

Systematics and affinity of the Lower Ordovician (Tulean; lower Floian) trilobite *Psalikilopsis*

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Psalikilopsis Ross, 1953, has been known from a single species and interpreted as a “hystricurine” ancestral to some, but not all, “bathyurids”. Comprehensive revision of the type species and the description of three new species demonstrate that the taxon is ingroup Bathyuridae. The unusual morphology of its more derived species is associated with a change from normal bathyurid sphaeroidal enrolment to spiral enrolment, with part of the pygidium tucked inside the cephalon, stopped medially by a pygidial spine docking against a medially modified anterior border. The oldest and apparently basal species lacks these modifications and is of “normal” bathyurid morphology. The genus occurs in lower Floian (Tulean) *Psalikilus spinosum*, *Hintzeia celsaora*, and *Psalikilopsis cuspidicauda* zones in Idaho, Utah, and Nevada, and its striking morphology and common occurrence make it biostratigraphically significant. A pygidium from the Fort Cassin Formation of New York, and two species illustrated in open nomenclature from the Shallow Bay Formation of Newfoundland demonstrate the occurrence of *Psalikilopsis* in eastern Laurentia. The eastern Laurentian species appear to be younger than those from western Laurentia. New species are *Psalikilopsis paracuspicauda* (*Psalikilopsis cuspidicauda* Zone), *P. redfordi* (*H. celsaora* Zone), and *P. newmani* (*Psalikilus spinosum* Zone).

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THE MONOGRAPHS of Ross (1951) and Hintze (1953) on Lower Ordovician trilobite faunas from the Great Basin included a number of new genera of uncertain systematic affinity. Many of these have remained difficult to interpret due to the limited scope of the original illustrations and lack of systematic work on the faunas in the half century since their original description. Comprehensive field-based revision of the Ross/Hintze faunas (Adrain *et al.* 2009, and references therein) is yielding much new information on problematic taxa as a result of highly stratigraphically resolved new sampling and large sample sizes. This paper is concerned with one such taxon, the previously monotypic *Psalikilopsis* Ross, 1953.

Psalikilopsis has rarely been commented upon since its original documentation and no additional material has been assigned to it from elsewhere in Laurentia or the world. When he proposed it, Ross (1953, p. 638) did not assign the genus to a family (as was his practice — he did not assign any of the taxa he described in his 1951 monograph to families, either). Poulsen (in Moore 1959, p. O278) assigned *Psalikilopsis* to a Subfamily Hystricurinae Hupé, 1953, of the Family Solenopleuridae Angelin, 1854. Hystricuridae has generally been treated at family level subsequent to the 1959 Treatise, but Adrain *et al.* (2003) emphasised the sprawling, phylogenetically suspect nature of the group as traditionally conceived. Adrain *et al.* (2003)

began the task of parsing the group into putatively monophyletic components, but much work remains to be done to understand hystricurid and general aulacopleuroidean phylogeny and classification. Nevertheless, to the extent that it has been considered at all, *Psalikilopsis* has been assigned to Hystricuridae either directly (Ross 1975, table 1; Lee & Chatterton 1999; Jell & Adrain 2003) or with question (Adrain *et al.* 2003).

Despite its relative obscurity, *Psalikilopsis* has played a role in the development of influential ideas about bathyurid phylogeny. Fortey & Owens (1975, pp. 228-229) presented the idea that Bathyuridae Walcott, 1886, included two main groups, classified as Bathyurinae and Bathyurellinae Hupé, 1953 (the groupings were initially proposed by Hupé [1953] and the idea was subsequently developed at length by Fortey [1979]). Bathyurinae was centered around genera with a posterior pygidial spine such as *Acidiphorus* Raymond, 1925, and *Goniotelina* Whittington & Ross in Whittington, 1953. Bathyurellinae was thought to include taxa with “a flat, wide pygidium, broad anterior border to the cranidium and blade-like genal spines...” (Fortey & Owens 1975, pp. 228-229) including *Peltabellia* Whittington, 1953, and *Licnocephala* Ross, 1951.

