have punctate cephalic sculpture. All have librigenae with the lateral and posterior border furrows deep and confluent in front of the genal angle, with the base of the genal spine swollen and difficult to distinguish from the rear of the posterior and lateral borders (e.g., Brett & Westrop 1996, fig. 17.3; Loch 2007, pl. 18, fig. 10). This contrasts strongly with the situation in *Bathyurina*, in which the furrows, while they may be confluent, are greatly shallowed in front of the genal angle, and are often crossed by sculpture originating on the field. The region around the base of the genal spine (where present) is always clearly distinguished from the lateral border and generally has distinctly different sculpture. In pygidia of species of *Strigigenalis*, it is typical for the first three pleural furrows to be clearly recognisable, and in some cases also the fourth (e.g., *S. derbyi* Loch 2007, pl. 17, figs 7–9). In those of species of *Bathyurina*, only the first two pleural furrows are always recognisable. Hence, it appears that the exclusively southern Laurentian *Strigigenalis* is a separate, though possibly related, clade.

Bathyurina megalops Poulsen 1937 (Fig. 4)

1937 *Bathyurina megalops*; Poulsen, p. 52, pl. 6, figs 14, 15, pl. 7, fig. 1.
1953 *Bathyurina megalops* Poulsen; Whittington, p. 669.
1979 *Bathyurina megalops* Poulsen; Fortey, p. 74, pl. 25, fig. 11.
1986 *Jeffersonia megalops* (Poulsen); Fortey, p. 18.
1989 *Bathyurina megalops* Poulsen; Boyce, p. 49.
1996 *Bathyurina megalops* Poulsen; Fortey & Droser, p. 83.
1998 *Bathyurina megalops* Poulsen; Zhou *et al*., p. 276.
2003 *Jeffersonia megalops* (Poulsen); Jell & Adrain, p. 347.
2005 *Bathyurina megalops* Poulsen; Adrain & Westrop, p. 1543.
2007 *Bathyurina" megalops* Poulsen; Loch, p. 37.

Holotype. Cranidium, MGUH 3699 (Poulsen 1937, pl. 6, fig. 14, pl. 7, fig. 15; Fig. 4A, C, E, H), from the Cape Weber Formation, Mt. Gunvor, Strindberg Land, eastern Greenland.

Diagnosis. Very similar to *B. plicolabeona*, differing in the possession of more strongly downturned frontal areas, an anteriorly broader glabella, somewhat larger palpebral lobes, a relatively longer (sag.; exsag.) SO and a relatively shorter LO.

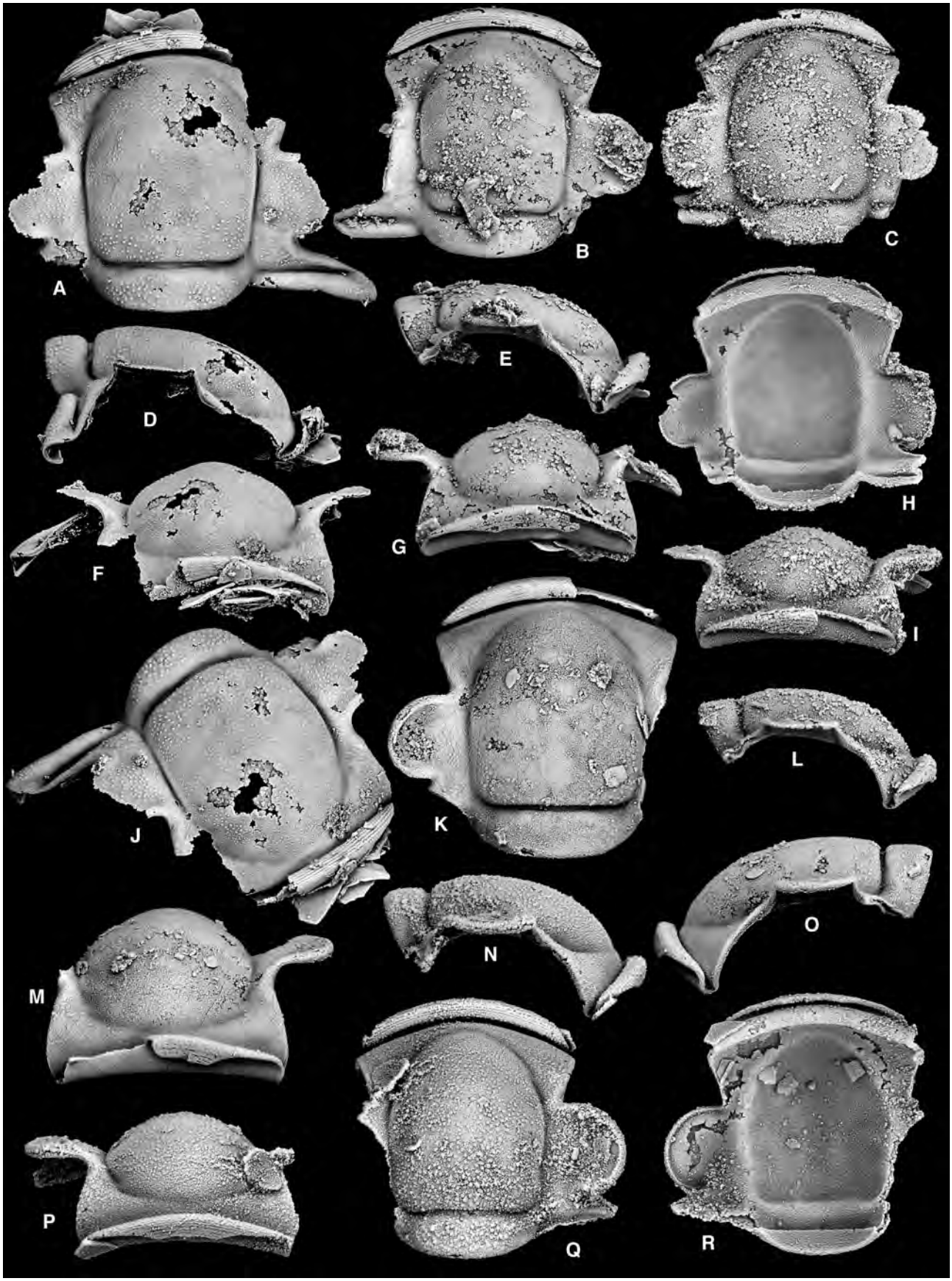
Remarks. The cranidial morphology of the species was discussed and compared with that of *B. plicolabeona* above under *Jeffersonia*. While two incomplete and largely exfoliated cranidia are a poor basis for a formally named species, similarity with cranidia of *B. plicolabeona* is so striking that the identity and content of the genus is now securely established. From what exists of the dorsal cranidial surface, it appears that the species had a sculpture of relatively widely scattered, tiny tubercles (see Fig. 4B especially), again almost identical with that of large cranidia of *B. plicolabeona*.

Bathyurina plicolabeona (Young 1973) (Figs 5–10)

1973 *Goniotelina* (?) *plicolabeonus*; Young, p. 99, pl. 5, figs 15–20 (only; pl. 5, figs 21, 22 = *Acidiphorus* sp. nov. 3 of Adrain *et al*. [2009, p. 570, fig. 17CC, DD]).
1973 Unassigned pygidium 8; Young, pl. 6, fig. 16.
1973 Unassigned pygidium 11; Young, pl. 6, figs 19, 22.
1979 *Strigigenalis plicalabeonus* [*sic*] (Young); Fortey, p. 90.
1986 *Strigigenalis plicalabeonus* [*sic*] (Young); Zhou & Fortey, p. 195.
1997 *Goniotelina*? *plicolabeonus* Young; Ross *et al*., pp. 19, 43.
2009 *Strigigenalis plicolabeona* (Young); Adrain *et al*., p. 570, fig. 17R, W.
2009a *Strigigenalis plicolabeona* (Young); McAdams & Adrain, p. 494.
2009b *Strigigenalis plicolabeona* (Young); McAdams & Adrain, p. 877.
2012 *Strigigenalis plicolabeona* (Young); Adrain & McAdams, p. 6.

Type material. Holotype, cranidium, BYU 2121 (Young 1973, pl. 5, figs 17–19), from Section H 191.7 m, Fillmore Formation (Floian; *Bathyurina plicolabeona* Zone), southern Confusion Range, Ibex area, Millard County, western Utah. Young (1973, p. 100) designated three paratypes, including two pygidia (BYU 2123, 2124) and one librigena (BYU 2125). The librigena was correctly assigned and remains

Figure 5. ***Bathyurina plicolabeona*** (Young 1973), from Section H 191.7 m, Fillmore Formation (Floian; *Bathyurina plicolabeona* Zone), southern Confusion Range, Ibex area, Millard County, western Utah. **A**, **D**, **F**, **J**, cranidium, SUI 124830, dorsal, (*continued opposite*)



right lateral, anterior, and oblique views, x5. **B**, **E**, **G**, cranidium, SUI 124831, dorsal, right lateral, and anterior views, x6. **C**, **H**, **I**, **L**, cranidium, SUI 124832, dorsal, ventral, anterior, and right lateral views, x6. **K**, **M**, **O**, cranidium, SUI 124833, dorsal, anterior, and left lateral views, x6. **N**, **P**–**R**, cranidium, SUI 124834, right lateral, anterior, dorsal, and ventral views, x7.5.

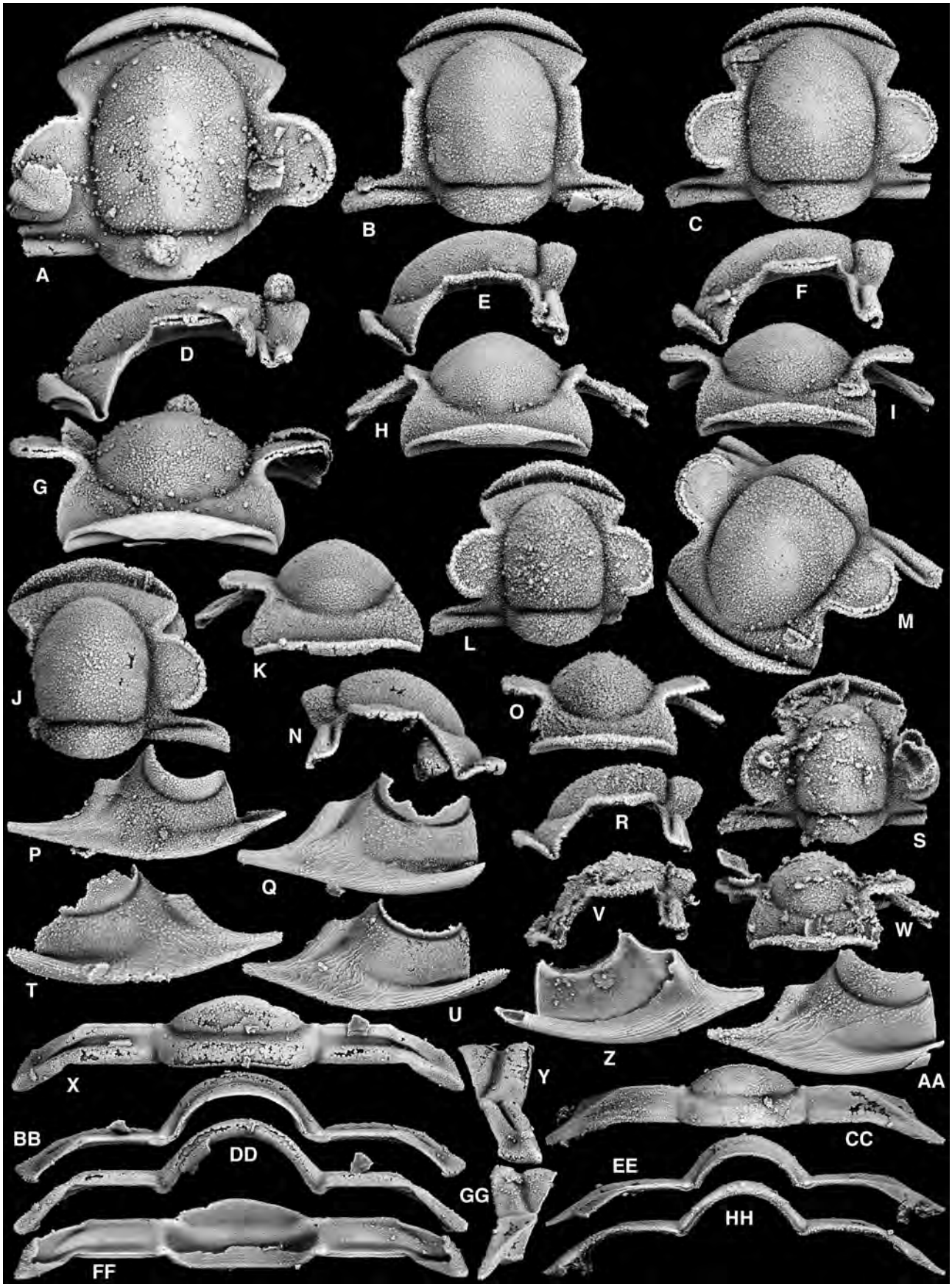


Figure 6. ***Bathyurina plicolabeona*** (Young 1973), from Section H 191.7 m, Fillmore Formation (Floian; *Bathyurina plicolabeona* Zone), southern Confusion Range, Ibex area, Millard County, western Utah. **A**, **D**, **G**, cranidium, SUI 124835, dorsal, left lateral, and anterior views, x10. **B**, **E**, **H**, cranidium, SUI 124836, dorsal, left lateral, and anterior views, x10. (*continued opposite*)

a valid paratype. However, both pygidia were incorrectly assigned and belong instead to a new species of *Acidiphorus* which will be described in a forthcoming work.

Additional material. Assigned specimens SUI 115335, 115336, 124830–124885, from Section H 185.6-191.7 m, Fillmore Formation (Blackhillsian; *Bathyurina plicolabeona* Zone), southern Confusion Range, Ibex area, Millard County, western Utah.

Diagnosis. Glabella not overhanging anterior border, preglabellar field visible in dorsal view; cranidial sculpture of large specimens of relatively widely scattered small tubercles; large librigenae with blunt genal spine; strong raised line sculpture on genal spine crosses inflated region interrupting posterior and lateral border furrows, confluent with raised line sculpture on field; large pygidia with narrow axis and border greatly extended into broad posterior point.

Description. Cranidial measurements were made on the largest and most complete specimens of Figure 5. Cranidium with width across posterior projections 144.8% sagittal length (Fig. 5A), width across midlength of palpebral lobes 120.7% (120.0-121.1) sagittal length; anterior border strongly flexed upward and backward against preglabellar field so that it obscures the anterior portion of the preglabellar field in dorsal view, two distinct sectors of border are visible in dorsal and anterior views, with third posteriorly facing sector; dorsally visible sector moderately short (sag., exsag.), with sagittal length less than half that of LO, of similar length along most of course, with distal tips tapering to a point abaxially, anterior and posterior margins describing gently curved arc with distal portions of anterior margin directed more strongly posterolaterally where facial suture cuts across border, inclined slightly toward anterior glabellar margin, with sculpture of approximately six raised lines, set subparallel to each other and following the same arc as the border, slightly more widely spaced on middle region; anteriorly visible sector is flattened and faces anteriorly to anteroventrally, oriented subparallel to the upturned posteriorly facing part of border, sculpture of raised lines covers anterior face, with lines more flattened than on the dorsal sector of the border; anterior border furrow extremely deep, trench-like, long (sag.), with anterior and posterior margins clearly distinct, describing arc similar to that of anterior border; preglabellar field long (sag.), but mostly obscured by upturned anterior border so that it appears much shorter in dorsal view and is hidden by border in anterior view, anteriormost portion slightly recurved under cranidium (Fig. 5D); preglabellar furrow much narrower and shallower than axial furrows; frontal areas with slight independent inflation, sloped strongly downward from anterior margin of palpebral lobe, with anterior portion more strongly downturned and nearly vertical, with moderately densely scattered small tubercles; anterior sections of facial suture moderately anteriorly divergent, gently laterally bowed across anterior border and frontal area, reaching widest point of divergence immediately behind intersection with rear of anterior border furrow; width across β 85.8% (84.3-87.7) cranidial sagittal length, and 70.6% (69.6-71.3) width across midlength of palpebral lobes; palpebral lobes very large, length (exsag.) 32.2% (29.5-34.6) cranidial sagittal length, distance across γ 75.2% (72.4-76.8) cranidial sagittal length, distance across ε 90.2% (87.7-94.1) cranidial sagittal length, lobe strongly laterally bowed, with curve slightly stronger posteriorly so that lobe appears slung posteriorly, lobe held below dorsal apex of glabella, dorsal surface nearly flat, with only gentle transverse convexity, and only slightly sloping toward glabella, sculpture of small scattered tubercles with expression ranging from distinct on larger specimens (Fig. 5A) to subdued on smaller specimens (Fig. 6A); margin of lobe defined by well developed narrow rim, sculpture of small, anastomosing, obliquely set raised lines, rim set off from main dorsal portion of lobe by distinct narrow furrow and strong independent inflation of rim; rim confluent posteriorly with narrow swollen area which runs along posterior section of facial suture on posterior projection, expressed distally all the way to point that fixigena is cut across by facial suture, rim confluent anteriorly with similar swollen area along anterior section of facial suture, expressed only for a short distance in front of the lobe; interocular fixigena distinguished from dorsal surface of palpebral lobe only by much steeper slope toward glabella, sculpture identical to that of palpebral lobe, narrow anteriorly so that anterior margin of palpebral lobe nearly abuts glabella, wider posteriorly where the posterior edge of palpebral lobe set more distal to glabella; posterior fixigena with inflation similar to frontal area, forming short (exsag.) strip, much shorter abaxially

Figure 7 (*overleaf*). ***Bathyurina plicolabeona*** (Young 1973), from Section H 191.7 m, Fillmore Formation (Floian; *Bathyurina plicolabeona* Zone), southern Confusion Range, Ibex area, Millard County, western Utah. **A**, right librigena, SUI 124848, external view, x6. **B**, **D**, right librigena, SUI 124849, external and ventrolateral views, x6. **C**, right librigena, SUI 124850, external view, x6. **E**, **H**, left librigena, SUI 124851, external and ventrolateral views, x10. **F**, left librigena, SUI 124852, external view, x6. **G**, **P**, right librigena, SUI 124853, external and internal views, x6. **I**, left librigena, SUI 124854, external view, x10. **J**, right librigena, SUI 124855, external view, x7.5. **K**, **M**, **Q**, right librigena, SUI 124856, external, ventrolateral, and internal views, x7.5. **L**, left librigena, SUI 124857, external view, x10. **N**, **U**–**X**, pygidium, SUI 124858, ventral, posterior, dorsal, right lateral, and anterior views, x15. **O**, **R**–**T**, final meraspid degree transitory pygidium, SUI 124859, right lateral, dorsal, posterior, and ventral views, x20.

Figure 8 (*Page 317*). ***Bathyurina plicolabeona*** (Young 1973), from Section H 191.7 m, Fillmore Formation (Floian; *Bathyurina plicolabeona* Zone), southern Confusion Range, Ibex area, Millard County, western Utah. **A**, **C**, **E**, **G**, **H**, pygidium, SUI 124860, dorsal, posterior, left lateral, ventral, and anterior views, x5. **B**, **D**, **F**, pygidium, SUI 124861, left lateral, dorsal, and posterior views, x6. **I**, **J**, **L**, pygidium, SUI 124862, left lateral, dorsal, and posterior views, x5. **K**, **M**, **P**, **R**, pygidium, SUI 124863, left lateral, dorsal, posterior, and ventral views, x6. **N**, **O**, **Q**, pygidium, SUI 124864, dorsal, left lateral, and posterior views, x6.