Notably, Fortey & Owens (1975) suggested that the groups had independent “hystricurine” origins. This opinion was repeated by Zhou & Fortey (1986). As pointed out by Adrain *et al.* (2003), if true this would mean Bathyuridae as thus recognised is an unnatural, polyphyletic group. Adrain *et al.* (2003) contested the idea of separate origins, asserting that new material supported instead a monophyletic Bathyuridae. The present study is part of the evidence for this view.

Fortey & Owens (1975) considered that *Pseudohystricuris orbis* Ross, 1953, was the “hystricurine” close to the derivation of Bathyurinae. This species was recently revised and assigned to *Litizicurus* Adrain, McAdams & Westrop, 2009. We regarded the taxon as possibly related to *Psalikilus* Ross, 1951, and assigned both to Hystricuridae, though their affinities will need to be explored in a broader analysis as more relevant data become available. It is conceivable that *Litizicurus* may be ingroup Bathyuridae, but it certainly bears no obvious close relationship to the much younger *Acidiphorus* group (*sensu* McAdams & Adrain 2007).

Fortey & Owens (1975) considered that *Psalikilopsis cuspidicauda* Ross, 1953 (which they misspelled “*cuspidicaudata*”), was the “hystricurine” close to the derivation of

Bathyurellinae. They pointed out the close morphological correspondence between what they called *Peltabellia* sp. B of Hintze (Hintze [1953, p. 175, pl. 9, figs 8, 11, 12] had assigned the taxon to *Jeffersonia* Poulsen, 1927) and *Psalikilopsis cuspidicauda*. Here we strongly agree: “*Peltabellia* sp. B” is described as *Psalikilopsis newmani* sp. nov. herein, and so we consider the species congeneric. Fortey & Owens, however, believed that *Psalikilopsis cuspidicauda* represented a hystricurine from which “*Peltabellia* sp. B” (and hence Bathyurellinae) was derived. As detailed in the genus discussion below, the polarity of this transition is likely reversed. *Psalikilopsis newmani* is the oldest member of the genus and has a conventional bathyurid morphology. The younger species of *Psalikilopsis* are not hystricurines, but rather are morphological derivatives of this general bathyurid morphology, modified to accommodate a transition from sphaeroidal to spiral enrolment. Hence, while Fortey & Owens (1975) correctly recognised the close relationship of *Psalikilopsis cuspidicauda* to what we here term *Psalikilopsis newmani*, we argue that this relationship indicates that *Psalikilopsis* is a derived ingroup bathyurid, and not the extra-bathyurid sister taxon to Bathyurellinae.

A review of the stratigraphic background and history of study of Great Basin localities was provided by Adrain *et al.* (2009). That work (and several other recent papers) also provided maps showing the location and lines of section of sections from which material is described herein, along with graphic logs of sections G and H at Ibex, western Utah. As this context has now been detailed several times, we do not repeat it herein. Details of the localities, stratigraphy, sampling and biostratigraphic zonation referred to herein are given by Adrain *et al.* (2009).

A small number of *Psalikilopsis* specimens collected by C. H. Kindle and H. B. Whittington from the Shallow Bay Formation, western Newfoundland, are also described herein. The material was recovered from their beds 8a and 8e (Kindle & Whittington 1958, fig. 2), which are correlative with beds 9.1 and 9.5 respectively of the James & Stevens (1986) Back Cove measured section (James & Stevens 1986, p. 109). Trilobites were recovered as disarticulated sclerites in large boulder sized clasts from these two debris flows. The *Psalikilopsis* material was recovered from two boulders referred to as 9.1/3 and 9.5/4 herein, with the first number indicating the bed from which it was collected and the second indicating the original Kindle and Whittington boulder sample number within that bed.

BIOSTRATIGRAPHY

Adrain *et al.* (2009) introduced a revised set of trilobite zones for the Tulean and Blackhillsian stages, increasing the biostratigraphic resolution from five zones (Ross *et al.* 1997) to 16. This scheme is followed herein. As work progresses, the scheme is likely to be further refined and amended as particular groups are studied in detail and new information becomes available. Close study of material representing *Psalikilopsis* has contributed to the discovery that the Tulean *Psalikilopsis cuspidicauda* Zone of Adrain *et al.* (2009; we misspelled the species throughout “*cuspidicauda*” following Fortey & Owens 1975, p. 228) is more complex than first thought. Initially, we assumed all of the material now recognised as *P. cuspidicauda* and *P. paracuspidauda* sp. nov. belonged to a single species. Only after photography was well advanced did it become apparent that the overall sample included two pervasively differentiated pygidial types, that the types were segregated by sample, and that in fact they were stratigraphically successive. The morphological details are discussed under the species below, but it is now apparent that the interval designated the *P. cuspidicauda* Zone includes two separate, stratigraphically successive faunas and that *P. cuspidicauda* itself is restricted to the lower one. Material of *Psalikilopsis* from the upper fauna is assigned below to *P. paracuspidauda*.