(*continued from opposite*) **C**, **F**, **I**, **M**, cranidium, SUI 124837, dorsal, left lateral, anterior, and oblique views, x10. **J**, **K**, **N**, cranidium, SUI 124838, dorsal, anterior, and right lateral views, x15. **L**, **O**, **R**, cranidium, SUI 124839, dorsal, anterior, left lateral views, x12. **P**, right librigena, SUI 124840, external view, x15. **Q**, right librigena, SUI 124841, external view, x12. **S**, **V**, **W**, cranidium, SUI 124842, dorsal, left lateral, and anterior views, x12. **T**, left librigena, SUI 124843, external view, x12. **U**, **Z**, right librigena, SUI 124844, external and internal views, x10. **X**, **Y**, **BB**, **DD**, **FF**, thoracic segment, SUI 124845, dorsal, left lateral, anterior, posterior, and ventral view, x6. **AA**, right librigena, SUI 124846, external view, x12. **CC**, **EE**, **GG**, **HH**, thoracic segment, SUI 124847, dorsal, anterior, right lateral, and posterior views, x10.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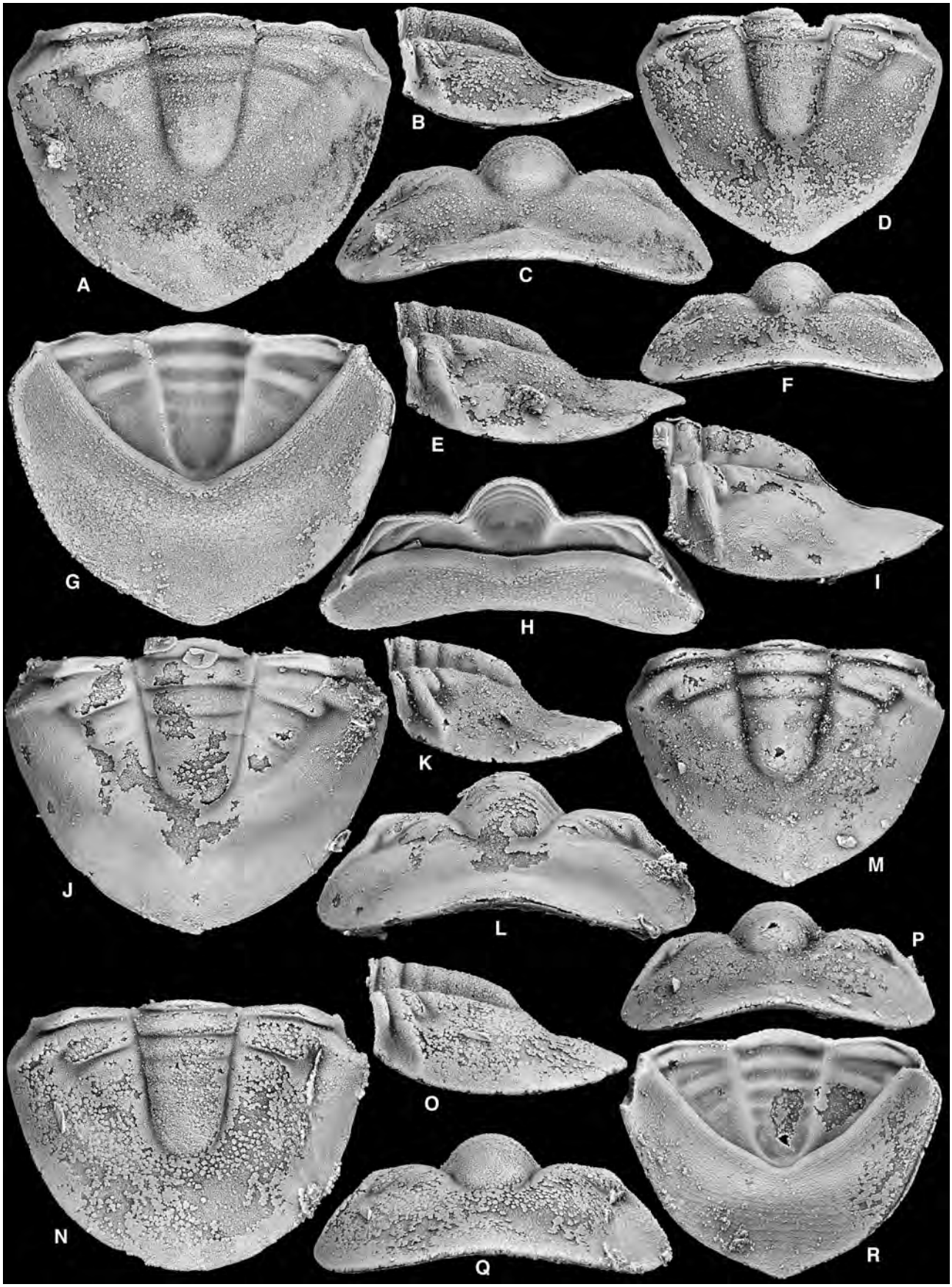
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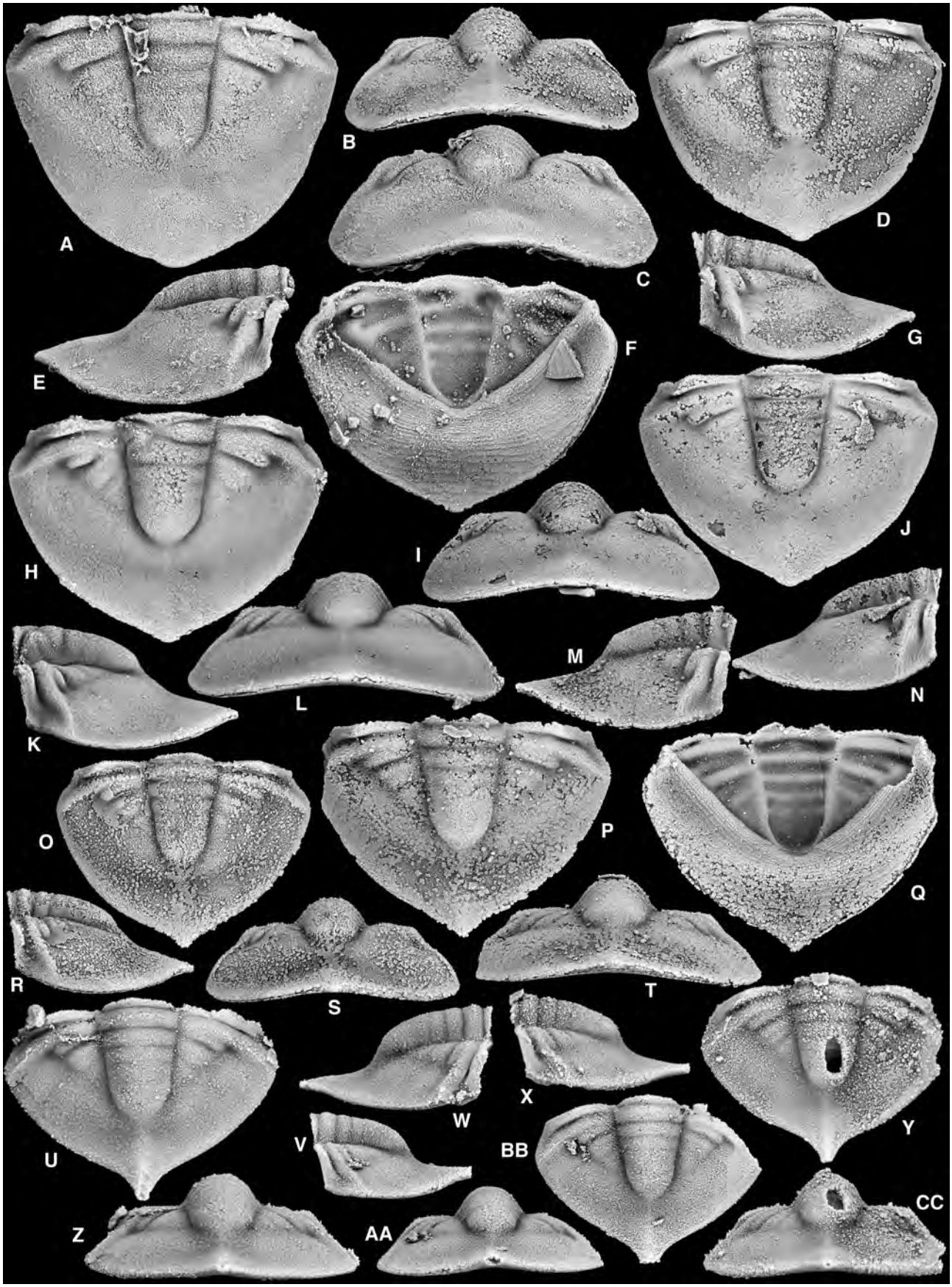


Figure 9. ***Bathyurina plicolabeona*** (Young 1973), from Section H 191.7 m, Fillmore Formation (Floian; *Bathyurina plicolabeona* Zone), southern Confusion Range, Ibex area, Millard County, western Utah. **A**, **C**, **E**, pygidium, SUI 124865, dorsal, posterior, and right lateral views, x6. **B**, **D**, **G**, pygidium, SUI 124866, posterior, dorsal, and left lateral views, x6. (*continued opposite*)

pinching out to a narrow point distally, small scattered tubercles continue from palpebral lobe and interocular fixigena onto posterior fixigena; posterior section of facial suture with strong posterolateral bow, so posterior fixigena extended strongly posterolaterally and almost parallel to transverse axis, adaxial portion of facial suture is directed strongly posterolaterally with gentle anteriorly convex bow, distal tip directed more strongly posterolaterally; posterior border furrow long (exsag.) medially, distal and proximal tips slightly shorter, very shallow at contact with axial furrow, then deeper adjacent to this contact, progressive deeper abaxially to point opposite where posterior fixigena pinches out, from this point abaxially furrow is much shallower, main portion directed nearly parallel to transverse axis with distal shallow portion directed strongly posterolaterally, with sharp contact posteriorly with posterior border and anteriorly with posterior fixigena; posterior border strongly dorsally inflated, almost subcylindrical in section (Fig. 5D), long (exsag.) proximally, lengthened distally, with distal tip strongly downturned, sculpture of small scattered tubercles similar to that present on posterior fixigena present on distal portion; posterior margin of posterior border nearly straight and directed slightly posterolaterally from contact with axial furrow to point about two thirds along length, from this point abaxially margin is directed more strongly posterolaterally; glabella with maximum width 85.5% (82.7-88.7) sagittal length (excluding LO), sagittal length 70.7% (69.2-71.8) that of cranidium, widest just behind anterior edge of palpebral lobe, glabella slightly waisted at L1, moderately dorsally inflated, sitting above fixigena in lateral view, anterior part coming nearly to a point medially in anterior view, anterior margin strongly arched medially; glabellar sculpture similar to that on dorsal surface of palpebral lobes, with slightly larger tubercles posteriorly; axial furrows shallow opposite LO, narrow and becoming deeper anteriorly, deepest near anterior edge of palpebral lobe, shallowed abruptly in front of palpebral lobe at contact with eye ridge, width across posterior contact of furrows with posterior margin 55.5% (55.4-55.6) cranidial sagittal length, axial furrows laterally confluent with posterior border furrow, but very shallow at contact; glabellar furrows not impressed, but expressed as dorsally smooth patches lacking tubercles; LO long, sagittal length 15.9% (15.3-16.5) that of cranidium, longer sagittally than exsagittally, posterior margin with slight posterior bow across median portion and distal tips directed strongly anterolaterally, anterior margin nearly transverse, but with distal tips strongly curved anterolaterally around posterolateral corners of glabella, with sculpture of scattered small tubercles as on glabella, covering most of LO except for distal tips which are smooth; SO deep, long (sag., exsag), anterior and posterior margins with sharp contact with rear of main glabella and LO respectively, almost exactly transverse, with distal tips significantly shorter, deeper opposite posterior margin of posterolateral corner of glabella, and strongly curved anteriorly to join axial furrow in smooth continuous curve; doublure underlying LO nearly semicircular, extending anteriorly to about midpoint of LO, with sculpture of very faint fine, closely spaced raised lines arranged subparallel to transverse plane.

Librigena with anterior section of facial suture with length about 36% exsagittal length of main body and posterior section of facial suture with length (across field) 22% exsagittal length of main body; anterior section with very slight convex bow adjacent to furrow bounding eye, remaining portion nearly straight to lateral border furrow; posterior section almost transversely straight to slightly sinuous across field, with strongly concave opposite border furrow so that suture is almost L-shaped, section cutting across posterior border is nearly transverse; visual surface long, tall, strongly convex, bounded by broad and deep furrow; main portion of field with strong dorsal convexity, sitting above border in ventrolateral view; field with prominent sculpture of raised anastomosing lines running from genal angle toward eye across posterior portion of field, lines stop short of furrow bounding eye and on some specimens lines only reach a short distance beyond genal angle onto field (Fig. 7F); broad band of prominent small tubercles present below visual surface of eye, band spans entire length of field opposite posterior facial suture, across anterior portion of field, to about half the length of the field opposite the anterior facial suture; smooth portion of field bounded by lateral border furrow, posterior half of anterior facial suture, posterior margin of tuberculate area, and anastomosing lines emanating from genal angle, sometimes posterior margin of tuberculate area creeps down into smooth sector forming a small region with a sculpture of short dashed lines; lateral border furrow deep and narrow anteriorly about halfway along course where lateral border is pushed upwards against field, posterior portion of furrow much shallower and broader, terminated by swollen area emerging from genal angle onto field; anterior portion of lateral border is strongly flexed upward against field, forming a distinct boundary to anterior portion of genal field, continuing anteriorly without obvious disruption into anterior projection, which is long, extending far beyond anterior facial suture and strongly turned downward from horizontal plane (Fig. 7B, D); sculpture of fine raised lines running subparallel to lateral margin running from lateral margin of genal angle, covering entire aspect of lateral border and anterior projection; broad dorsoventrally flattened portion of lateral border present adjacent to genal angle, merges smoothly into anterior upturned portion of lateral border, sculpture of raised lines also continuous, but lines are coarser and arranged in a more anastomosing pattern than on anterior portion of lateral border; lateral border with lateral margin gently bowed outward opposite dorsoventrally flattened portion of border; posterior border narrow and more dorsoventrally flattened in contrast to anterior portion of lateral border, widest at intersection with posterior facial suture, narrowing toward genal angle; posterior border furrow forming deep, broad, trough-like pit, smooth, clearly separating posterior border from main portion of field; sculpture of prominent, raised, anastomosing lines present on posterior border and broad swollen region at base of genal angle, sculpture continues onto field towards eye from genal angle and mingles with band of tubercles below eye, lines are much more coarse than those on anterior portion of lateral border and anterior projection; genal angle developed into short blade-like

F, **H**, **K**, **L**, pygidium, SUI 124867, ventral, dorsal, left lateral, and posterior views, x7.5. **I**, **J**, **N**, pygidium, SUI 124868, posterior, dorsal, and right lateral views, x7.5. **M**, **P**, **Q**, **T**, pygidium, SUI 124869, right lateral, dorsal, ventral, and posterior views, x10. **O**, **R**, **S**, pygidium, SUI 124870, dorsal, left lateral, and posterior views, x7.5. **U**, **W**, **Z**, pygidium, SUI 124871, dorsal, right lateral, and posterior views, x15. **V**, **AA**, **BB**, pygidium, SUI 124872, left lateral, posterior, and dorsal views, x15. **X**, **Y**, **CC**, pygidium, SUI 124873, left lateral, dorsal, and posterior views, x15.

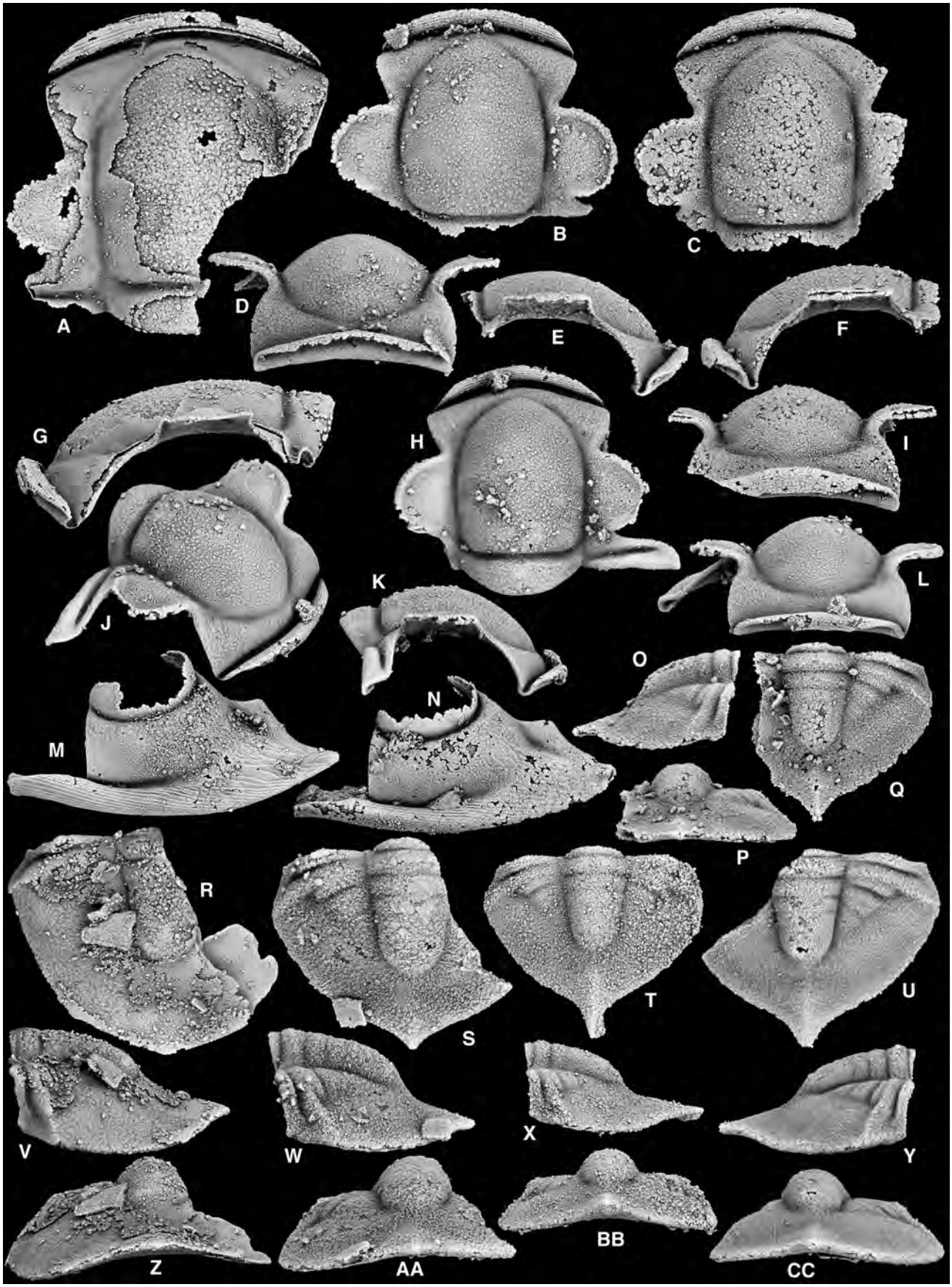


Figure 10. ***Bathyurina plicolabeona*** (Young 1973), from Section H 185.6–187.4 m, Fillmore Formation (Floian; *Bathyurina plicolabeona* Zone), southern Confusion Range, Ibex area, Millard County, western Utah. **A**, **G**, cranidium, SUI 124874, dorsal and left lateral views, x5 (H 186.2 m). **B**, **D**, **E**, cranidium, SUI 124875, dorsal, anterior, and right lateral views, x10 (H 186.2 m). (*continued opposite*)

projection, sculpture of anastomosing lines emanates from tip of projection in a series of three of four strongly curved lines before running outward across field perpendicular to eye; doublure widest beneath genal angle and posterior border, narrows significantly below lateral border and anterior projection, inner margin of doublure describes smooth continuous arc without any distinct change in course between posterior border and lateral border, doublure forming small depressed region adjacent to inner margin at genal angle; entire doublure with sculpture of very fine, closely spaced raised lines running subparallel to posterior and lateral borders externally, lines meet at a sharp angle toward tip of genal angle, but are more gently curved toward inner margin of doublure, lines slightly more widely spaced toward inner margin; large Panderian notch developed adjacent to posterior facial suture (e.g., Fig. 7P, Q).

Hypostome and rostral plate not identified.

Description of thoracic morphology based on the segments of Figure 6. Thoracic segments with axis strongly convex and sitting high above pleurae; axial ring shorter sagittally than exsagittally, slightly wider (tr.) anteriorly; ring furrow is deep, long (sag., exsag.), with medial potion nearly transverse and distal tip more strongly bowed anterolaterally; articulating half ring large with sagittal length nearly one and a half times as long as that of axial ring, nearly semicircular in outline, with anterior margin strongly anteriorly bowed and posterior margin gently posteriorly bowed to nearly transverse medially; axial furrows deep and pit-like posteriorly opposite posterior pleural band, significantly shallower anteriorly; small, rounded, anteriorly directed process developed at intersection of axial furrow with anterior margin of anterior pleural band (Fig. 6CC), articulates with small depression in posterior end of next segment anteriorly; pleural furrow long (exsag.) between fulcrum and axial furrow, this portion of furrow is deepest at fulcrum and shallows adaxially on larger segment (Fig. 6X), but on smaller segment (Fig. 6CC) this portion of furrow is shallower overall; section of pleural furrow from fulcrum distally is deeper, much shorter, and slit-like, pinching out and not reaching margin so that anterior and posterior pleural bands appear merged distally; anterior and posterior pleural bands with independent inflation, clearly differentiated into anterior and posterior bands for majority of course, merged into single strip distally, terminating in distinct posterolaterally directed point; very narrow ridge-like rim bounds anterior margin of anterior band between articulating process at anterior margin of axial furrow and fulcrum, rim articulates with a transverse groove ventrally beneath the posterior edge of the pleurae of the next segment anteriorly (Fig. 6FF); anterior margin of pleura developed into small anterolaterally directed subtriangular spike, situated just past point opposite of where anterior and posterior pleural bands merge distally, ventrally spike is clearly visible at contact of doublure with anterior margin of segment, spike articulates with small, deep notch on the posterior margin of the next segment anteriorly; on smaller segment spike is expressed as larger triangular facet (Fig. 6GG); ventrally, doublure incomplete on recovered specimens, but forms long (sag.) articulating surface beneath the axial ring, with a sculpture of fine raised lines running subparallel to margin; doublure also present distally beneath tip of pleura, inner margin developed into prominent notch with a slightly rounded hole medially that extends even further towards distal tip of segment, anteriorly doublure extends only to contact with articulating spike, posteriorly doublure extends nearly to fulcrum; fulcrum is set about at midpoint of pleura, with the portion of pleura distal to the fulcrum strongly downturned from horizontal plane and directed strongly posterolaterally, compared to rest of segment which is nearly transverse.

Pygidium with maximum with across anterior margin of third axial segment (on some specimens maximum width is achieved across posterior margin of second axial segment) 128.6% (125.3-133.2) sagittal length; axis composed of five segments, with maximum axial width across first segment 29.9% (25.2-31.5) maximum pygidial width, width across anterior margin of fifth segment 68.2% (65.6-72.1) width across first segment, length of axis excluding articulating half ring 52.0% (50.5-53.9) total sagittal length of pygidium; articulating half ring very short (sag., exsag.), sagittal length 4.7% (3.9-6.7) total pygidial length, sliver-like with anterior margin anteriorly convex, half ring sitting slightly below first axial ring in general sagittal profile of axis, sculpture of fine granules appears to be present, but surface not well preserved on any recovered specimens; first ring furrow deep along entire course, slightly deeper just before contact with axial furrow, very short (sag., exsag.), and gently anteriorly bowed; second ring furrow with morphology similar to first, but slightly shallower medially, and slightly deeper and slit-like distally before contact with axial furrow; third ring furrow similar to second, but overall slightly shallower; fourth ring furrow mostly effaced dorsally, but clearly expressed ventrally; fifth ring furrow expressed dorsally only by slight indentation along axial margin, ventrally more clearly visible, especially at contact with axial furrow; pseudo-articulating half ring of second and subsequent segments not clearly differentiated; first axial ring of similar length sagittally and exsagittally, slightly longer than second ring, nearly transverse; posterior rings progressively smaller and more poorly expressed, but with generally similar morphology; axis terminated by broad terminal piece, with posterior margin strongly rounded and clearly distinct from post axial region; dorsal surface of axis not well preserved, but sculpture of small to medium sized tubercles present on medial portion (Fig. 8J), lateral portions of axis smooth; post axial field extremely long (sag.), with length (sag.) 42.3% (41.0-44.3) pygidial length; fulcrum set moderately close to axis, with portion of pleurae between axis and fulcrum held nearly parallel to horizontal plane (Fig. 8H) in anterior view; first pleural segment with maximum exsagittal pleural length 14.4% (13.2-15.5) sagittal axial length, anterior margin straight and nearly transverse to slightly anterolaterally directed to fulcrum; margin directed slightly posterolaterally distal to fulcrum, with course disrupted by prominent anterolaterally directed subtriangular spike developed about halfway between fulcrum and margin, portion of anterior margin distal to spike directed strongly

C, **F**, **I**, cranidium, SUI 124876, dorsal, left lateral, and anterior views, x10 (H 186.2 m). **H**, **J**–**L**, cranidium, SUI 124877, dorsal, oblique, right lateral, and anterior views, x12 (H 186.2 m). **M**, left librigena, SUI 124878, external view, x10 (H 186.2 m). **N**, left librigena, SUI 124879, external view, x6 (H 186.2 m). **O**–**Q**, pygidium, SUI 124880, right lateral, posterior, and dorsal views, x12 (H 186.2 m). **R**, **V**, **Z**, pygidium, SUI 124881, dorsal, left lateral, and posterior views, x6 (H 187.4 m). **S**, **W**, **AA**, pygidium, SUI 124882, dorsal, left lateral, and posterior views, x12 (H 187.4 m). **T**, **X**, **BB**, pygidium, SUI 124883, dorsal, left lateral, and posterior views, x10 (H 186.2 m). **U**, **Y**, **CC**, pygidium, SUI 124884, dorsal, right lateral, and posterior views, x12 (H 185.6 m).

posterolaterally; spike articulates with last thoracic segment, in ventral view spike is triangular in outline, inner margin of doublure extends continuously to tip of spike (Fig. 8G); facet relatively small, strongly downturned from horizontal plane, with sculpture of fine raised lines; anterior pleural band set off from margin by narrow ridge-like rim and shallow furrow similar to that on thorax (Fig. 8J); anterior pleural band short (exsag.) proximally, lengthens abaxially to fulcrum, tapers from articulating spike abaxially to margin, short posterolaterally directed process developed at fulcrum disrupting course of band, process is better developed on some specimens (e.g., Fig. 8J) than others (e.g., Figs 8N, 9H); posterior pleural band longer (sag., exsag.) than anterior band, course not obviously disrupted at fulcrum, but with more gentle bow, sculpture of faint tubercles present along posterior margin adaxially adjacent to fulcrum, portion of band distal to fulcrum covered with sculpture of fine raised lines running subparallel to margin of band; pleural furrow moderately short (exsag.), deepest between fulcrum and articulating spike, significantly shallower from spike distally so that anterior and posterior pleural bands appear almost merged; portion of pleural furrow between fulcrum and axis on some specimens is shallow becoming more shallow toward axial furrow (Fig. 8J), but on others it is deeper then becoming abruptly shallow just before contact with axial furrow (Fig. 9A); interpleural furrow largely effaced between axis and fulcrum, forming a deep depression at fulcrum that is confluent with pleural furrow of second band and clearly outlines abaxial extent of anterior band of second pleurae, very shallow between fulcrum and pygidial margin just barely setting on posterior margin of posterior pleural band of first pleura; second pleural band with anterior and posterior bands expressed between fulcrum and axis, but effaced abaxially from fulcrum, with pleural furrow deep and narrow clearly differentiating anterior and posterior bands, but effaced adaxially so that it either does not contact or just barely makes contact with axial furrow; subsequent pleural bands not well expressed, with third pleural furrow slightly impressed, and pleural bands slightly dorsally inflated; distinct change in slope at fulcrum between termination of second and subsequent pleural bands and remainder of pleural field (Fig. 9K); border furrow and border not well expressed, differentiated from pleural field by change in slope, forming a broad smooth area with pleural field; pygidial margin poorly preserved, but sculpture of fine raised lines apparently developed along margin, lines slightly encroach on pleural region posteriorly; posterior pygidial margin forming a gentle, slightly rounded, point medially, in transverse profile margin is strongly bowed upward medially forming a prominent arc, in sagittal profile margin forms smooth, gentle arc; in ventral view extremely broad doublure visible, extending adaxially to point opposite inner margin of short articulating spike developed on first pleural band and smooth with slight deflection around posterior margin of terminal piece medially; doublure divided into two sections, a broad flat portion that makes up the majority of the doublure and a much shorter upturned section present along the inner margin of the doublure; the flatter section is very broad, reaching maximum length sagittally, covered with fine raised lines that are relatively widely spaced posteriorly and running nearly parallel to transverse axis, about two thirds of the way across the broad flattened section the doublure is slightly depressed and the sculpture of fine raised lines becomes more closely spaced and the lines begin to run more subparallel to inner margin of doublure, lines are deflected medially and more closely spaced around ventral expression of terminal piece as is inner margin of doublure; the shorter upturned section also possesses sculpture of fine raised lines that run continuously from flattened section, but they are much more closely spaced.

Ontogeny. The anterior borders of small cranidia (Fig. 6J) are more dorsally flattened with the bottom of the anterior border furrow more fully visible in dorsal view. Through ontogeny the border becomes progressively turned up and back against the preglabellar field, resulting in the deep trench-like furrow characteristic of larger specimens. This is associated with a change in the expression of the preglabellar field, which is clearly visible in dorsal and anterior views in smaller specimens, but becomes progressively obscured throughout ontogeny. The shape of the glabella also undergoes modification, with small specimens having a more parallel-sided and less elongate glabella, but larger specimens possessing a glabella that is more laterally expanded near the front edge of the palpebral lobe and much more anteriorly extended and medially pointed. The glabella is also more dorsally convex in smaller specimens, flattening out throughout ontogeny. Small cranidia (Fig. 6J, L) have a sculpture of closely crowded granules or flattened tubercles which are gradually replaced by fairly dense, small, but more distinct, tubercles. On some larger specimens the tubercles are effaced, especially on the frontal areas and anterior region of the glabella.

The most obvious ontogenetic change of the librigena is the presence of a long, slender, and blade-like genal spine on smaller specimens (Fig. 6P). The spine becomes shorter and much broader in larger specimens (Fig. 7A). The sculpture of anastomosing lines and tubercles is more subdued on smaller specimens, becoming more prominent and distinct on the largest.

Pygidial changes throughout ontogeny are also noticeable, with smaller tails having the posterior margin developed into prominent post-axial spine and also having a clearly defined post-axial ridge (Figs 7R, 8U). The spine becomes greatly reduced and the margin broadly pointed posteriorly and the post-axial ridge becomes obscured throughout ontogeny. Pygidia also become longer with respect to width throughout ontogeny with the post-axial field occupying much more of the overall pygidial length in the largest specimens compared to the smallest.

Remarks. Bathyurina plicolabeona was compared with *B. megalops*, apparently the most similar species despite lack of knowledge of sclerites other than cranidia, above and under discussion of *Jeffersonia*. When Young (1973) described the species, he confused correctly associated cephalic material with pygidia of one of the two co-occurring species of *Acidiphorus* Raymond 1925. He illustrated some of the correct pygidia in open nomenclature (Young 1973, pl. 6, figs 16, 19, 22), but assigned them to two different species, presumably owing to the considerable ontogenetic change displayed.

Bathyurina plicolabeona is similar to the oldest known species, *B. morrisi* sp. nov, in the possession of a glabella which does not overhang the anterior border, with the preglabellar field visible dorsally. It differs from that species in the possession of a much more anteriorly expanded glabella, larger, more laterally extended palpebral lobes, a blunt genal spine versus a rounded genal angle; and pygidia with the border greatly extended posteriorly versus poorly

differentiated from the pleurae and not extended at all.

Bathyurina curtisi sp. nov. (Figs 11–13)

2009 *Strigigenalis* sp. nov. 1; Adrain *et al*., p. 571.

Material. Holotype, cranidium, SUI 124885 (Fig. 11A, B, D, E, G), from Section H 222.1 m, and assigned specimens SUI 124886–124910 from Section H 222.1 m and 226T m, Fillmore Formation (Floian; *Carolinites nevadensis* Zone), southern Confusion Range, Ibex area, Millard County, western Utah.

Etymology. After Ian Curtis.

Diagnosis. Glabella narrow anteriorly, coming to a prominent point overhanging anterior border; genal spine nearly effaced in large specimens, but retained as distinct point at genal angle; large pygidia vaulted and considerably effaced, especially posteriorly, with only first two ring furrows impressed.

Description. Cranidial measurements were made on Figures 11A, I and 12A, C. Cranidium with maximum width across posterior projections 136.6% sagittal length (Fig. 12A); width across midlength of palpebral lobes 113.7% (112.9-114.5) sagittal length; anterior border less than half as long (sag.) as LO, border tapering to a distinct point abaxially, strongly flexed posteriorly against anterior margin of cranidium so that border furrow, part of preglabellar field, and anterior tip of glabellar are crowded out; in anterior view, border forms a near vertical subtriangular face (ventral margins on larger specimens are incomplete, but smaller specimens show subtriangular outline), obscures anterior tip of glabella, ventral margin terminated above ventral extent of anterior border so that ventral surface of border is visible (Fig. 11F); entire border with sculpture of fine raised lines set parallel to margin, in dorsal view lines are set slightly closer together on part of border opposite anterior glabellar margin, sculpture of raised lines on near vertical anterior face peaked medially running subparallel to dorsal arc of border; anterior border furrow is very deep, with distinct break anteriorly and posteriorly, slightly deflected around anterior margin of glabella, sculpture of fine raised lines marks posterior margin of border furrow in lateral view (Fig. 11H); preglabellar field nearly vertical to almost curving under glabella in sagittal profile (Fig. 11D), anterior tip of glabella overhangs preglabellar field and preglabellar furrow medially obscuring it in dorsal view, field and furrow obscured medially in anterior view due to encroachment of anterior border; frontal areas dorsally convex, sloped strongly downward from anterior margin of palpebral lobe becoming near vertical to slightly curved under anteriorly, facing anteriorly, anterior part of frontal area smooth, posterior and lateral portions with widely spaced raised lines; preglabellar furrow moderately shallow, narrower than and confluent with axial furrows; anterior sections of facial sutures laterally convex opposite anterior border, forming very small concave notch opposite rear of anterior border furrow, and laterally divergent and very slightly laterally convex to nearly straight opposite frontal areas, with width across maximum point of divergence (β) 80.5% (77.2-82.7) cranidial sagittal length and 72.3% (72.2-72.4) width across midlength of palpebral lobe; palpebral lobes large, length (exsag.) 34.0% (32.8-35.3) cranidial sagittal length, distance across γ 71.0% (69.4-74.0) cranidial sagittal length, distance across ε 79.8% (78.0-83.2) cranidial sagittal length; lobe strongly laterally bowed and slung strongly posteriorly, with distinct, narrow, inflated rim-like border around margin, sculpture of fine raised lines appears to continue from frontal area onto rim (Fig. 12A, C), but not well preserved on any recovered specimens, lobe held well below dorsal apex of glabella, nearly horizontal, sloping very slightly toward palpebral furrow in anterior view; palpebral furrow faint, narrow, but distinct; interocular fixigena sloping more strongly toward axial furrow in anterior view; posterior fixigena forming short laterally extended, inflated strip, distal tip extending just past lateral extent of palpebral lobe; posterior section of facial suture directed almost parallel to transverse axis; posterior border furrow short (exsag.), deep abaxially past fulcrum toward distal tip, but does not reach facial suture, slightly lengthened and significantly shallower adaxially, directed slightly anterolaterally, with more gradational contact along anterior margin and slightly more distinct contact posteriorly with posterior border; posterior border dorsally inflated, short (exsag.) proximally, lengthened distally, subtriangular in outline with distal tip forming laterally convex arc running smoothly around anterolateral corner, posterolateral corner forming sharp angle, posterior margin of posterior border transversely straight; posterior projection, except for abaxial portion of posterior border furrow, covered with sculpture of fine granules; glabella bullet-shaped in plan view, with maximum width 77.1% (74.6-78.9) sagittal length (excluding LO), sagittal length 74.9% (74.0-76.3) that of cranidium, moderately dorsally inflated, sitting well above fixigena in sagittal profile, sagittal profile moderately curved, with highest point reached opposite palpebral lobes, moderately sized, densely spaced tubercles on median dorsal part of glabella give way to smaller and more widely spaced tubercles on posterolateral corners of glabella and LO, anteriorly tubercles morph into short dashed lines, which give way to a series of several fine raised lines running in a strongly bowed arc subparallel to anterior glabellar margin, anterior tip of glabella smooth (Fig. 12H); S1 and S2 visible on some specimens (Fig. 12A, B) as obliquely directed smooth areas, S1 is very slightly impressed at intersection with axial furrow; L1 and L2 not prominent and without any obvious independent inflation; axial furrows shallow and slightly laterally bowed around LO, width across posterior contact of furrows with posterior margin 57.2% (52.2-64.5) cranidial sagittal length, laterally confluent with posterior border furrow, slightly shallower at intersection with SO, uniformly deep around main portion of glabella, narrower anteriorly from anterior margin of palpebral lobe, running smoothly into preglabellar furrow; SO deep, anterior and posterior edges with sharp contact with rear glabellar margin and LO respectively, nearly transverse with slight posterior bow, distal tips strongly curved joining axial furrow in smooth curve, but with axial furrow shallower to the rear of this contact; LO long, sagittal length 16.0% (15.2-16.7) that of cranidium, longer sagittally than exsagittally, posterior margin strongly posteriorly bowed, anterior margin slightly posteriorly bowed to nearly transverse, with sculpture of scattered moderately sized tubercles, of similar size and spacing to those on posterior part of glabella, covering most of LO except for distal tips which are smooth; doublure underlying LO not completely preserved (Fig. 11B), with sculpture of fine, closely spaced raised lines.

Librigenal measurements were made on the largest specimen of Figure 12. Main body of librigena (excluding

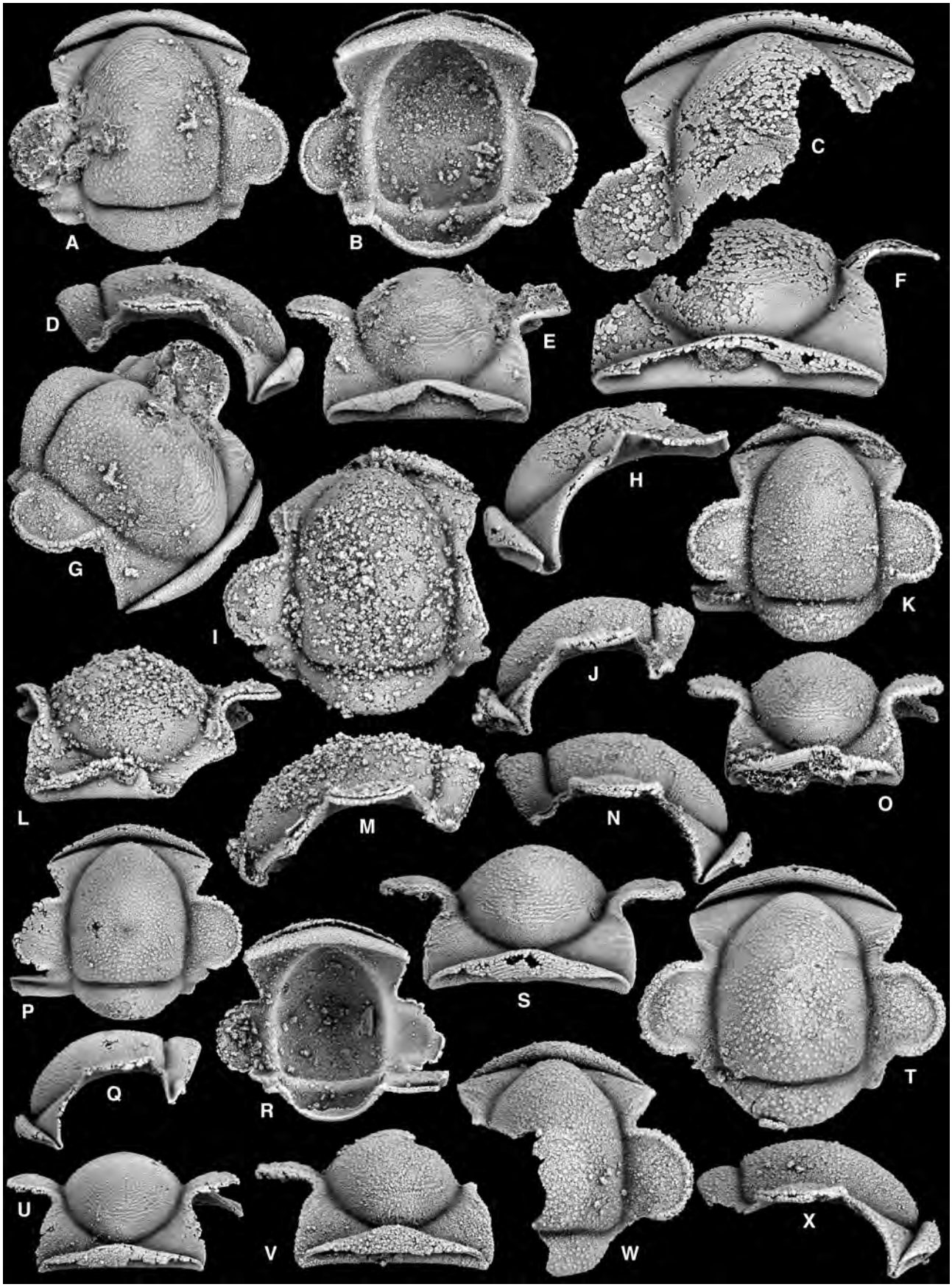


Figure 11. ***Bathyurina curtisi*** sp. nov., from Section H 222.1 m, Fillmore Formation (Floian; *Carolinites nevadensis* Zone), southern Confusion Range, Ibex area, Millard County, western Utah. **A**, **B**, **D**, **E**, **G**, cranidium, holotype, SUI 124885, dorsal, ventral, right lateral, anterior, and oblique views, x10. **C**, **F**, **H**, cranidium, SUI 124886, dorsal, anterior, and left lateral views, x10. (*continued opposite*)

anterior projection) with maximum width 55.8% exsagittal length; anterior section of facial suture with length 65.2% exsagittal length of main body and posterior section of facial suture with length 48.6% exsagittal length of main body; anterior section gently convex across field, with slight concave bow just before anterior projection; posterior section concave opposite border furrow almost transversely straight across posterior border and field; visual surface long, tall, and bulbous, bounded by narrow and deep furrow; field with prominent sculpture of fine raised anastomosing lines running from eye straight across to border furrow; lateral border furrow very broad and shallow posteriorly, significantly deeper and narrower anteriorly; posterior border furrow similar to main portion of lateral border furrow, deeper toward intersection with posterior facial suture; lateral border with main portion broad, dorsoventrally flattened, with moderate inflation, widest at genal angle and narrowing anteriorly, anterior portion of lateral border, from point opposite where furrow becomes deeper and narrower, is flexed upward against genal field, forming a prominent and distinct ridge-like border bounding anterior portion of genal field, continuing without obvious disruption into anterior projection; anterior projection incomplete on largest specimen, but prominent; posterior border similarly broad and dorsoventrally flattened as portion of lateral border adjacent to genal angle, widest at genal angle, narrowing significantly toward posterior facial suture; main flattened portion of lateral and posterior borders lacking obvious sculpture, sculpture of prominent fine raised lines running continuously from genal angle anteriorly along lateral aspect of lateral border and doublure onto anterior projection, lines running lengthwise along projection, sculpture present on all aspects of projection, lines much finer that those on genal field; genal angle slightly greater than 90°, describing slightly rounded corner on largest specimens without being extended into spine; lateral and posterior border furrows shallowest at intersection at genal angle; doublure divided into two sections, a flat portion beneath posterior border along posterior margin and beneath lateral border along outer margin, an upturned portion beneath adaxial part of lateral and posterior borders and anterior projection; sections divided by ridge originating from middle of lateral margin, following smooth arc across doublure, ridge more prominent closer to lateral margin becoming weaker adaxially across doublure and turning into shallow depression opposite genal angel; inner margin of doublure describes continuous arc, lacking any obvious change in course between posterior border and lateral border; doublure beneath posterior border with faint, fine raised lines running subparallel to posterior margin, continues around genal angle onto flattened portion of doublure beneath lateral border, middle portion of flattened area smooth; sculpture of more prominent fine raised lines subparallel with inner margin of doublure running continuously from ventral aspect of anterior projection onto upturned portion of doublure, lines are more closely spaced on anterior projection up to base of ridge dividing two sections of doublure, lines become more widely spaced on upturned portion toward posterior facial suture; sculpture of raised lines on both sections of doublure intersect at posterior facial suture; large Panderian notch (Fig. 12E) developed adjacent to posterior facial suture.