Similar subtle but pervasive differentiation has been encountered as work on other groups progresses. For example, species of *Gladiatoria* Hupé, 1955, are also distinct and restricted to either the lower or higher of the assemblages (Adrain *et al.*, this volume). Species of *Psalikilus* Ross, 1951, also appear to be differentiated, as are those of the pliomerid *Protopliomerella* Harrington, 1957. There do, however, appear to be some species that definitely occur in both assemblages. It is difficult to anticipate how thoroughly differentiated the assemblages will be and we are reluctant to formally name a new zone until systematics of more groups are well advanced. For the time being we refer to a lower and upper *Psalikilopsis cuspidicauda* Zone, though the name bearer itself is restricted to the lower part. The distinction has already proved useful and regionally significant, as the fauna of an isolated exposure of the Yellow Hill Limestone in eastern Nevada (Locality YH E herein) can be directly correlated with the upper part of the zone based on the occurrence of *P. paracuspidauda*.

SYSTEMATIC PALAEONTOLOGY

Repository. Type and figured material is housed in the Paleontology Repository, Department of

Geoscience, University of Iowa, Iowa City, with number prefix SUI, and the Geological Survey of Canada, Ottawa, with number prefix GSC.

Descriptions. Throughout the descriptions, where ratios are reported, the first value is the mean, followed by the recorded range in parentheses.

Family BATHYURIDAE Walcott, 1886

Psalikilopsis Ross, 1953

Type species. *Psalikilopsis cuspidicauda* Ross, 1953, from the Garden City Formation, Idaho, and the Fillmore Formation, Utah.

Other species. *Psalikilopsis newmani* sp. nov., Fillmore Formation, Utah; *P. paracuspidauda* sp. nov., Fillmore Formation, Utah, and Yellow Hill Limestone, Nevada; *P. redfordi* sp. nov., Garden City Formation, Idaho, and Fillmore Formation, Utah; *Psalikilopsis* sp. nov. 1, Shallow Bay Formation, Newfoundland; *Psalikilopsis* sp. nov. 2, Shallow Bay Formation, Newfoundland; *Acidiphorus?* sp. indet. of Brett & Westrop (1996, fig. 16.9, 16.10), Fort Cassin Formation, New York State.

Diagnosis. Most dorsal surfaces with dense sculpture of small to medium tubercles; glabella strongly inflated and “humped” in sagittal profile; frontal area and preglabellar field sloped strongly down from interocular fixigena and glabella; palpebral lobes large, with inflated rim and strong palpebral furrow; librigenal field broad and inflated; thoracic anterior and posterior pleural bands separated by long (exsag.), trough-like pleural furrow, merged distally to form posteriorly directed spine with raised line sculpture; posterior region of thoracic and pygidial articulating half-rings with transverse band of scattered small tubercles.

Remarks. When he named the genus, Ross (1953, p. 639) made comparison to *Hystericurus* Raymond, 1913 (which was then very broadly interpreted) and *Psalikilus* Ross, 1951. He particularly emphasised similarity with the latter in pygidial morphology, in the shape of the preglabellar field, and the shape of the palpebral lobes. *Psalikilus* remains largely unrevised and generally poorly known. We have, however, amassed large samples of all known species and multiple new species (see faunal lists and illustrations of Adrain *et al.* 2009), and described the zonal name bearer *Psalikilus hestoni* Adrain, McAdams & Westrop, 2009. While the morphology of both *Psalikilopsis* and

Psalikilus is unusual and broadly similar, there are no obvious synapomorphies and the unique features of either genus are likely independently derived. We have recovered a stratigraphically low species of *Psalikilus* (*Psalikilus* sp. nov. 1 of Adrain *et al.* 2009, fig. 7A, E) and below we describe a stratigraphically low new species of *Psalikilopsis*, *P. redfordi*, as well as a lower species of “normal” bathyurid morphology, *P. newmani*, which we consider the basal species of *Psalikilopsis*. Assuming each genus is monophyletic (which seems highly likely), assessment of relationship of the genera should involve these presumptively basal species and not later, more derived forms (such as those available to Ross for comparison). These basal forms bear no obvious synapomorphic resemblance to each other. While their broader relationship needs to be explored in a comprehensive analysis of bathyurid phylogeny, it seems clear that similarity between more derived species of *Psalikilus* and *Psalikilopsis* is superficial.