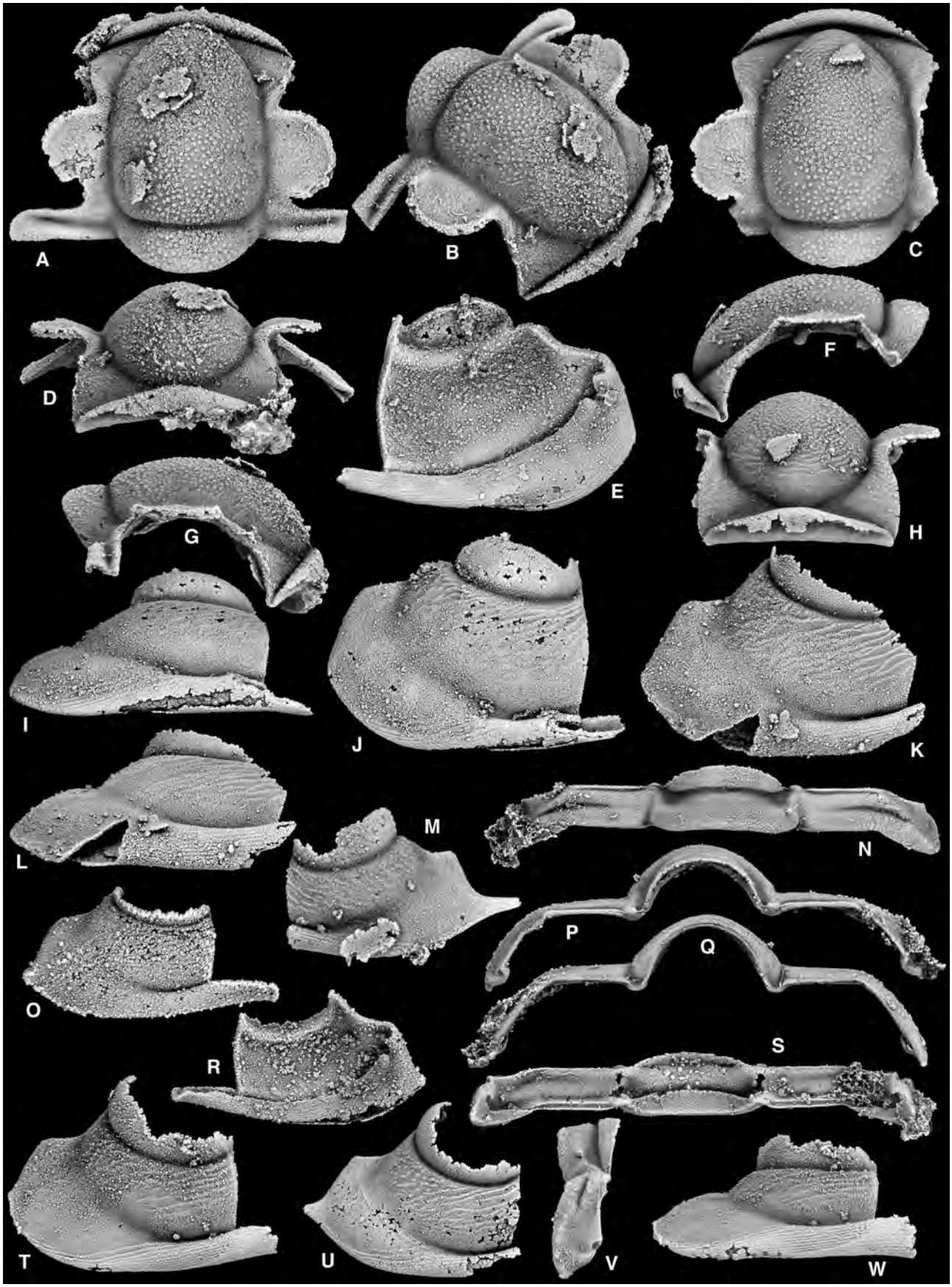
Hypostome and rostral plate not identified.

Thoracic segment description based on single recovered sclerite (Fig. 12N, P, Q, S, V); axial ring slightly wider posteriorly, sagittally long, posterior margin generally transverse with distal tips angled anterolaterally, anterior margin with medial portion transverse and lateral portions with prominent posterior bow, surface smooth; deep ring furrow that is short medially and significantly longer abaxially so that lateral portions form prominent subtriangular depression; articulating half ring with sagittal length about one third that of axial ring, anterior margin gently bowed with posterior margin less so; axial furrows deep posteriorly terminating in a pit-like depression at intersection with posterior margin, shallower anteriorly and completely effaced at intersection with anterior margin; short, rounded, anteriorly directed process developed at intersection of axial furrow with anterior margin of anterior pleural band, articulates with pit-like depression in posterior end of next segment anteriorly; fulcrum is set so that portion of pleura adaxial and abaxial to fulcrum appear nearly equal in dorsal view, with the portion of the pleura distal to the fulcrum turned down from about 55° horizontal; pleural furrow very short (exsag.), deep, and slit-like adjacent to either side of fulcrum, otherwise effaced, not reaching axial furrow or distal tip of pleura; anterior and posterior pleural

Figure 12 (*overleaf*). ***Bathyurina curtisi*** sp. nov., from Section H 222.1 m and H 226T m, Fillmore Formation (Floian; *Carolinites nevadensis* Zone), southern Confusion Range, Ibex area, Millard County, western Utah. **A**, **B**, **D**, **G**, cranidium, SUI 124892, dorsal, oblique, anterior, and right lateral views, x12 (H 226T m). **C**, **F**, **H**, cranidium, SUI 124893, dorsal, left lateral, and anterior views, x12 (H 226T m). **E**, **I**, **J**, right librigena, SUI 124894, internal, ventrolateral, and external views, x7.5 (H 222.1 m). **K**, **L**, right librigena, SUI 124895, external and ventrolateral views, x12 (H 222.1 m). **M**, left librigena, SUI 124896, external view, x15 (H 226T m). **N**, **P**, **Q**, **S**, **V**, thoracic segment, SUI 124897, dorsal, anterior, posterior, ventral, and right lateral views, x12 (H 222.1 m). **O**, **R**, right librigena, SUI 124898, external and internal views, x10 (H 222.1 m). **T**, **W**, right librigena, SUI 124899, external and ventrolateral views, x12 (H 226T m). **U**, right librigena, SUI 124900, external view, x12 (H 222.1 m).

Figure 13 (*Page 327*). ***Bathyurina curtisi*** sp. nov., from Section H 222.1 m and H 226T m, Fillmore Formation (Floian; *Carolinites nevadensis* Zone), southern Confusion Range, Ibex area, Millard County, western Utah. **A**, **B**, **D**, **J**, pygidium, SUI 124901, dorsal, left lateral, posterior, and ventral views, x7.5 (H 222.1 m). **C**, **G**, **I**, pygidium, SUI 124902, dorsal, right lateral, and posterior views, x7.5 (H 222.1 m). **E**, **F**, **H**, pygidium, SUI 124903, dorsal, right lateral, and posterior views, x7.5 (H 222.1 m). **K**, **L**, **P**, pygidium, SUI 124904, posterior, dorsal, and left lateral views, x12 (H 226T m). **M**, **N**, **Q**, **U**, **Y**, pygidium, SUI 124905, dorsal, ventral, left lateral, posterior, and anterior views, x15 (H 222.1 m). **O**, **S**, **T**, pygidium, SUI 124906, dorsal, posterior, and left lateral views, x12 (H 226T m). **R**, **W**, **X**, pygidium, SUI 124907, right lateral, posterior, and dorsal views, x12 (H 226T m). **V**, **Z**, **BB**, pygidium, SUI 124908, left lateral, dorsal, and posterior views, x15 (H 222.1 m). **AA**, **DD**, **EE**, pygidium, SUI 124909, left lateral, dorsal, and posterior views, x12 (H 222.1 m). **CC**, **FF**, **GG**, pygidium, SUI 124910, right lateral, posterior, and dorsal views, x15 (H 222.1 m).

(*continued from opposite*) **I**, **L**, **M**, cranidium, SUI 124887, dorsal, anterior, and left lateral views, x10. **J**, **K**, **O**, cranidium, SUI 124888, left lateral, dorsal, and anterior views, x12. **N**, **S**, **T**, cranidium, SUI 124889, right lateral, anterior, and dorsal views, x15. **P**–**R**, **U**, cranidium, SUI 124890, dorsal, left lateral, ventral, and anterior views, x12. **V**–**X**, cranidium, SUI 124891, anterior, dorsal, and right lateral views, x15.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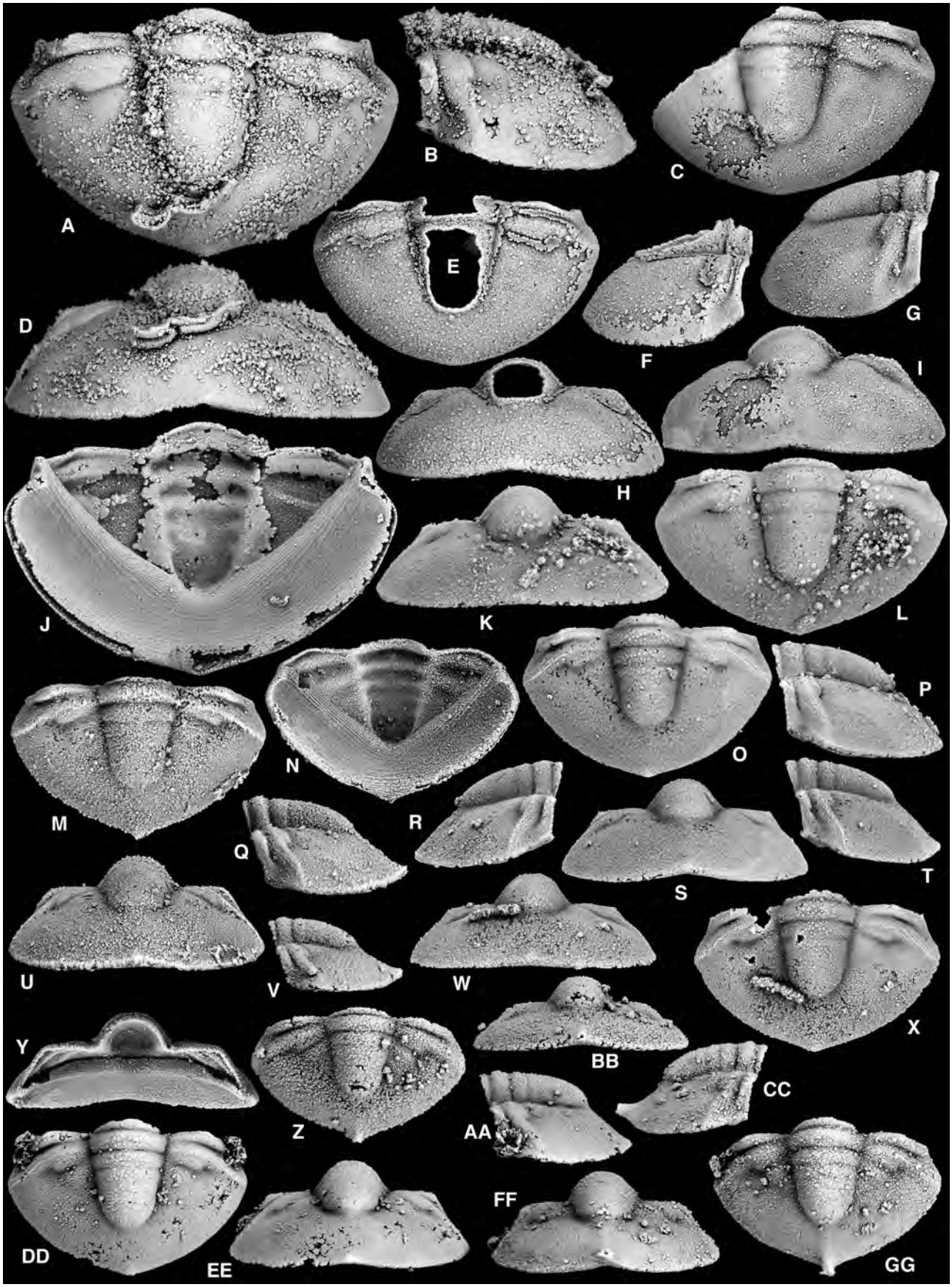
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bands with slight independent inflation, merged into single strip opposite axial furrow, clearly differentiated into anterior and posterior bands adjacent to fulcrum, merged to single strip distally; deep, narrow, transverse furrow set adjacent to anterior margin of anterior band from articulating process at anterior margin of axial furrow to fulcrum; furrow sets off anterior edge margin of pleural band forming a narrow ridge-like rim, which articulates with a narrow ventral transverse groove (Fig. 12S) beneath the posterior edge of the pleurae of the next segment anteriorly; short anterolaterally directed spike present about equidistant between fulcrum and pleural tip along anterior margin of band, spike articulates with small notch on the posterior margin of the next segment anteriorly (Fig. 12P); ventrally, doublure forms a lenticular articulating surface beneath the axial ring, doublure also present distally beneath tip of pleura.

Pygidial measurements were made on the largest, nearly or completely intact specimens of Figure 13. Pygidium with maximum with across third segment 157.5% (155.4-159.7) sagittal length; axis of five segments clearly defined, maximum axial width across first segment 31.0% (30.2-31.8) maximum pygidial width, width across fifth segment 69.2% (66.2-72.3) width across first segment, length of axis excluding articulating half ring 65.8% (64.9-66.7) total sagittal length of pygidium; articulating half ring small and medially short, sagittal length 6.3% (4.2-8.5) total pygidial length, anterior margin gently anteriorly convex, ring sloped slightly backward and down from general sagittal profile of axis, gently dorsally convex in sagittal profile and inflated so that appears independent from axis, apparently smooth and lacking any obvious sculpture, but surface not well preserved on any recovered specimens; first ring furrow deep, narrow, and gently anteriorly bowed; second ring furrow as deep as first abaxially, slightly shallower medially on most specimens, bowed similarly to first ring furrow; third ring furrow much fainter than second but still clearly expressed; fourth ring furrow much less well expressed, completely effaced medially, best observed in sagittal profile as shallow depression along axis or in ventral view (Fig. 13J); fifth ring furrow very faintly expressed dorsally, but clearly visible ventrally; pseudo-articulating half ring of second segment partially outlined by faint, smooth, furrow situated medially on first axial segment; pseudo-articulating half rings of subsequent segments not clearly differentiated; first axial ring of similar length sagittally and exsagittaly, slightly longer sagittally (including merged second pseudo-articulating half ring) than second ring; posterior rings progressively smaller and more poorly expressed, but with similar morphology; sculpture of medium sized, densely spaced tubercles present medially along at least first three axial segments of larger specimens (Fig. 13C), tubercles become more effaced posteriorly; axis terminated by long, broad terminal piece, with posterior margin rounded and distinctly differentiated from relatively long post axial region; first pleural segment with maximum exsagittal pleural length 20.8% (20.2-21.5) sagittal axial length, anterior margin with slight anterolateral bow to fulcrum, which is set slightly closer to axis than pygidial margin, margin directed sharply posterolaterally distal to fulcrum; prominent anterolaterally directed spike developed along anterior margin at fulcrum, which articulates with last thoracic segment, in ventral view spike is clearly triangular in outline and inner margin extends continuously from doublure; anterior pleural band well inflated, faint and narrow furrow present along anterior margin, sculpture of fine granules, sometimes arranged into lines oriented subparallel to anterior margin on portion distal to fulcrum, band is slightly longer (exsag.) abaxially to fulcrum, shortens slightly from fulcrum distally; posterior pleural band longer (exsag.) than anterior band, longest at fulcrum, sculpture of fine granules, granules form series of raised lines oriented subparallel to band from fulcrum distally, lines continue just adaxial to fulcrum on some specimens, with posterior margin developed into short posteriorly direct process just before fulcrum; pleural furrow short (exsag.) and deep, terminated past fulcrum, but before pygidial margin, in contact with axial furrow on larger specimens; interpleural furrow short, deep, clearly outlining posteriorly directed process of posterior plueral band, becoming very shallow and nearly effaced just before fulcrum distally, in contact with axial furrow; subsequent pleural bands, pleural and interpleural furrows not expressed, leaving pleural region smooth, strongly downturned from horizontal plane; border furrow and border not well expressed or distinctly differentiated from pleural field, form smooth area with pleural field, strongly downturned distally from fulcrum; posterior pygidial margin forming smooth laterally convex arc, developed into short point posteromedially on larger specimens, in transverse profile margin slightly bowed upward medially, in sagittal profile forming smooth, gently convex arc; very broad doublure visible ventrally, extending adaxially to point opposite posteriorly directed process of first posterior pleural band and slightly deflected around posterior margin of terminal piece, sculpture of prominent fine raised lines running parallel to margin, lines more closely spaced along inner and outer margins becoming more widely spaced on medial portion of doublure; in anterior view inner margin of doublure rolled upward forming near vertical short wall (Fig. 13Y), sculpture of fine, closely spaced lines continues from ventral aspect of doublure.

Ontogeny. Smaller cranidia possess slightly more space between the anterior margin of the glabella and the anterior border so that the preglabellar field is nearly visible in plan view. Smallest recovered librigena (Fig. 12M) possess prominent genal spine, which becomes progressively reduced into a rounded corner on larger specimens; lateral and posterior borders meet at acute angle on smaller specimens, angle becomes wider and eventually obtuse on larger specimens; overall genal field and border (especially posterior border) become broader; anterior projection long on smaller specimen. Pygidial changes include reduction of prominent posteromedian spine and associated postaxial ridge (Fig. 13GG) into medially pointed posterior margin with pygidium smooth behind terminal piece, and associated change of posterior pygidial margin in sagittal profile from being slightly upturned to describing smooth convex curve; sculpture of fine tubercles covering axis become slightly larger and more concentrated on medial portion of axis.

Remarks. Bathyurina curtisi, *B. sumneri* sp. nov. and *B. hooki* sp. nov., are quite similar to one another, with the latter two in particular differentiated in only a few pervasive characters. The species share a cephalic sculpture of fairly densely crowded small tubercles on posterior regions, and strong raised lines traversing the anterior part of the glabella, frontal areas, and the anterior region of the librigenal field. All have the genal spine greatly reduced, but it is retained as a distinct point in even the largest species of *B. curtisi*, while completely effaced in large specimens of the other two species. The librigenal field of *B. curtisi* also has the

raised line sculpture expressed posteriorly, whereas the other two have strong tubercles in this region. Small pygidia of *B. curtisi* closely resemble similar sized specimens of *B. sumneri* (cf. Figs 13DD, 17O), but in the latter species the same basic morphology is retained with size whereas in *B. curtisi* larger specimens are increasingly dorsally vaulted and posteriorly effaced.

Bathyurina sumneri sp. nov. (Figs 14–17, 18I, L, M, P, Q, S)

2009 *Strigigenalis* sp. nov. 2; Adrain *et al*., p. 573, fig. 19T, V.

Material. Holotype, cranidium, SUI 124912 (Fig. 14B, C, G, I, J), from Section H 256.0–261.0T m, and assigned specimens SUI 115379, 115380, 124913–124938, 124940–124944, 128983, 128984, from Section H 256.0–267.0T m, Fillmore Formation (Floian; *Presbynileus ibexensis* Zone), southern Confusion Range, Ibex area, Millard County, western Utah.

Etymology. After Bernard Sumner.

Diagnosis. Raised line sculpture strongly expressed on anterior part of glabella and distributed posteriorly nearly to level of palpebral lobes; raised line sculpture extended posteriorly on librigenal field; sculpture prominent on flattened region around genal spine; genal spine completely lost relatively early in ontogeny, mid-sized specimens lacking spine; pygidium relatively wide versus median length.

Description. Cranidial measurements were made on the largest and most intact specimens of Figure 14. For measurements made on only one specimen the figure number is indicated. Cranidium with maximum cranidial width across posterior projections 152.6% sagittal length (Fig. 14A); width across midlength of palpebral lobes 117.1% (114.5-118.6) sagittal length; anterior border flexed strongly upward and posteriorly against border furrow and anterior tip of glabella so that is appears almost folded in half against itself (Fig. 14I), a short dorsal face is visible in plan view and a steeply inclined anteroventral face is visible in anterior and lateral views; dorsal face of anterior border short (sag., exsag.), even shorter medially on largest specimens, with middle portion of posterior margin deflected anteriorly around anterior glabellar margin, distal tips pinching out abaxially, anterior margin forming gently evenly bowed arc, sculpture of very densely spaced fine raised lines, lines closer to posterior margin are deflected around anterior margin of glabella; in anterior view, border obscures anteriormost tip of glabella (Fig. 14R), with dorsal margin of anteroventral face describing gentle dorsal arc, ventral margin subdivided into three independently dorsally arched segments, a narrow (tr.) median portion and two wider flanking segments that cut slightly obliquely across border, about six fine raised lines cover anteroventral face and display same dorsal arc as border in anterior view; anterior border furrow is deep, shorter medially and distally, dorsally concave, anterior and posterior margins distinct, strongly deflected around anterior glabellar margin, furrow recurved slightly under cranidium in lateral view (Fig. 14F); distinct inflated ridge bounding posterior margin of anterior border furrow visible where anterior border has been broken (Fig. 14E), distal corners also just visible in anterior view where border is intact (Fig. 14G), upper portion of ridge faces anteriorly and lower portion faces more anteroventrally and is slightly recurved under cranidium, with sculpture of fine raised lines running subparallel to anterior margin of cranidium; preglabellar field nearly vertical and largely obscured by anterior border; preglabellar furrow deep, laterally confluent with axial furrows, obscured in dorsal view by overhanging anterior margin of glabella, obscured in anterior view by upturned anterior border; frontal areas sloped strongly downward from anterior margin of palpebral lobe, with anterior portion more strongly downturned and nearly curved under cranidium, anterolateral corners turned slightly outward, sculpture of prominent raised lines running obliquely from axial furrow anterolaterally, lines become slightly more widely spaced anteriorly, with anterior portion smooth and lacking lines; width across β 86.4% (80.1-92.1) cranidial sagittal length, 73.8% (70.0-77.6) width across midlength of palpebral lobe; anterior sections of facial sutures moderately anteriorly divergent, nearly straight from γ to β, forming a small notch where suture cuts across anterior border furrow, laterally convex opposite anterior border; distance across γ 76.8% (70.4-80.8) cranidial sagittal length, distance across ε 84.9% (78.5-88.7) cranidial sagittal length; palpebral lobes moderately large, length (exsag.) 32.9% (29.4-35.5) cranidial sagittal length, margin strongly laterally bowed, slight dorsal inflation on main middle portion, lobe held below, but close to dorsal apex of glabella, abaxial portion held nearly horizontal, adaxial portion sloping more strongly toward palpebral furrow in anterior view, sculpture of prominent small densely spaced tubercles covers main middle portion of lobe; distinct, broad, inflated border bounds margin of lobe, sculpture of fine raised lines continues from frontal area onto rim (Fig. 14C), sculpture present on entire rim; border extended into very short eye ridge cutting obliquely across frontal area (Fig. 14A); very broad, shallow, furrow running inside inflated rim separating border from main middle portion of lobe, furrow slightly narrower anteriorly and posteriorly, largely smooth, but sculpture of prominent small tubercles continues onto adaxial portion from main lobe; interocular fixigena narrow, sloping strongly toward axial furrow, with sculpture identical to that of palpebral lobe; posterior section of facial suture overall extended out far laterally, with adaxial portion directed just slightly anterolaterally, and distal tip directed more strongly posterolaterally; posterior fixigena with inflation similar to frontal area, forming very short (exsag.) laterally extended strip, much shorter abaxially, very small scattered tubercles continue from palpebral lobe and interocular fixigena onto posterior fixigena; posterior border furrow short (exsag.), very shallow from contact with axial furrow just past fulcrum, forming deep slit abaxially past fulcrum, but shallower distally toward contact facial suture, directed slightly anterolaterally; posterior border moderately dorsally inflated, short (exsag.) proximally, lengthened distally, subtriangular in outline with distal tip strongly downturned, sculpture of small scattered tubercles similar to that present on posterior fixigena, posterior margin of border with slight concave bow, overall directed slightly posterolaterally; short articulating groove present ventrally along posterior margin of posterior border (Fig. 14B); posterior projection extends far laterally past lateral extent of palpebral lobe; glabella with maximum width 83.5.0% (82.7-84.8) sagittal length (excluding LO), sagittal length (excluding LO) 74.3% (71.5-76.8) that of cranidium, widest across point opposite anterior margin of palpebral furrow, slightly waisted opposite S2, moderately dorsally inflated, with apex sitting slightly above fixigena in anterior and lateral views, sagittal profile

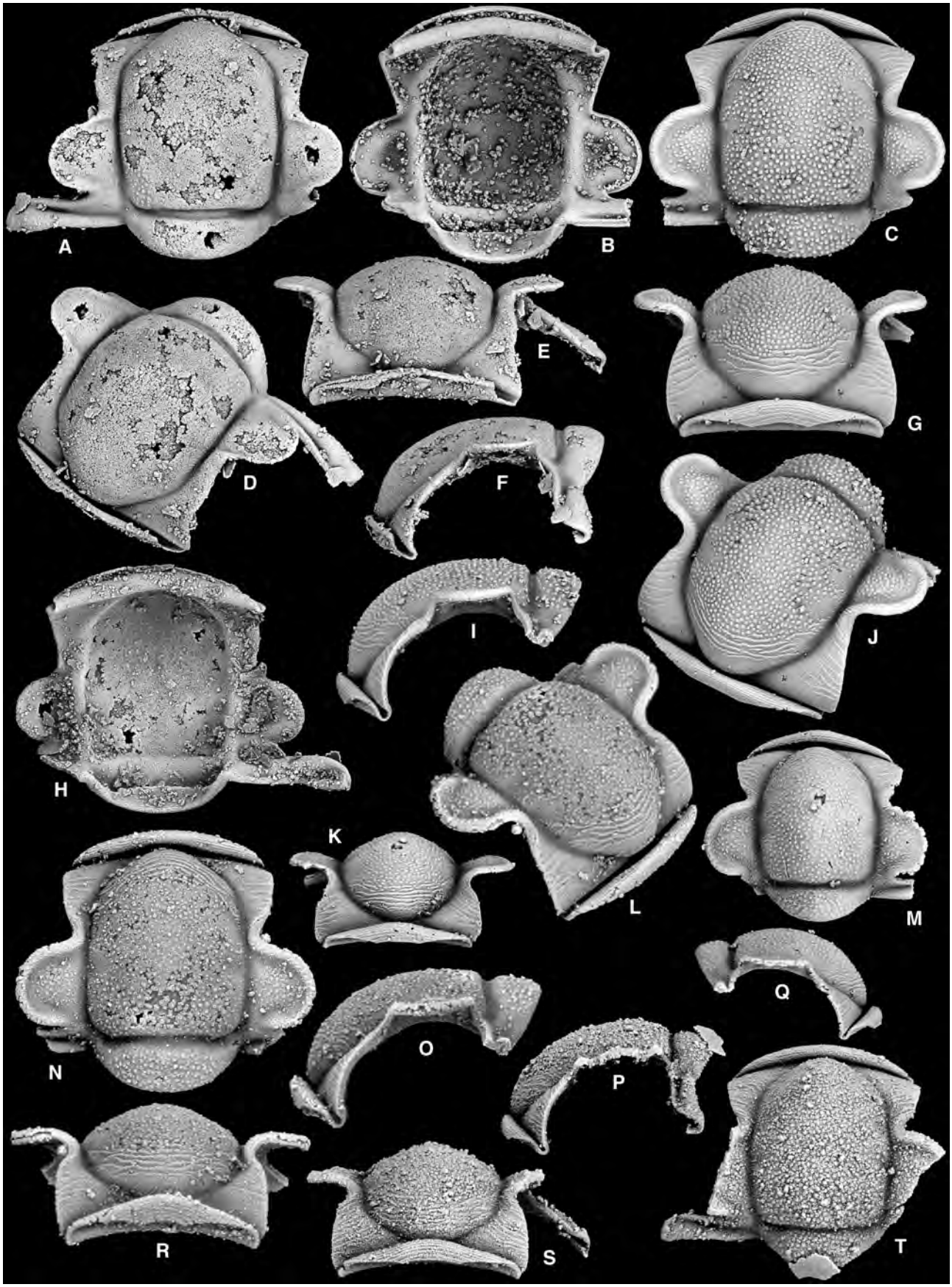


Figure 14. ***Bathyurina sumneri*** sp. nov., from Section H 256.0–267.0T m, Fillmore Formation (Floian; *Presbynileus ibexensis* Zone), southern Confusion Range, Ibex area, Millard County, western Utah. **A**, **D**–**F**, **H**, cranidium, SUI 115379, dorsal, oblique, anterior, left lateral, and ventral views, x6 (H 256.0–261.0T m). **B**, **C**, **G**, **I**, **J**, cranidium, holotype, SUI 124912, (*continued opposite*)

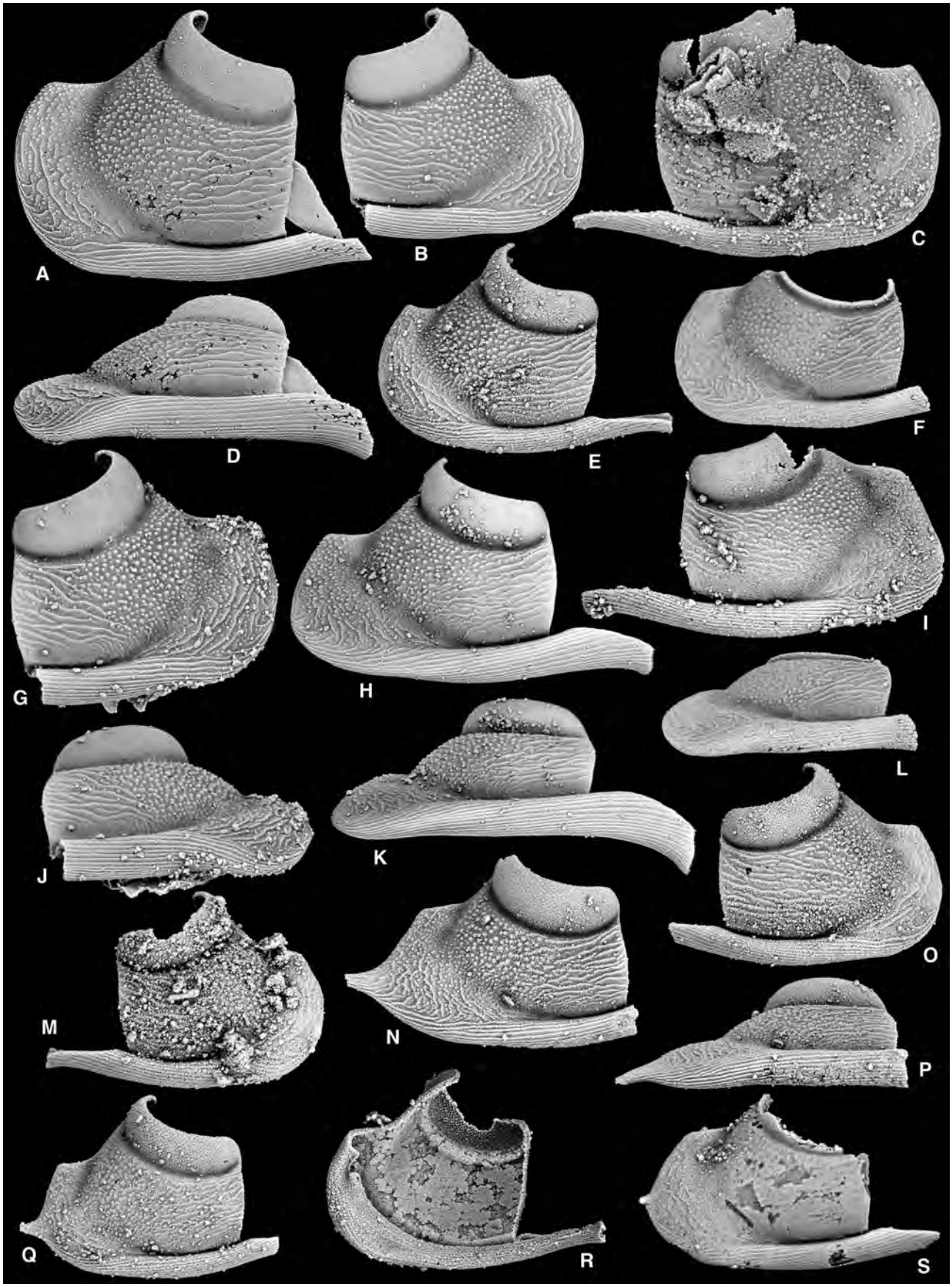
moderately curved, with anterior tip of glabella more strongly downturned; glabellar sculpture consisting of moderately sized, densely spaced tubercles, except for S1-S2 (smooth), and anterior portion of glabella, which is covered with a series of fine raised anastomosing lines visible in plan view just along the anterior glabellar margin, in anterior view lines can be seen running across anterior fixigena and across anterior portion of glabella, anteriormost tip of glabella is nearly smooth, with a few extremely fine anastomosing lines running up from contact with preglabellar furrow and just barely visible in anterior view (Fig. 14C); S1-S2 expressed (Fig. 14C) as obliquely directed smooth areas lacking any other obvious sculpture, S1-S2 very slightly impressed at intersection with axial furrow, obscured in lateral view by palpebral lobe and fixigena; L1 and L2 primarily defined by S1-S2, with very slight independent inflation and slight disruption at axial furrow; axial furrows moderately deep, deeper opposite base of S1 and S2, slightly laterally bowed around L2-L2, narrower at contact with preglabellar furrow and running without obvious break into preglabellar furrow, width across posterior contact of furrows with posterior margin 58.0% (56.5-59.3) cranidial sagittal length, axial furrows laterally confluent with posterior border furrow, but much shallower at intersection; SO deep, long (sag., exsag), anterior and posterior edges with sharp contact with rear glabellar margin and LO respectively, almost exactly transverse, with distal tips significantly shorter, deeper, and strongly curved anteriorly to join axial furrow in smooth continuous curve; LO long, sagittal length 16.7% (15.3-18.1) that of cranidium, longer sagittally than exsagittally, posterior margin with strong posterior bow, anterior margin nearly transverse, with sculpture of scattered moderately sized tubercles as on glabella, covering most of LO except for distal tips which are smooth, median node not prominent; doublure underlying LO nearly semicircular, not reaching expression of SO ventrally, with sculpture of very faint fine, closely spaced raised lines.

Librigenal measurements were made on the largest and most complete specimens of Figure 15. Main body of librigena (excluding anterior projection) with maximum width behind eye 68.4% (64.6-73.4) exsagittal length; field broad, with width opposite anterior section of facial suture with length 44.6% (42.1-48.2) exsagittal length of main body, strong dorsal convexity, sitting high above border in anteroventral view, prominent sculpture of fine raised anastomosing lines running perpendicular to anterior facial suture and covering portion of field anterior to genal angle, sculpture is a continuation of that present on frontal area of cranidium, posterior portion of field covered fine prominent densely spaced tubercles, that are finer and continue across border furrow; visual surface long, tall, set off from field by broad, deeply incised furrow; anterior section of facial suture with convex bow forming a gentle peak mid way across field, drastic change in direction at lateral border furrow; posterior section of facial suture almost transversely straight across field and posterior border, but with strong inward bow at border furrow; lateral border furrow deep and narrow anteriorly where lateral border is pushed upwards against field, posterior portion of furrow much shallower and broader merging smoothly around genal angle into posterior border furrow; anterior portion of lateral border is flexed upward against genal field, forming a prominent, strongly inflated face bounding the anterior portion of the genal field, continuing without obvious disruption into anterior projection, sculpture of fine raised lines running subparallel to lateral margin clearly differentiates this portion of border, sculpture starts at genal angle and covers entire aspect of lateral border and anterior projection; smaller dorsoventrally flattened portion of lateral border present adjacent to genal angle, confluent with posterior border; anterior projection with length 41.5% (36.0-45.6) librigenal length (excluding anterior projection), extending far beyond genal field, with anterior portion curved downward from horizontal plane anteriorly (Fig. 15K); posterior border broad and strongly dorsoventrally flattened in contrast to lateral border, widest at genal angle, narrowing slightly toward posterior facial suture, sculpture of small scattered tubercles continues from field, across border furrow and onto posterior border, tubercles are much smaller than those on field, additional sculpture of fine, raised, anastomosing lines also present on portion of posterior borders adjacent to genal angle, and sometimes continuing onto posterior border in addition to

Figure 15 (overleaf). ***Bathyurina sumneri*** sp. nov., from Section H 256.0–267.0T m, Fillmore Formation (Floian; *Presbynileus ibexensis* Zone), southern Confusion Range, Ibex area, Millard County, western Utah. **A**, **D**, right librigena, SUI 124916, external and ventrolateral views, x7.5 (H 264.0–267.0T m). **B**, left librigena, SUI 124917, external view, x10 (H 264.0–267.0T m). **C**, left librigena, SUI 124918, external view, x10 (H 264.0–267.0T m). **E**, right librigena, SUI 124919, external view, x12 (H 256.0–261.0T m). **F**, **L**, right librigena, SUI 124920, external and ventrolateral views, x10 (H 256.0–261.0T m). **G**, **J**, left librigena, SUI 124921, external and ventrolateral views, x10 (H 256.0–261.0T m). **H**, **K**, right librigena, SUI 124922, external and ventrolateral views, x10 (H 256.0–261.0T m). **I**, left librigena, SUI 124923, external view, x10 (H 256.0–261.0T m). **M**, **R**, left librigena, SUI 124924, external and internal views, x12 (H 256.0–261.0T m). **N**, **P**, right librigena, SUI 124925, external and ventrolateral views, x15 (H 256.0–261.0T m). **O**, left librigena, SUI 124926, external view, x12 (H 256.0–261.0T m). **Q**, right librigena, SUI 124927, external view, x15 (H 256.0–261.0T m). **S**, right librigena, SUI 124928, external view, x12 (H 256.0–261.0T m).

Figure 16 (*Page 333*). ***Bathyurina sumneri*** sp. nov., from Section H 256.0–267.0T m, Fillmore Formation (Floian; *Presbynileus ibexensis* Zone), southern Confusion Range, Ibex area, Millard County, western Utah. **A**, **B**, **E**, cranidium, SUI 124929, dorsal, anterior, and right lateral views, x20 (H 264.0–267.0T m). **C**, **D**, **G**, cranidium, SUI 124930, anterior, dorsal, and left lateral views, x20 (H 256.0–261.0T m). **F**, left librigena, SUI 124931, external view, x20 (H 256.0–261.0T m). **H**, left librigena, SUI 124932, external view, x15 (H 256.0–261.0T m). **I**, **J**, left librigena, SUI 124933, internal and external views, x15 (H 256.0–261.0T m). **K**, **M**, **O**, **S**, **V**, thoracic segment, SUI 124934, dorsal, anterior, posterior, left lateral, and ventral views, x10 (H 264.0–267.0T m). **L**, **N**, **P**, **R**, **U**, thoracic segment, SUI 124935, dorsal, anterior, posterior, right lateral, and ventral views, x12 (H 256.0–261.0T m). **Q**, **W**, **Y**, **AA**, **CC**, thoracic segment, SUI 124936, right lateral, dorsal, anterior, posterior, and ventral views, x12 (H 264.0–267.0T m). **T**, **X**, **Z**, **BB**, **DD**, thoracic segment, SUI 124937, left lateral, dorsal, anterior, posterior, and ventral views, x15 (H 264.0–267.0T m).