Psalikilopsis (?) *alticapitis* Young, 1973, is not related to *Psalikilopsis*, but rather is a dimeropygid which is now assigned to *Heckethornia* McAdams & Adrain, 2009.

The relationship between *P. cuspidicauda*, *P. paracuspicauda* and *P. redfordi* is obvious, as they share uniquely derived pygidial morphology and modification of the anterior border to accommodate it during enrolment. Assignment of *P. newmani* to the genus is less obvious, as in isolation it would likely be assigned to the plesiomorphic and currently paraphyletic *Peltabellia* (indeed, exactly this assignment was made by Fortey & Owens [1975, p. 228] in referring to material of the species described in open nomenclature by Hintze [1953, p. 175, pl. 9, figs 8, 11, 12]). However, despite its conventional pygidial and anterior border morphology, *P. newmani* seems clearly to be the sister species of the more derived species. It is nearly identical in cranial morphology posterior to the preglabellar field, sharing the inflated, posteriorly “humped” glabella, the large palpebral lobes with prominent, inflated rims, and the occipital node placed forward on LO and faintly expressed. Librigenae differ only in proportion of the lateral border and length of the genal spine. The librigena of *P. newmani* seems quite different from those of *P. cuspidicauda* and *P. paracuspicauda*, which have long genal spines, but compares closely with that of the stratigraphically intermediate species *P. redfordi*. The librigena of *P. redfordi* has a genal spine which is long and similar to that of *P. paracuspicauda* in small specimens, but which becomes progressively shorter with size, so that the largest specimens have a spine

only moderately longer than that of *P. newmani*. In thoracic morphology, *P. newmani* is nearly indistinguishable from the more derived species, differing only in the retention of larger articulating facets on the distal part of the anterior pleura and in the possession of smaller distal spines. The most obvious difference is the morphology of the pygidium, which at first glance seems to be of radically different construction. When examined in detail, however, the differences, while striking, involve modifications of structures already present in the pygidium of *P. newmani*, and many parts of the pygidia remain nearly identical. In particular, the morphology of the axis and of the pleural region on which bands and furrows are expressed is essentially the same across all of the species, in keeping with the nearly identical thoracic morphology. *Psalikilopsis newmani* exhibits a general bathyurid border morphology, in which the distal parts of the pleural regions behind the first segment are flattened out into an apparent border. This region is faintly transgressed by continuations of the pleural and interpleural furrows in many bathyurid taxa, and this is the case also, faintly, in *P. newmani*. This region is matched ventrally by a broad, ventrally concave shelf. At the inner edge of this shelf is a prominent raised rim — again, a feature seen in other bathyurids. Silicified material reveals that this rim is matched by an upturned region of doublure (Fig. 29J, O).

Compared with the pygidial border of conventional trilobite pygidia, against which pleural segmentation typically terminates, the flattened dorsal region of bathyurids is probably not homologous, but rather a modified part of the pleura. Instead, it seems likely that the ventral rim, which is itself underlain by a separate vertically upturned doublural sector, is the homologue of a conventional border, moved ventrally and anteriorly to lie in front of a secondarily derived border.