(*continued from opposite*) ventral, dorsal, anterior, left lateral, and oblique views, x10 (H 256.0–261.0T m). **K**, **M**, **Q**, cranidium, SUI 124913, anterior, dorsal, and right lateral views, x15 (H 256.0–261.0T m). **L**, **N**, **O**, **R**, cranidium, SUI 124914, oblique, dorsal, left lateral, and anterior views, x12 (H 264.0–267.0T m). **P**, **S**, **T**, cranidium, SUI 124915, left lateral, anterior, and dorsal views, x12 (H 256.0–261.0T m).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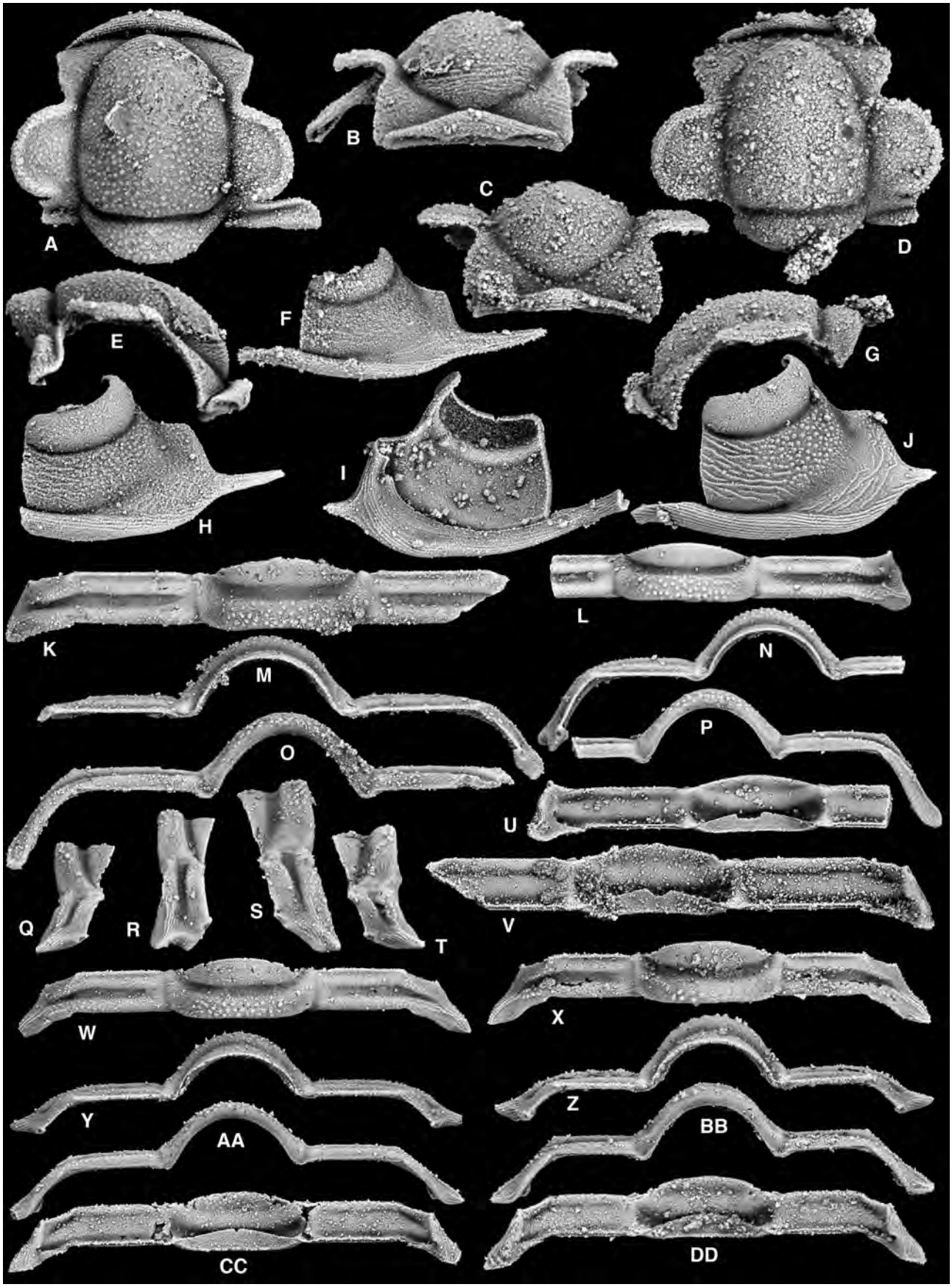
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small tubercles; posterior border furrow and rear portion of lateral border furrow are broad and shallow, sculpture of fine tubercles present on posterior border furrow (Fig. 15A); genal angle broadly rounded forming an obtuse angle, strongly deflected downward from horizontal plane (Fig. 15D, J), sculpture of a few raised lines present on external margin of posterior border continues around genal angle and smoothly onto lateral border; doublure widest beneath genal angle and posterior border, narrows significantly below lateral border and anterior projection, inner margin of doublure describes smooth continuous arc between posterior border and lateral border, course disrupted by large Panderian notch (Fig. 15R) developed adjacent to posterior facial suture; entire doublure with sculpture of very fine, closely spaced raised lines running subparallel to inner and outer margins, with lines slightly more widely spaced on medial portion of doublure beneath genal angle.

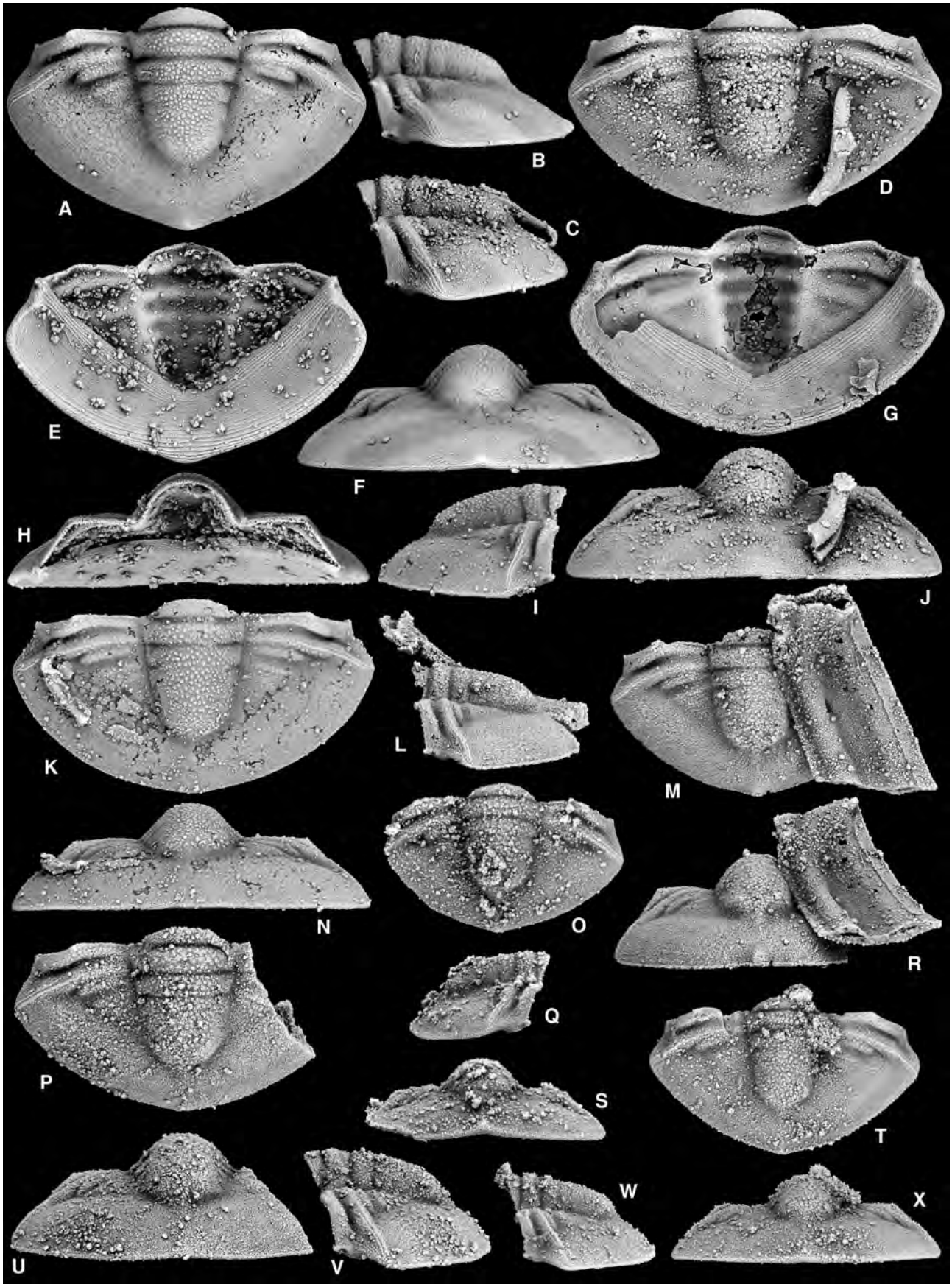
Hypostome suboval shaped; anterior wings not completely preserved on recovered specimens, but anterior wing process prominent in lateral view (Fig. 18L); middle body strongly inflated, longer (sag.) than wide, with anterior lobe much longer (sag.; exsag.) than posterior lobe, sculpture of prominent raised lines present on anterior margin of anterior lobe, main portion of anterior lobe covered by closely spaced net-like mesh of very fine raised lines and granules, granules are present on anterior portion of anterior lobe and merge into short segments of anastomosing raised lines posteriorly, this sculpture continues onto posterior lobe, but becomes more widely spaced; middle furrows moderately deep, slightly sinuous, directed posteromedially, but do not meet so that anterior and posterior lobes of middle body are confluent medially, anterior tips shallow, but intersect lateral border furrow at shoulder; posterior lobe of middle body V-shaped, with anterior tips continuing far anteriorly to shoulder, posterior margin composed of three distinct sections: an anterior section that nearly parallel to sagittal axis or slightly directed posteromedially, a middle portion that is more strongly directed posteromedially, and a more broadly rounded section bounding the posterior tip of the lobe; lateral and posterior border furrows broad, moderately deep; lateral border furrow narrows and slightly deepens anteriorly opposite shoulder; lateral and posterior borders forming narrow, strongly inflated rim bounding middle body, sculpture of fine raised lines covering ventral aspects of border; lateral border composed of two sections, anterior section from shoulder to point about opposite posterior tip of middle furrow is directed just slightly posterolaterally, second section starting from this point and continuing to intersection with posterior border is directed more strongly posteromedially; posterior border directed even more strongly posteromedially from intersection with lateral border, forming a rounded point posteriorly, sitting above posterior lobe in posterior view; posterior wing small, but prominent in lateral view (Fig. 18L).

Rostral plate not identified.

Morphology of entire thorax unknown, but recovered segments possess the following morphology. Thoracic segment with axial ring slightly wider anteriorly, covered by small scattered tubercles; lateral margins of axial ring developed into subtle inflated ridge opposite axial furrows, ridge terminating with an extremely small, rounded, anteriorly directed process developed at intersection with anterior margin of segment, articulates with depression in posterior end of next segment anteriorly; ring furrow deep, long (sag., exsag.), main portion with gentle posterior bow, distal tips slightly shorter and directed anterolaterally; articulating half ring large, sagittal length slightly shorter than that of axial ring, lenticular in outline; axial furrows deepest posteriorly, significantly shallower anteriorly and almost completely effaced at intersection with anterior margin; pleural furrow very long (exsag.) and deep along majority of course, but terminated abruptly before reaching axial furrow, deeper, shorter and slit-like from fulcrum abaxially, then pinching out before reaching distal pleural tip; anterior and posterior pleural bands with moderate independent inflation, merged into single strip adjacent to axial furrow, clearly differentiated into anterior and posterior bands for majority of course, merged into single strip distally, terminating in distinct posterolaterally directed point; sculpture of small tubercles present along posterior band from just past axial furrow to just before distal pleural tip, tubercles also present on anterior band on portion just abaxial of fulcrum, portion of anterior pleural band from fulcrum adaxially is smooth, distal tip of pleurae covered with prominent anastomosing lines running toward pleural tip; shallow, narrow, transverse furrow running along anterior margin of anterior band from articulating process at anterior margin of axial furrow to fulcrum, furrow sets off narrow ridge-like rim along anterior edge of the pleural band, which articulates with a narrow and deep ventral transverse groove beneath the posterior edge of the pleurae of the next segment anteriorly; short anteriorly directed spike developed distally along anterior margin, situated about equidistant between fulcrum and pleural tip, spike articulates with small notch on the posterior margin of the next segment anteriorly; ventrally, the doublure forms a crescent-shaped articulating surface beneath the axial ring; doublure also present distally beneath tip of pleura, inner margin developed into strong V-shaped notch, with sculpture of fine anastomosing lines; fulcrum is set so that portion of pleura adaxial to fulcrum is slightly longer, with the portion of the pleura distal to the fulcrum strongly downturned from horizontal plane.

Pygidial measurements were made on the largest, nearly or completely intact specimens of Figure 17. Pygidium with maximum width across anterior margin of fourth segment 175.3% (160.8-184.2) sagittal length; axis of five segments, maximum axial width across first segment 28.5% (25.2-31.5) maximum pygidial width, length of axis (excluding articulating half ring) 61.2% (58.3-62.6) total sagittal length of pygidium, width across fifth segment 68.2% (66.5-68.2) width across first segment, strongly inflated sitting above pleural field; articulating half ring moderately small, sagittal length 8.6% (7.6-9.4) total pygidial length, semicircular with anterior margin strongly anteriorly convex and posterior margin almost exactly transverse to slightly bowed, half ring sitting just below first axial ring and sloped slightly backward and down from general sagittal profile of axis, surface smooth; first axial ring (including merged

Figure 17. ***Bathyurina sumneri*** sp. nov., from Section H 256.0–267.0T m, Fillmore Formation (Floian; *Presbynileus ibexensis* Zone), southern Confusion Range, Ibex area, Millard County, western Utah. **A**, **B**, **E**, **F**, **H**, pygidium, SUI 124938, dorsal, left lateral, ventral, posterior, and anterior views, x12 (H 256.0–261.0T m). **C**, **D**, **G**, **J**, pygidium, SUI 115380, left lateral, dorsal, ventral, and posterior views, x12 (H 256.0–261.0T m). **I**, **K**, **N**, pygidium, SUI 124940, right lateral, dorsal, and posterior views, x10 (H 264.0–267.0T m). **L**, **M**, **R**, pygidium, SUI 124941, left lateral, dorsal, and posterior views, x15 (H 256.0–261.0T m). (*continued opposite*)



O, **Q**, **S**, pygidium, SUI 124942, dorsal, right lateral, and posterior views, x15 (H 264.0–267.0T m). **P**, **U**, **V**, pygidium, SUI 124943, dorsal, posterior, and left lateral views, x15 (H 256.0–261.0T m). **T**, **W**, **X**, pygidium, SUI 124944, dorsal, left lateral, and posterior views, x12 (H 264.0–267.0T m).

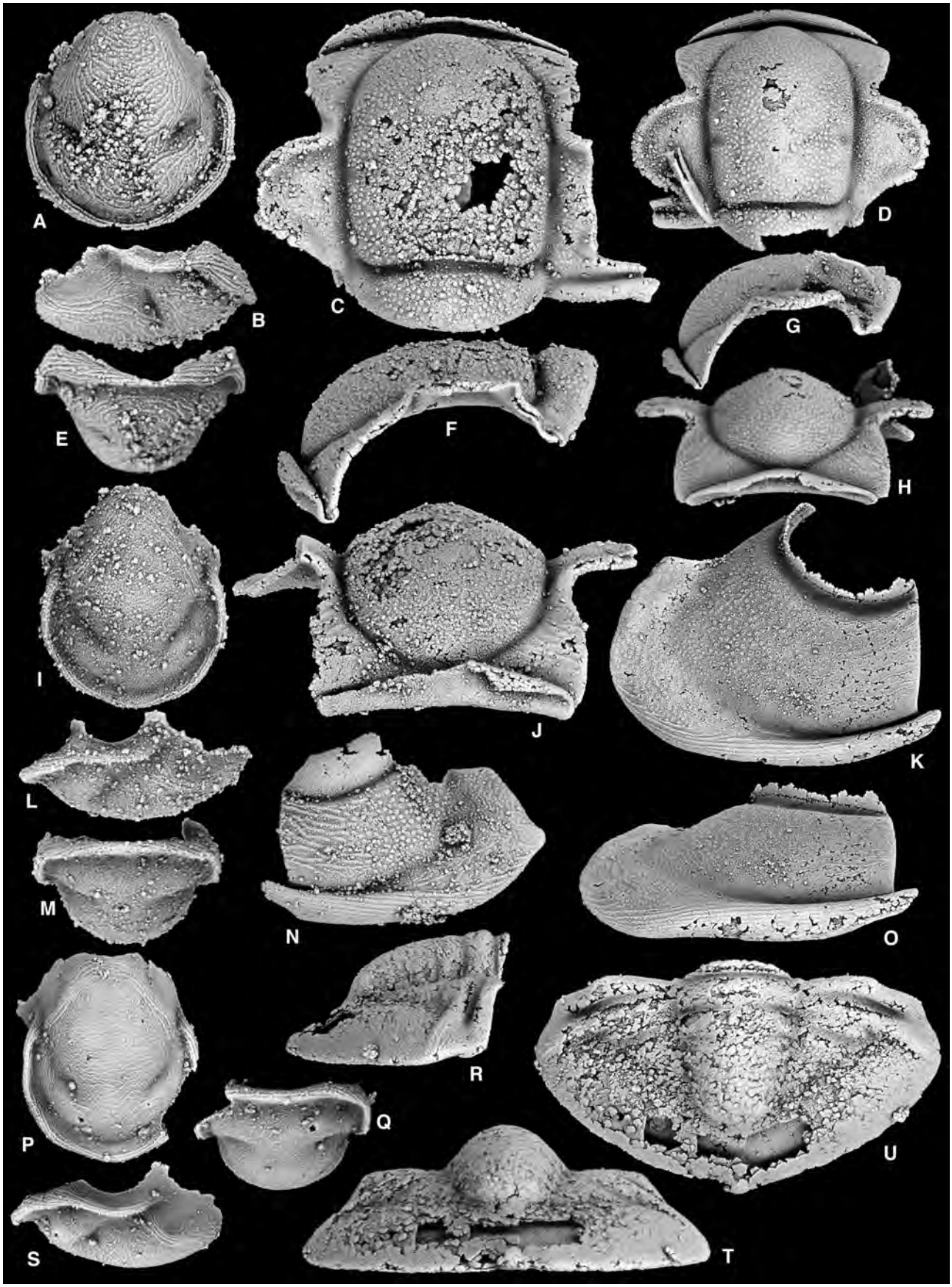
pseudo-articulating half ring of second axial ring) slightly longer sagittally than exsagittally, longer than second ring; subsequent axial rings progressively smaller and more poorly defined; axis terminated by moderately long, broad terminal piece, with posterior margin rounded and distinct from postaxial region; first ring furrow deep along entire course, narrow, and very slightly anteriorly bowed; second ring furrow shallower than first medially, distal tips slightly deeper and longer (exsag.) than medial portion; third ring furrow much shallower and narrower than second but still clearly expressed with distal tips deeper and pit-like at contact with axial furrows; fourth ring furrow much less well expressed, almost completely effaced medially, but incised adjacent to axial furrow on some specimens (Fig. 17A); fifth ring furrow very faint, expressed dorsally by slight depression at contact with axial furrow; pseudo-articulating half ring of second segment almost completely merged with first axial ring, very faintly outlined by furrow situated just posterior to mid-point of first axial segment; pseudo-articulating half rings of subsequent segments not clearly differentiated; sculpture of medium sized, densely spaced tubercles present on entire axis, except for narrow strip along abaxial margins of first four axial segments, which are smooth, sculpture of tubercles present on lateral posterior margin of terminal piece; post axial field with length (sag.) 26.2% (25.2-28.1) pygidial length; very faint post axial ridge present on some specimens (e.g., Fig. 17A); pleural region broad, with portion between axis and fulcrum held nearly parallel to horizontal plane, portion distal to fulcrum more strongly downturned from horizontal; first pleural segment with maximum exsagittal length 21.8% (20.9-22.4) sagittal length of pygidium, anterior margin straight and directed slightly anterolaterally to fulcrum, which is set relatively close to axis, portion of margin distal to fulcrum directed more sharply posterolaterally, but course disrupted by short anterolaterally directed spine developed about mid way between fulcrum and margin; spike articulates with last thoracic segment, in ventral view spike is triangular in outline, inner margin of doublure extends continuously to tip of spine; facet strongly downturned from horizontal plane; anterior pleural band with strong independent inflation, sculpture of fine and very faint tubercles present on portion between axis and fulcrum; anterior margin of first pleural band set off from margin by faint, narrow furrow and associated narrow ridge; posterior pleural band with length (exsag.) similar to anterior band, sculpture of fine faint tubercles present on posterior half of portion between fulcrum and axis, anterior half of band with prominent raised lines running subparallel to margins of pleural band, raised line sculpture also present on distal tip of anterior pleural band and continues to pygidial margin; pleural furrow long (exsag.) and deep from fulcrum abaxially, but terminated before pygidial margin, furrow much shallower adaxial of fulcrum, shortens and shallows significantly towards contact with axial furrow; interpleural furrow very shallow, but forming a deep pit at fulcrum, largely effaced between fulcrum and pygidial margin; second pleural band with anterior and posterior bands expressed between fulcrum and axis, but effaced abaxially from fulcrum; subsequent pleural bands not expressed, leaving pleural region smooth without any obvious sculpture; border furrow and border not well expressed or distinctly differentiated from pleural field, forming a broad smooth area with pleural field; very narrow rim around pygidial margin with sculpture of fine raised lines that continue from distal tips of first pleural band around entire pygidial margin; posterior pygidial margin forming smooth laterally convex arc, on some specimens slightly concave just before very short posteromedially directed projection, others are more smoothly rounded posteriorly; in posterior view some specimens show margin very slightly bowed upward medially (Fig. 17F); in lateral view margin forms smooth, gentle arc from posterior margin of first pleural band to posterior margin of pygidium; in ventral view very broad doublure visible, extending adaxially to point opposite inner margin of short articulating spike developed on first pleural band and slightly deflected around posterior margin of terminal piece; doublure divided into two sectors, a broad flat portion that makes up the majority of the doublure and a shorter upturned section present along the inner margin of the doublure; the flatter section is very broad, covered with fine raised lines that are relatively widely spaced and running subparallel to pygidial margin, the middle of this sector is slightly depressed medially and the lines are slightly more widely spaced; the shorter upturned portion also possesses sculpture of fine raised lines, but they are much more closely spaced.

Ontogeny. Changes in the cranidium throughout ontogeny are as follows. The preglabellar field is just visible on one of the smallest specimens in anterior view (Fig. 16C), but it is progressively obscured by the upward encroachment of the anterior border throughout ontogeny. It is clearly hidden from view in larger specimens. The anterior border furrow is more evenly bowed and less strongly deflected around the anterior glabellar margin on smaller specimens. The anterior margin of the glabella is more rounded and becomes more medially pointed and the glabellar furrows are slightly more deeply impressed. The palpebral lobes are large, occupying over half the glabellar length (sag.), and they become smaller throughout ontogeny, but remain posteriorly positioned in larger specimens. The palpebral furrow is very narrow and not deeply impressed on smallest specimens compared to the broad furrow on the largest specimens. LO is longer (sag.) with more strongly curved posterior margin, becoming shorter (sag.) and less strongly bowed on larger specimens.

The most significant librigenal change is the loss of the genal spine. The genal angle is developed into prominent genal spine on the smallest specimens, with the spine relatively long, thin, and blade like. Throughout ontogeny the spine becomes shorter and smaller and eventually absent leaving the genal angle forming a slightly rounded nearly 90° corner. The genal angle then becomes progressively more rounded and the angle more obtuse on larger specimens. The sculpture on the genal field also becomes more prominent on larger specimens.

Smaller pygidia possess a faint post axial ridge that becomes largely effaced throughout ontogeny and a pygidial border that is more clearly differentiated from the pleural

Figure 18. A–H, **J**, **K**, **N**, **O**, **R**, **T**, **U**. ***Bathyurina hooki*** sp. nov., from Section H 274.4 m, Fillmore Formation (Floian; *Presbynileus ibexensis* Zone), southern Confusion Range, Ibex area, Millard County, western Utah. **A**, **B**, **E**, hypostome, SUI 128977, ventral, left lateral, and posterior views, x20. **B**, **F**, **J**, cranidium, SUI 128978, dorsal, left lateral, and anterior views, x12. **D**, **G**, **H**, cranidium, SUI 128979, dorsal, left lateral, and anterior views, x15. **K**, **O**, right librigena, SUI 128980, external and ventrolateral views, x10. **N**, left librigena, SUI 128981, external view, x12. **R**, **T**, **U**, pygidium, SUI 128982, right lateral, posterior, and dorsal views, x15. (*continued opposite*)



I, **L**, **M**, **P**, **Q**, **S**. ***Bathyurina sumneri*** sp. nov., from Section H 256.0–261.0T m, Fillmore Formation (Floian; *Presbynileus ibexensis* Zone), southern Confusion Range, Ibex area, Millard County, western Utah. **I**, **L**, **M**, hypostome, SUI 128983, ventral, right lateral, and posterior views, x15. **P**, **Q**, **S**, hypostome, SUI 128984, ventral, posterior, and right lateral views, x15.

Figure 19. ***Bathyurina hooki*** sp. nov., from Section H 274.4 m, Fillmore Formation (Floian; *Presbynileus ibexensis* Zone), southern Confusion Range, Ibex area, Millard County, western Utah. **A**, **D**, **I**, **M**, **P**, cranidium, holotype, SUI 124945, dorsal, anterior, ventral, right lateral, and oblique views, x10. **B**, **E**, **G**, cranidium, SUI 124946, dorsal, left lateral, and anterior views, x10. (*continued opposite*)

field. The posterior pygidial margin also becomes less pointed medially and more gently rounded.

Remarks. Bathyurina sumneri was compared with *B. curtisi* above, and the ways in which these species and *B. hooki* differ from other species were listed. It is compared with *B. hooki* in an extended differential description below.

Bathyurina hooki sp. nov. (Figs 18A–H, J, K, N, O, R, T, U, 19–21, 22A–V)

Material. Holotype, cranidium, SUI 124945 (Fig. 19A, D, I, M, P), and assigned specimens SUI 124946–124972, 128977–128982, all from Section H 274.4 m, Fillmore Formation (Floian; unzoned interval above *Presbynileus ibexensis* Zone), southern Confusion Range, Ibex area, Millard County, western Utah.

Etymology. After Peter Hook.

Diagnosis. Anterior region of glabella with sculpture dominated by tubercles; raised line sculpture muted and restricted to anteriormost parts; raised line sculpture on librigenal field restricted to anteriormost region; sculpture on flattened area in front of genal angle very subdued; genal spine retained until relatively late in ontogeny, entirely absent only from largest specimens; pygidium with relatively broad border, narrow compared with sagittal length.

Description. Bathyurina hooki and *B. sumneri* are very similar and a comparative description of the former is provided herein along with the standard measurements provided for the other described species. Cranidial measurements were made on the largest and most intact specimens of Figure 19. Cranidium with maximum width across posterior projections 147.0% (142.9-151.2) sagittal length; width across midlength of palpebral lobes 123.2% (122.5-123.8) sagittal length; width across β 86.5% (84.4-89.7) cranidial sagittal length, and 69.0% (68.8-69.1) width across midlength of palpebral lobe; palpebral lobes with length (exsag.) 35.8% (34.6-37.2) cranidial sagittal length; distance across γ 78.0% (75.6-79.6) cranidial sagittal length; distance across ε 89.5% (86.1-93.1) cranidial sagittal length; glabella with maximum width 86.1% (83.5-89.5) sagittal length excluding LO; glabella with sagittal length (excluding LO) 73.2% (71.5-75.0) that of cranidium; width across posterior contact of axial furrows with posterior margin 55.1% (53.4-56.2) sagittal length of cranidium; LO sagittal length 17.6% (16.1-18.6) that of cranidium.

Cranidia of *B. hooki* differ from those of *B. sumneri* in the following: the anteriormost tip of the glabella and the anterior portion of the frontal area is covered with a sculpture of fine raised lines whereas this area is more smooth on cranidia of *B. sumneri*; the anterior border is slightly more upturned toward the glabella and obscures slightly more of the anterior margin of the glabella in anterior view than those of *B. sumneri*, and the border is more peaked medially with the sculpture of raised lines more strongly bowed than *B. sumneri*; in dorsal view, the anterior tip of the glabella does not extend as far past the anterior border furrow as on cranidia of *B. sumneri*; the anterior sections of the facial sutures are slightly more outwardly convex; palpebral furrow with sculpture of very fine tubercles compared to that of *B. sumneri*, which is smooth; the glabellar furrows are also slightly more impressed.

Librigena of *B. hooki* are nearly identical to those of *B. sumneri*, but they differ in having a sculpture of small tubercles rather than anastomosing raised lines on the posterior border. This sculpture of small tubercles also continues onto the genal angle, unlike librigena of *B. sumneri*. The genal angle of *B. hooki* appears slightly more angular and less rounded than that of *B. sumneri*.

The hypostome (Figs 18A, B, E, 19J-L) of *B. hooki* possesses a more rounded lateral and posterior margin. The posterior lobe of the middle body is smaller than the anterior lobe, but closer in size (i.e., length and overall area), whereas the posterior lobe of *B. sumneri* is shorter and smaller. The net-like sculpture characteristic of the main portion of the anterior lobe of the middle body of the *B. sumneri* is absent and instead a sculpture of prominent fine raised lines covers entire middle body. The hypostome of *B. hooki* is also more strongly inflated.

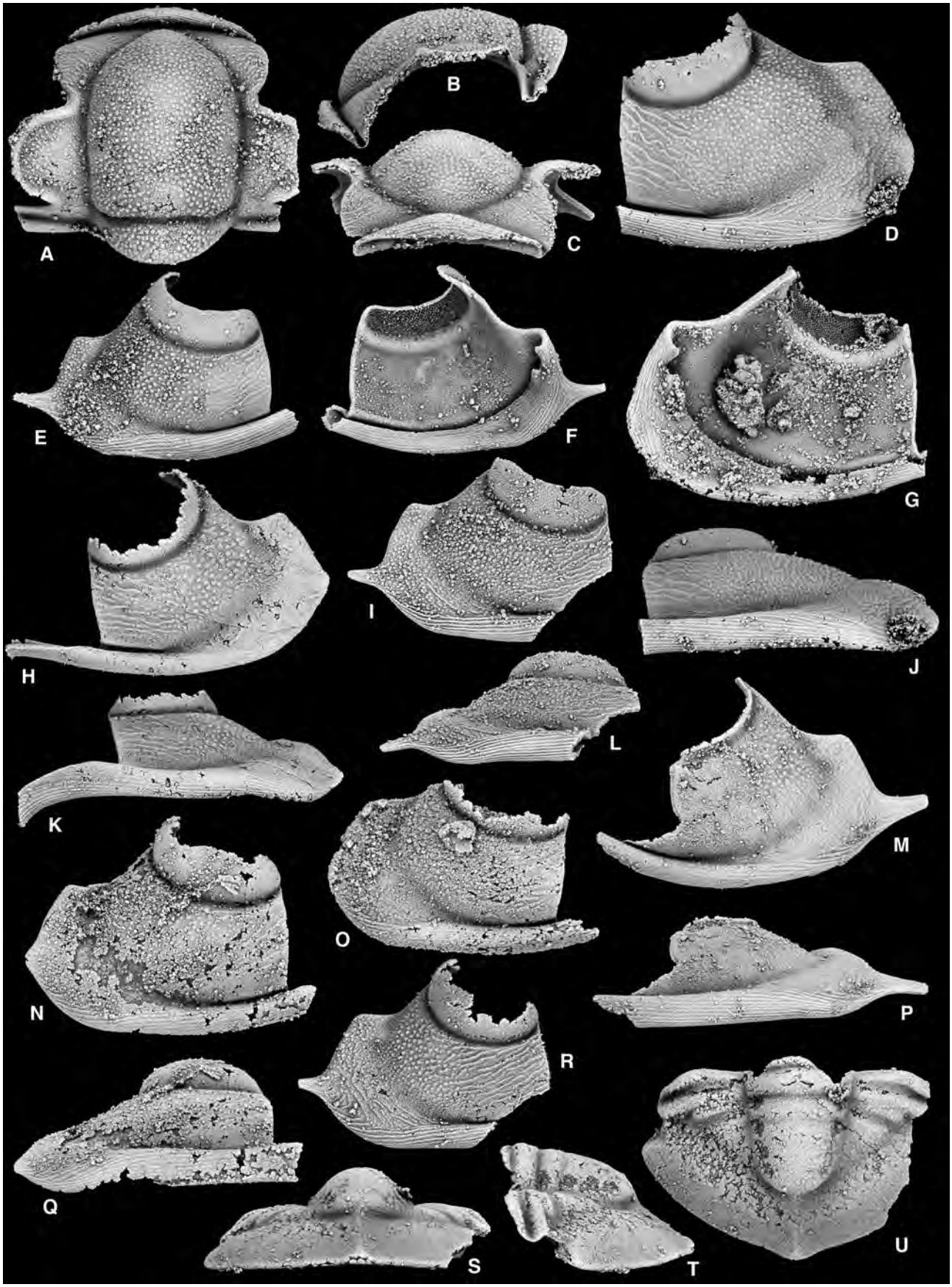
Rostral plate not recovered. Thoracic segments essentially similar.

Pygidial measurements were made on the largest specimens of Figure 21 and are given in general terms as most specimens are incomplete. Pygidium with maximum width across third segment about 161% sagittal length; maximum axial width across first segment about 33% maximum pygidial width; width across fifth segment about 74% width across first segment; length of axis excluding articulating half ring about 60% total sagittal length of pygidium. Additional differences include: axis slightly shorter and broader than *B. sumneri* and with postaxial region

Figure 20 (*overleaf*). ***Bathyurina hooki*** sp. nov., from Section H 274.4 m, Fillmore Formation (Floian; *Presbynileus ibexensis* Zone), southern Confusion Range, Ibex area, Millard County, western Utah. **A**–**C**, cranidium, SUI 124950, dorsal, left lateral, and anterior views, x12. **D**, **G**, **J**, left librigena, SUI 124951, external, internal, and ventrolateral views, x10. **E**, **F**, right librigena, SUI 124952, external and internal views, x10. **H**, **K**, left librigena, SUI 124953, external and ventrolateral views, x10. **I**, **L**, right librigena, SUI 124954, external and ventrolateral views, x12. **M**, **P**, left librigena, SUI 124955, external and ventrolateral views, x12. **N**, **Q**, right librigena, SUI 124956, external and ventrolateral views, x10. **O**, right librigena, SUI 124957, external view, x12. **R**, right librigena, SUI 124958, external view, x12. **S**–**U**, pygidium, SUI 124959, posterior, left lateral, and dorsal views, x12.

Figure 21 (*Page 341*). ***Bathyurina hooki*** sp. nov., from Section H 274.4 m, Fillmore Formation (Floian; *Presbynileus ibexensis* Zone), southern Confusion Range, Ibex area, Millard County, western Utah. **A**, **F**, **I**, **K**, **N**, pygidium, SUI 124965, dorsal, ventral, right lateral, posterior, and anterior views, x7.5. **B**, **D**, **G**, pygidium, SUI 124966, dorsal, left lateral and posterior views, x7.5. **C**, **E**, **H**, pygidium, SUI 124967, dorsal, posterior, and left lateral views, x7.5. **J**, **L**, **Q**, **T**, pygidium, SUI 124968, left lateral, dorsal, posterior, and ventral views, x10. **M**, **O**, **R**, pygidium, SUI 124969, dorsal, left lateral, and posterior views, x7.5. **P**, **S**, **W**, pygidium, SUI 124970, dorsal, posterior, and left lateral views, x10. **U**, **V**, **Z**, pygidium, SUI 124971, right lateral, dorsal, and posterior views, x12. **X**, **Y**, **AA**, pygidium, SUI 124972, right lateral, dorsal, and posterior views, x15.

(*continued from opposite*) **C**, **F**, **H**, cranidium, SUI 124947, dorsal, anterior, and left lateral views, x10. **J**–**L**, hypostome, SUI 124948, right lateral, posterior, and ventral views, x12. **N**, **O**, **Q**–**S**, cranidium, SUI 124949, oblique, anterior, ventral, dorsal, and right lateral views, x10.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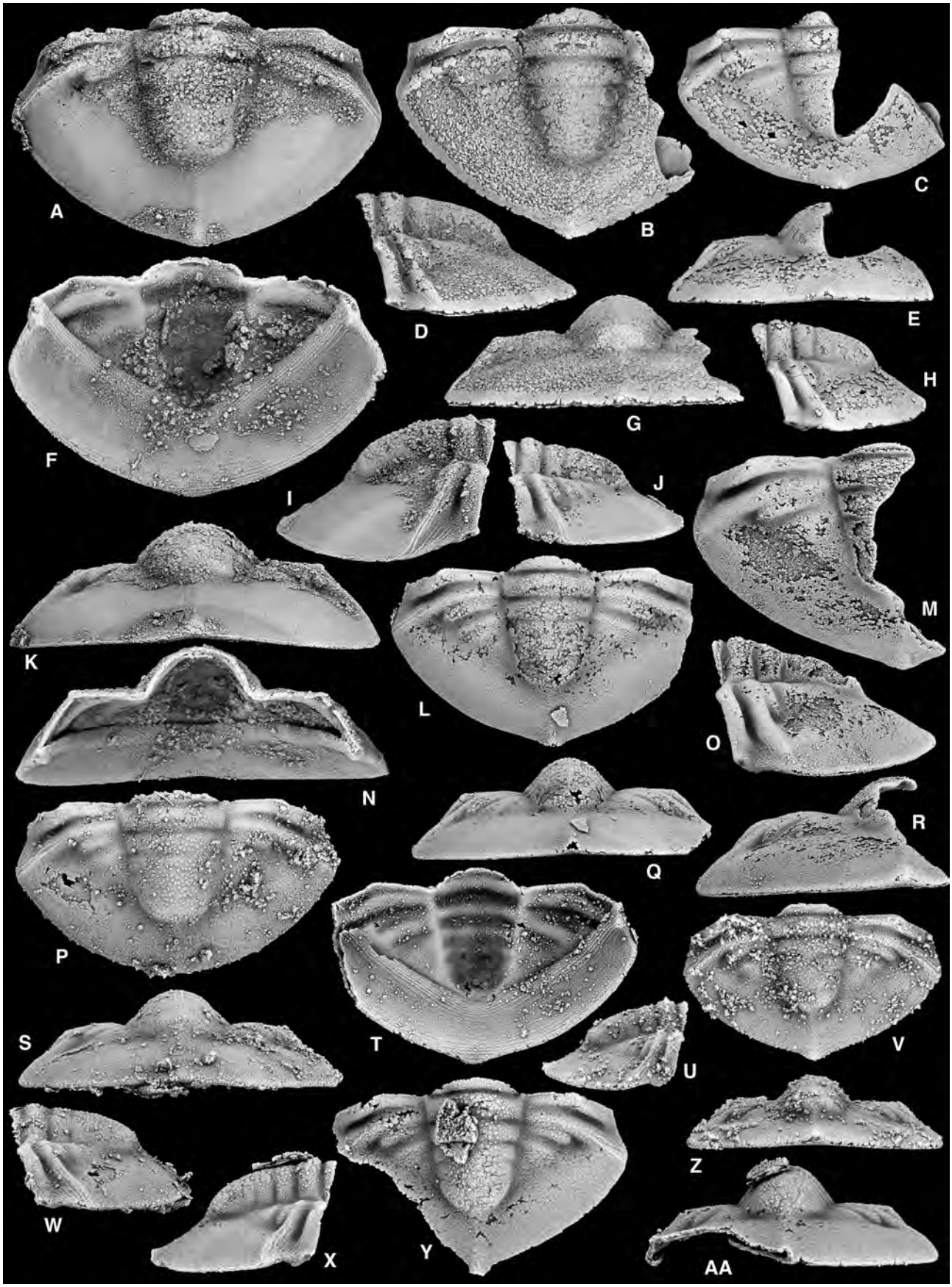
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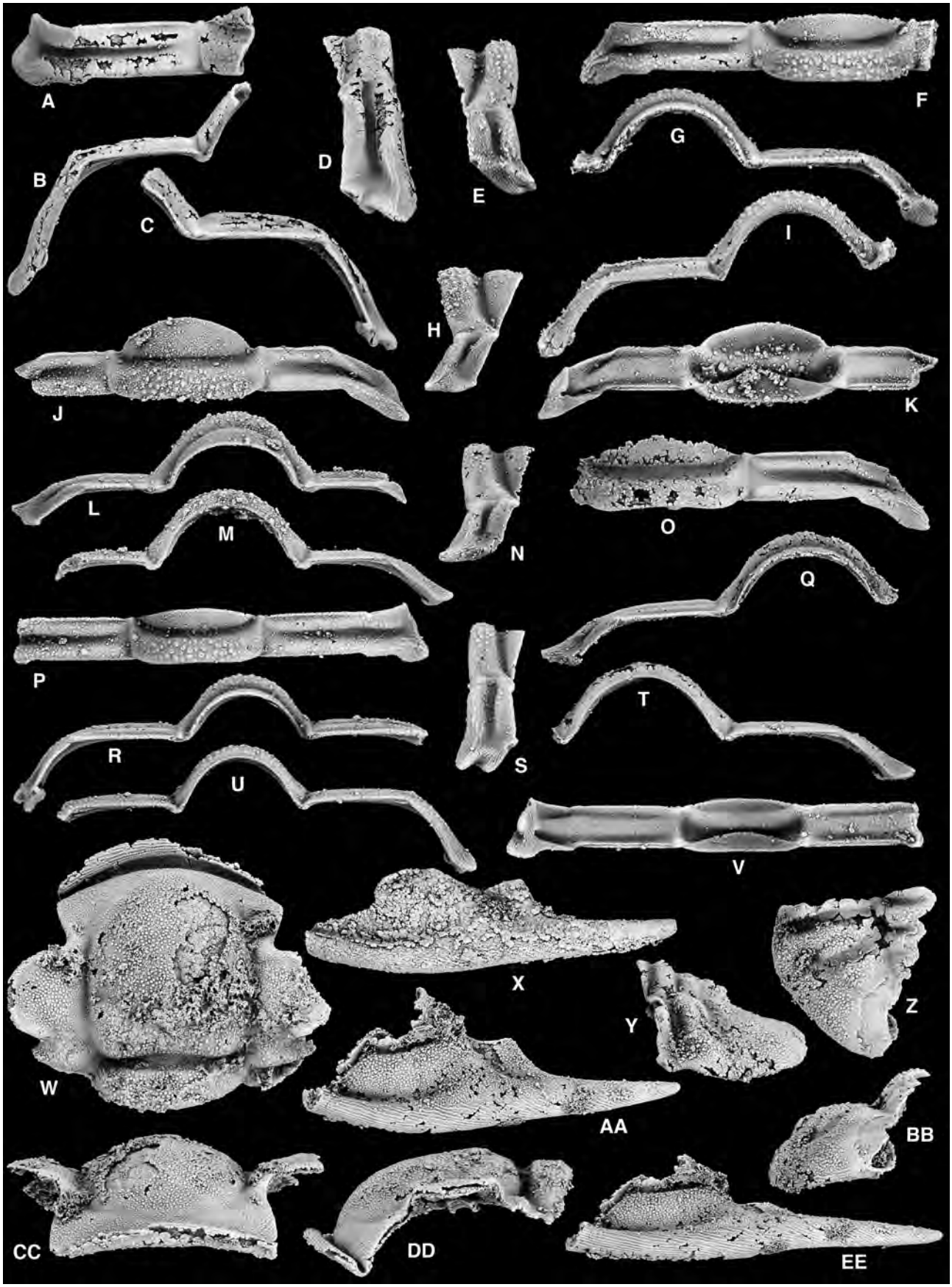