In any case, the homologies proposed here between the more conventional bathyurid pygidium of *P. newmani* and those of the derived species are as follows. The flattened dorsal secondary border region of *P. newmani* is greatly reduced in *P. redfordi* to the flattened dorsal surface of the lobate median spine, and a narrow furrow-like region between the rim-like border and the impressed pleural regions. These areas are lost entirely in *P. cuspidicauda* and *P. paracuspicauda*. The rear margin of the pygidium in *P. newmani*, which is slightly swollen into a rim separating the dorsal and ventral faces of the secondary border (Fig. 29G, I, Y), and which bears several raised lines, is the homologue of the raised ridge which bounds the impressed

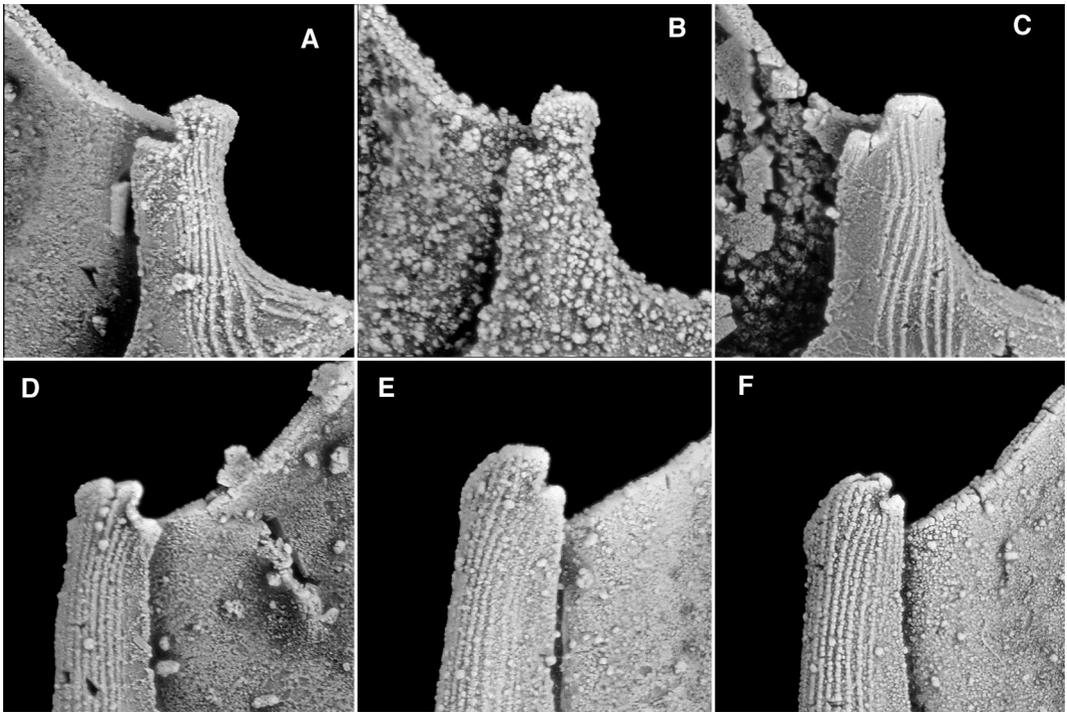


Figure 1. Detail views of the Panderian notch in species of *Psalikelopsis*, which is in all cases very small and set nearly adjacent to the posterior facial suture. All magnifications are x30. **A**, *Psalikelopsis newmani* sp. nov., SUI 128947 (see Fig. 27G, J, K). **B**, **C**, *Psalikelopsis redfordi* sp. nov., **B**, SUI 128914 (see Fig. 22 J, K), from Section HC5 186.5 m, **C**, SUI 128926 (see Fig. 24A, D), from Section G 118.6 m. **D**, *Psalikelopsis cuspidicauda* Ross, 1953, SUI 128813 (see Fig. 8F, I), from Section D 88.9 m. **E**, **F**, *Psalikelopsis paracuspidauda* sp. nov., SUI 128853 (see Fig. 15M, O), SUI 128847 (see Fig. 15A, B, D), both from Section D 106.4 m.

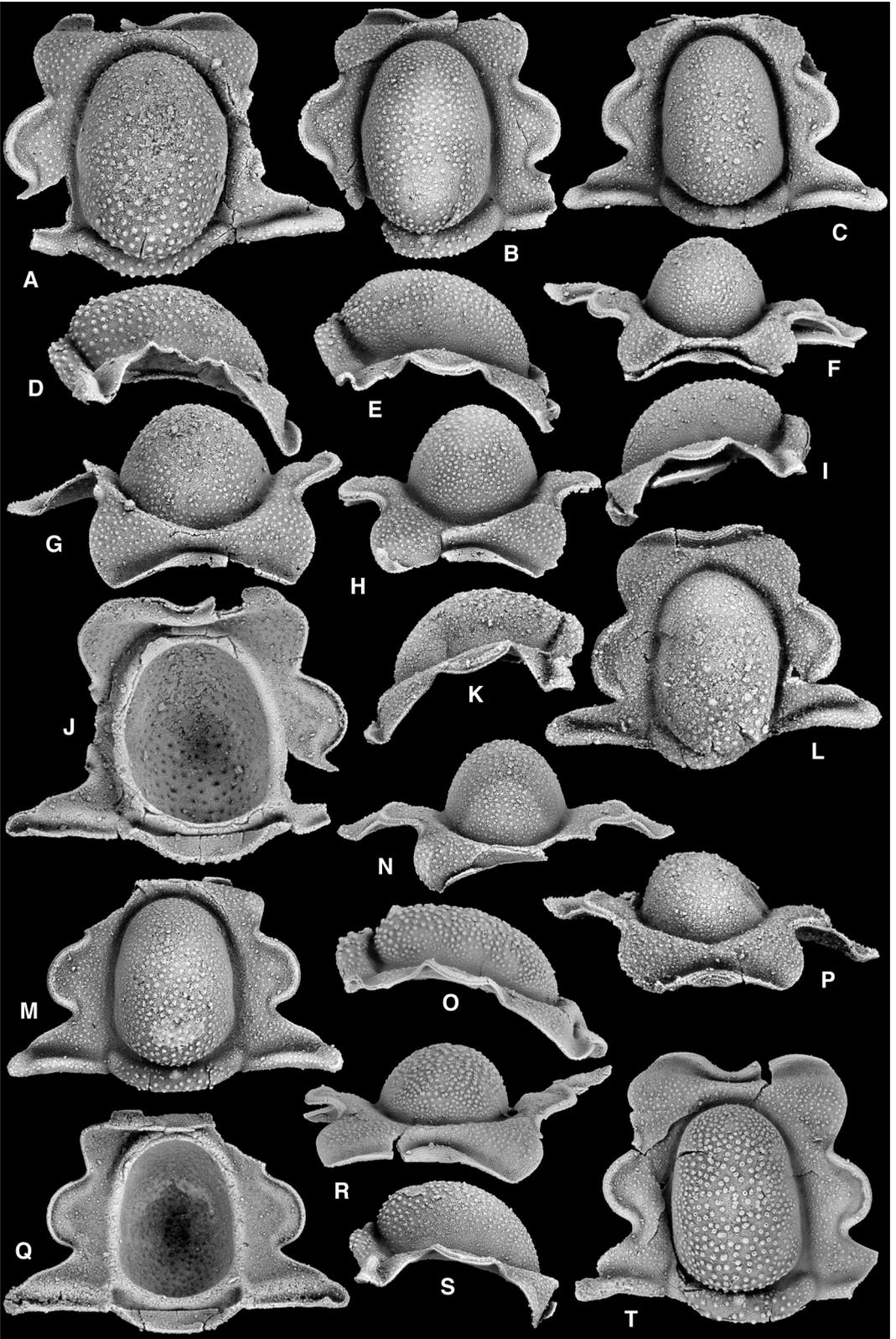
pleural regions in the more derived species. The concave ventral aspect of the secondary border region is the homologue of the vertically oriented “wall” in the more derived species, which is also gently outwardly concave. The inflated anterior ventral rim in *P. newmani* is the homologue of the rim ventrally bounding the wall in the more derived species. Finally, the narrow strip of true doublure visible in anterior view in *P. newmani* is the homologue of the nearly identical strip in the same position in the more derived species (e.g., Fig. 18J).

When these (putative) homologies are recognised, it becomes apparent that what appear to be radically different pygidia are derivatives of the basic bathyurid condition, adapted for a different style of enrolment. In the derived species, the vertical “wall” slipped inside the cephalon during enrolment. The pygidial median spine acted as a stopper, and the cranidia are modified in the medial anterior border region to form a median notch for reception of this spine during enrolment. Most of the morphological differences between the derived species and *P. newmani* reflect modifications to accommodate this transition from a sphaeroidal to a spiral

enrolment mechanism.