Figure 22. A–V, *Bathyurina hooki* sp. nov., from Section H 274.4 m, Fillmore Formation (Floian; *Presbynileus ibexensis* Zone), southern Confusion Range, Ibex area, Millard County, western Utah. **A**–**D**, thoracic segment, SUI 124960, dorsal, posterior, anterior, and left lateral views, x10. **E**–**G**, **I**, thoracic segment, SUI 124961, left lateral, dorsal, anterior, and posterior views, x15. (*continued opposite*)

less strongly downturned; axial ring furrows are in general shallower than on *B. sumneri*; second pleural segment slightly less well defined on *B. hooki* compared to *B. sumneri*.

Remarks. Bathyurina hooki is very similar to the older *B. sumneri* and it was initially assumed that it was conspecific. However, with a large sample size obtained from H 274.4 m, several universal differences can be catalogued and it is clear that distinct, subtly but clearly differentiated species are involved. Cranidia are nearly identical in dimensions, but there is a strong sculptural difference, unambiguous on all known specimens. In *B. sumneri*, when cranidia are viewed anteriorly, the raised line sculpture is very prominent on the anterior part of the glabella and extends to the exclusion of tuberculate sculpture nearly to the level of the bases of the palpebral lobes. In *B. hooki*, the raised line sculpture is poorly expressed, in all cases mixed with tuberculate sculpture, and in most specimens the raised lines are present only at the very front of the glabella, and only about half the distance to the bases of the palpebral lobes. Similar distinctions can be seen on the librigenae, with the raised line sculpture in *B. sumneri* prominent and occupying a greater anterior area of the field than in *B. hooki*. Sculpture on the flattened region in front of the genal angle is much more prominent in *B. sumneri*. There is a clear ontogenetic difference in the reduction of the genal spine with size. The spine is retained much later in ontogeny in *B. hooki*, and completely lost only in the largest specimens. It disappears in relatively smaller specimens of *B. sumneri*. Similarly sized specimens show a tubular spine in *B. hooki* (e.g. Fig. 20M) versus a completely rounded angle in *B. sumneri* (e.g., Fig. 15O). Pygidia are very similar, but those of *B. hooki* are consistenly narrower relative to their length, with slightly broader borders.

Bathyurina morrisi sp. nov. (Fig. 23)

2009 *Peltabellia* sp. nov. 4; Adrain *et al*., p. 557, fig. 8P, T.

Material. Holotype, cranidium, SUI 115133 (Fig. 23A, B, E, F, J), from Section G 99.3 m, and assigned specimens SUI 115134, 128978–128982, 128984, from Section G 99.3 m and G 99T m, Fillmore Formation (Floian; *Psalikilus spinosum* Zone), southern Confusion Range, Ibex area, Millard County, western Utah.

Etymology. After Stephen Morris.

Diagnosis. Glabella not strongly expanded anteriorly; palpebral lobes relatively small and not extended far laterally; glabella not overhanging anterior border, preglabellar field visible in dorsal view; cephalic sculpture of very subdued tiny tubercles, raised lines not present; genal spine lost in all known specimens, genal angle gently rounded; pygidium with very weakly differentiated border, with little change in slope between pleurae and border.

Description. Cranidium with width across midlength of palpebral lobes 118.0% sagittal length; width across β 84.2% cranidial sagittal length and 71.4% width across midlength of palpebral lobe; anterior border short (sag., exsag.), about half the sagittal length of LO, tapering abaxially, posterior and anterior margins describing gentle arc in dorsal view, in anterior view dorsal margin describing strongly convex arc, ventral margin similarly bowed medially with lateral portions cut obliquely and with strong concave bow; in lateral view anterior border is flexed strongly upward and posteriorly so that border crowds out anterior portion of preglabellar field, anterior portion of border forms steep face vertical to slightly overhanding face; sculpture of very densely spaced fine raised lines covers entire border, lines more closely spaced in dorsal view than anterior view, about six lines cover anteroventral face of border in anterior view and are bowed medially similar to anterior border; anterior border furrow very deep, distinct, slightly longer medially, medially arched similar to anterior border; preglabellar field strongly downturned from horizontal plane, very thin strip visible in dorsal and anterior views, pinched out medially by contact of preglabellar and anterior border furrows (Fig. 23B); preglabellar furrow short, shallow, just barely in contact medially with anterior border furrow; frontal areas strongly sloped downward from anterior margin of palpebral lobe, with anterior portion nearly vertical and facing mostly anteriorly with slight oblique turn becoming more pronounced abaxially; anterior sections of facial sutures laterally convex across anterior border, curve strongest just anterior to intersection with anterior border furrow, forming angular notch across anterior border furrow and adjacent portions of anterior border and frontal area, directed posterolaterally across anterior portion of frontal area, from this point posteriorly to γ suture strongly posteromedially convergent and sinuous; palpebral lobes large, length (exsag.) 14.0% cranidial sagittal length, distance across γ 79.6% cranidial sagittal length, distance across ε 92.4% cranidial sagittal length, lateral margin strongly bowed, with curve strongest posteriorly, lobe held well below dorsal apex of glabella in anterior and lateral view, proximal portion sloping toward glabella and distal portion just slightly sloping away from glabella; broad, inflated border bounds lateral margin of lobe, inner margin poorly defined by very faint, shallow, and narrow palpebral furrow, border extended anteriorly into eye ridge cutting obliquely across frontal area (Fig. 23A); interocular fixigena narrow, sloping toward glabella more strongly than proximal portion of palpebral lobe, with sculpture identical to that of palpebral lobe and glabella; glabella with maximum width 90.2% sagittal length (excluding LO), sagittal length 70.7% that of cranidium, widest opposite midpoint of palpebral lobes, moderately dorsally inflated, sitting above fixigena in lateral and anterior views, lateral profile moderately curved posteriorly, with anterior portion of glabella more strongly curved so that anterior tip is strongly downturned and nearly vertical; glabellar furrows not clearly expressed; axial furrows moderately deep, deeper from opposite γ posteriorly, gently bowed opposite palpebral lobes, slightly deeper and bowed inward at fossulae, shallower anteriorly from fossulae, running without obvious break into preglabellar furrow, width across intersection with

H, **J**–**M**, thoracic segment, SUI 124962, right lateral, dorsal, ventral, anterior, and posterior views, x10. **N**, **O**, **Q**, **T**, thoracic segment, SUI 124963, right lateral, dorsal, anterior, and posterior views, x10. **P**, **R**, **S**, **U**, **V**, thoracic segment, SUI 124964, dorsal, anterior, right lateral, posterior, and ventral views, x15. Figs **W**–**EE**. ***Bathyurina* sp. nov. A**, from Section H 172.5 m, Fillmore Formation (Floian; *Psalikilus pikum* Zone), southern Confusion Range, Ibex area, Millard County, western Utah. All magnifications are x7.5. **W**, **CC**, **DD**, cranidium, SUI 124973, dorsal, anterior, and left lateral views. **X**, left librigena, SUI 124974, external view. **Y**, **Z**, **BB**, pygidium, SUI 124975, left lateral, dorsal, and posterior views. **AA**, **EE**, left librigena, SUI 124976, external and ventrolateral views.

Figure 23. ***Bathyurina morrisi*** sp. nov., from Section G 99Tm and G 99.3 m, Fillmore Formation (lower Floian; *Psalikilus spinosum* Zone), southern Confusion Range, Ibex area, Millard County, western Utah. **A**, **B**, **E**, **F**, **J**, cranidium, holotype, SUI 115133, dorsal, anterior, ventral, oblique, and right lateral views, x10 (G 99.3 m). **C**, **D**, left librigena, SUI 128978, (*continued opposite*)

posterior cranidial margin 60.1% cranidial sagittal length, much shallower from contact with SO posteriorly, furrows clearly confluent with SO, intersection with posterior border furrow shallow and less obvious than that with SO; fossulae very faintly expressed dorsally, not clearly visible on ventral surface; SO deep, longest sagittally, anterior and posterior margins with distinct with posterior glabellar margin and anterior margin of LO respectively, very gentle concave bow medially, distal tips slightly shorter and more strongly curved anteriorly around posterolateral corners of glabella; LO long, with sagittal length 15.5% that of cranidium, slightly longer sagittally than exsagittally, posterior margin with moderately strong posterior bow, anterior margin with more gentle posterior bow; posterolateral projection incomplete with only adaxial portion preserved, directed just slightly posteriorly past horizontal plane; posterior fixigena forming very short (exsag.) strip, much shorter abaxially; posterior section of facial suture with proximal portion directed slightly posterolaterally; posterior border furrow very shallow and nearly effaced from contact with axial furrow to a short distance abaxially, deeper and longer (exsag.) from this point abaxially, deep section with sharp contact posteriorly with posterior border and anteriorly with posterior fixignea; posterior border with distinct convexity, shorter (exsag.) proximally, lengthened distally; sculpture of densely distributed, very small faint tubercles covers majority of cranidium, tubercles appear to cover LO, but surface not well preserved; doublure underlying LO crescent shaped, anterior margin incomplete, but does not appear to reach posterior margin of SO ventrally, sculpture of very faint and fine raised lines running nearly transverse with slight posterior bow; very short articulating groove present ventrally beneath posterior margin of posterior border (Fig. 23E).

Librigenal specimens not particularly well preserved, with visual surface not preserved on any recovered specimens; anterior section of facial suture almost transversely straight across field to border furrow, then with almost 90° change in direction and transversely straight across anterior projection; posterior section of facial suture gently concave across field and posterior border with apex of curve at intersection with posterior border furrow; field moderately inflated, sitting above lateral and posterior borders; lateral border furrow deep and relatively broad anteriorly where lateral border is pushed upwards against field, posterior portion of furrow adjacent to genal angle much shallower; slightly swollen region at genal angle separates lateral and posterior border furrows (Fig. 23D); lateral border is gently flexed upward against genal field, with anteriormost portion more strongly flexed, strongly inflated, forming a near vertical wall along lateral margin anteriorly, continuing without obvious disruption into anterior projection, in ventrolateral profile border is shortest at genal angle and lengthens into anterior projection; sculpture of fine raised lines running subparallel to lateral margin covers border and continues without obvious disruption onto anterior projection, lines become slightly more widely spaced toward anterior projection; anterior projection relatively long, extending beyond genal field, with anterior portion very slightly curved downward from horizontal plane anteriorly (Fig. 23H); lateral border with lateral margin gently bowed adjacent to genal angle, nearly straight with only a very slight curve along main portion and anterior projection; posterior border broad and more strongly dorsoventrally flattened than lateral border; posterior border furrow shallow, broad; genal angle gently rounded forming an obtuse angle, deflected downward from horizontal plane; doublure wide beneath genal angle, narrows below lateral border and into anterior projection, inner margin of doublure from genal angle to anterior projection describes continuous arc that is more strongly curved at genal angle; doublure beneath lateral border and anterior projection with sculpture of fine, closely spaced raised lines running subparallel to inner and outer margins; small section of double beneath genal angle visible on one specimen (Fig. 23C), appears smoother with raised line present much more faint, and with slight depression medially.

Hypostome, rostral plate, and thorax not identified.

Pygidial measurements were made on the best preserved specimens of Figure 23 with some measurements given in more general terms due to preservation issues. Pygidium with maximum width across posterior margin of third segment about 180% sagittal length; axis composed of five segments, with maximum axial width across first segment 35.5% (35.0-35.7) maximum pygidial width, length of axis (excluding articulating half ring) about 65% total sagittal length of pygidium, width across fifth segment 67.6% (61.8-72.1) width across first segment; articulating half ring small, sagittal length about 9% total pygidial length, lenticular in outline with anterior margin more strongly bowed than posterior margin; first ring furrow deep along entire course, broad, distal tips slightly turned anterolaterally and deeper; second ring furrow shallow and narrow, distal tips deeper and longer (exsag.) than medial portion; third ring furrow shallower and narrower than second, almost completely effaced medially, distal tips deeper at intersection with axial furrows; fourth ring furrow much less well expressed, almost completely effaced, but very faint distally with slight depression at contact with axial furrow; fifth ring furrow very faint, expressed dorsally by slight depression at intersection with axial furrow, clearly visible ventrally adjacent to axial furrow (Fig. 23X); pseudo-articulating half ring of second segment faintly visible, those of subsequent segments not expressed; first axial ring of similar length sagittally and exsagittaly (including merged pseudo-articulating half ring), slightly longer than second ring; posterior rings progressively smaller and more poorly expressed, but with essentially the same morphology; terminal piece moderately short, broad, posteriorly rounded, with posterior margin faintly, but clearly differentiated from postaxial region; pleural region with first segment clearly differentiated, subsequent segments less so; first pleural segment with maximum exsagittal pleural length about 24% sagittal axial length, anterior margin overall anteriorly convex with tightest point of curve directed anterolaterally, fulcrum set relatively close to axis, portion of margin between axis and fulcrum directed slightly posterolaterally, portion of margin distal to fulcrum directed more strongly posterolaterally, with course disrupted by short anterolaterally directed spike developed about

internal and external views, x10 (G 99.3 m). **G**, **K**, **L**, pygidium, SUI 128979, right lateral, dorsal, and posterior views, x10 (G 99T m). **H**, **I**, **M**, right librigena, SUI 128980, ventrolateral, internal, and external views, x10 (G 99.3 m). **N**–**P**, **Q**, pygidium, SUI 128981, dorsal, posterior, right lateral, and ventral views, x10 (G 99T m). **R**, **S**, **U**, pygidium, SUI 128982, posterior, dorsal, and right lateral views, x12 (G 99T m). **T**, **X**, **Y**, **AA**, **BB**, pygidium, SUI 115134, dorsal, ventral, posterior, left lateral, and anterior views, x12 (G 99T m). **V**, **W**, **Z**, **CC**, pygidium, SUI 128984, right lateral, dorsal, ventral, and posterior views, x12 (G 99.3 m).

mid way between fulcrum and margin, portion from spike abaxially is more strongly directed posterolaterally; spike is clearly visible in ventral view as small triangular process along margin at contact with doublure; very faint and narrow furrow present along anterior margin of first pleural band; facet downturned from horizontal plane, with sculpture of fine raised lines; first segment with anterior pleural band more strongly inflated than posterior band, shortest (exsag.) at contact with axial furrow, lengthens abaxially; posterior pleural band longer (exsag.) at contact with axial furrow than anterior band, shortens slightly abaxially; sculpture of fine granules present on first pleural band adaxial of fulcrum; pleural furrow long (exsag.), deepest at fulcrum and slightly shallower adjacent to fulcrum, effaced at point opposite marginal articulating spike to pygidial margin so that anterior and posterior bands appear merged, furrow shallow between fulcrum and axis becoming nearly effaced at contact with axial furrow; interpleural very shallow and almost effaced, deepest at and from fulcrum distally; second pleural band with anterior and posterior bands differentiated at and adjacent to fulcrum, with very little independent inflation; subsequent pleural bands not as clearly expressed dorsally, with only pleural furrows faintly incised between axis and fulcrum, pleural region distal to fulcrum largely smooth and more strongly downturned from horizontal plane; pleural bands and furrows more clearly differentiated on ventral surface; border furrow and border not distinctly differentiated from pleural field; very narrow rim around pygidial margin with sculpture of fine raised lines present around pygidial margin, best seen in posterior view (Fig. 23O); posterior pygidial margin forming smooth and broad laterally convex arc; in ventral view broad doublure visible, extending adaxially to point opposite inner margin of short articulating spike developed on first pleural band and slightly deflected medially around posterior margin of terminal piece; doublure divided into two distinct sections, a broad flat portion and a shorter upturned portion present along the inner margin of the doublure; flatter section is very broad, covered with fine raised closely spaced lines adjacent to pygidial margin, whereas middle portion is smoother with only a few more widely spaced fine lines, this portion is also slightly depressed toward ventral surface of pygidium; shorter upturned section of doublure with sculpture of fine raised closely spaced lines that merge continuously from flatter section.

Remarks. *Bathyurina morrisi* is the oldest known and presumptively most plesiomorphic species. Membership in *Bathyurina* is indicated by the arcuate anterior border with strong dorsal raised line sculpture, nearly vertical preglabellar field, and the upturning of the anterior border to lie against the preglabellar field, with a deep, trench-like anterior border furrow, and the overall cephalic sculpture of scattered, tiny tubercles. It can be distinguished from all of the younger species in its relatively anteriorly narrow glabella, narrow palpebral lobes, and particularly in its pygidium with the border poorly differentiated from the pleurae.

Bathyurina sp. nov. A (Fig. 22W–EE)

Material. Assigned specimens SUI 124973–124976, from Section H 172.5 m, Fillmore Formation (Floian; *Psalikilus pikum* Zone), southern Confusion Range, Ibex area, Millard County, western Utah.

Remarks. A poorly known species from the *Psalikilus pikum* Zone is most similar to the slightly younger *B. plicolabeona*, differing in its relatively shorter glabella, longer (sag., exsag.) anterior border furrow, smaller palpebral lobes, and particularly in the retention in large specimens of a long genal spine.

ACKNOWLEDGEMENTS

Support from (U.S.) National Science Foundation grant DEB 0716065 is gratefully acknowledged. Tiffany Adrain provided assistance with specimen numbers and curation. Dave Harper facilitated loan of Poulsen's 1927 and 1937 specimens. Derek Siveter facilitated loan of Poulsen's 1946 specimens. Claire Mellish, Richard Fortey and Greg Edgecombe provided invaluable assistance during rephotography of Poulsen's 1946 material at the Natural History Museum (London) in 2010. Neo McAdams provided much assistance with photography. Jim Loch and an anonymous reviewer provided helpful comments on the manuscript.

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