The phylogeny of this small group seems very clear, so much so that there seems little point presenting a tiny formal analysis. *Psalikelopsis newmani* is the basal species, with pygidial morphology of broadly distributed general bathyurid type, and *P. redfordi* is both stratigraphically and morphologically intermediate between it and the closely similar sister pair of *P. cuspidicauda* and *P. paracuspidauda*. Hence the cladogram is (*P. newmani* (*P. redfordi* (*P. cuspidicauda*, *P. paracuspidauda*))), which is fully congruent with stratigraphic order.

Despite this, where to draw the basal node of *Psalikelopsis* is a valid question. Inclusivity of a taxon is a subjective decision in light of a phylogeny, and the main obvious modifications associated with secondary spiral enrolment supporting a node subtending *P. redfordi*, *P. cuspidicauda* and *P. paracuspidauda* might support restricting the taxon to these species. The options for *P. newmani* are: 1) to retain it in an expressly paraphyletic taxon, in this case likely *Peltabellia*, as a matter of convenience; 2) to erect a monotypic genus for it; or 3) to include it within *Psalikelopsis*. Initially, we



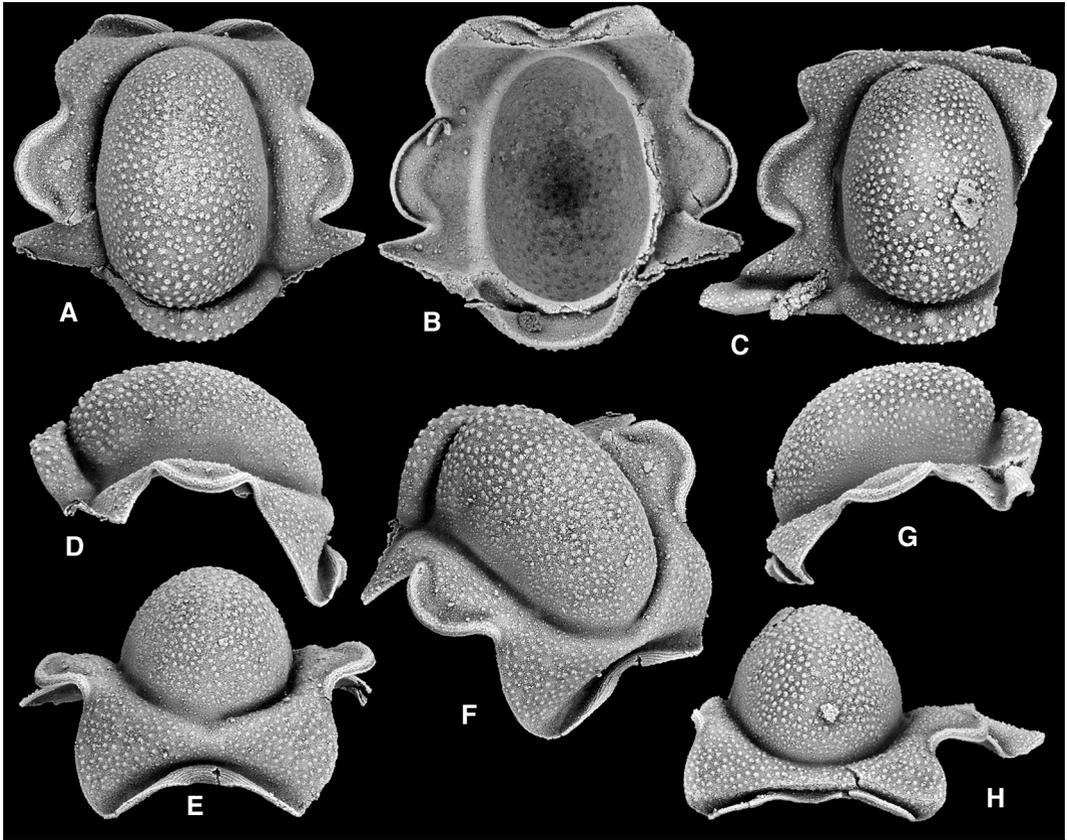


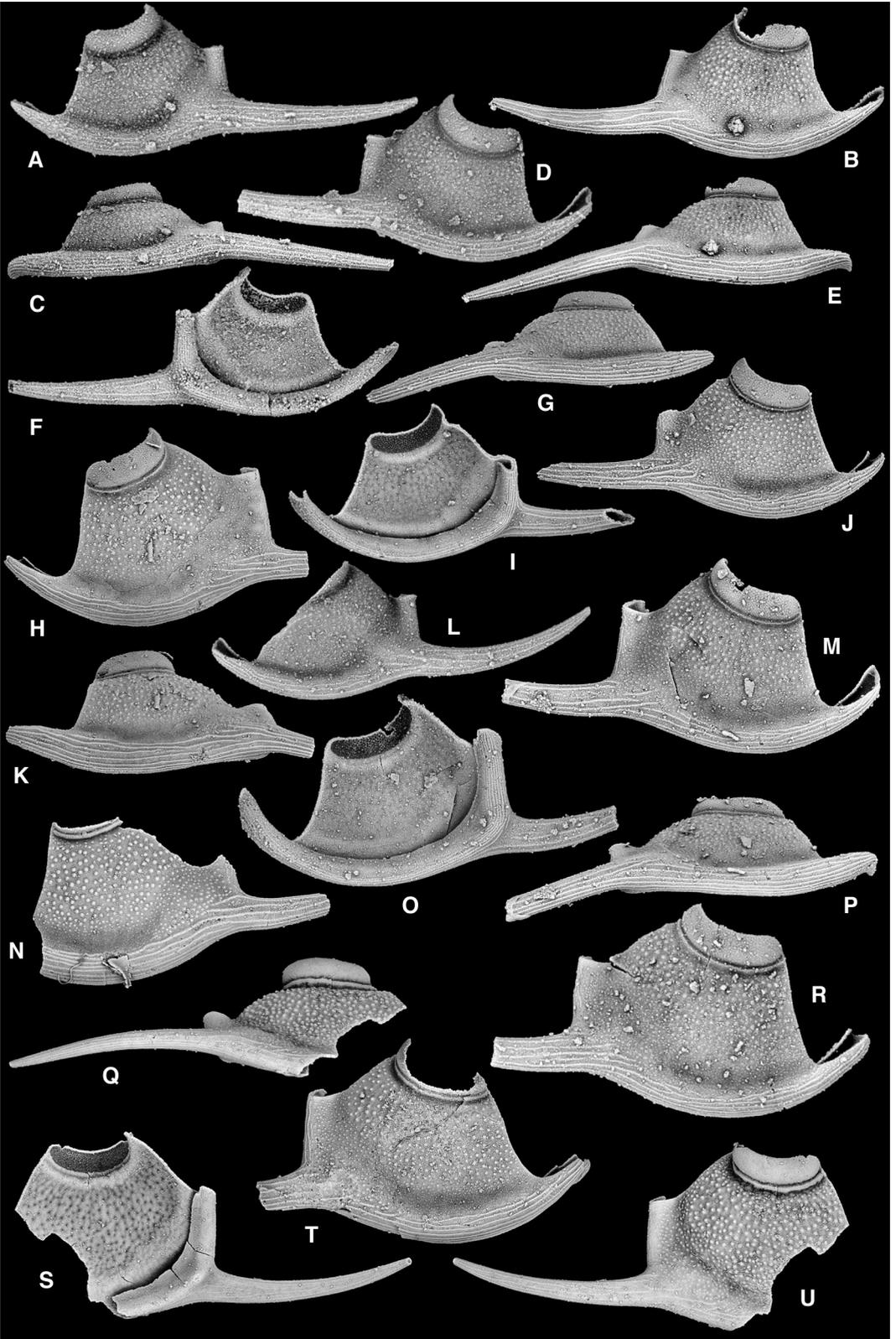
Figure 3. *Psalikelopsis cuspidicauda* Ross, 1953, from Section HC5 195.7 m, Garden City Formation (lower Floian; Tulean; low *Psalikelopsis cuspidicauda* Zone), east side of Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho, USA. All magnifications are x10. **A, B, D-F,** cranium, SUI 115171, dorsal, ventral, right lateral, anterior, and oblique views. **C, G, H,** cranium, SUI 128785, dorsal, left lateral, and anterior views.

provisionally assigned the species to *Peltabellia* (*Peltabellia* sp. nov. 3 of Adrain *et al.* [2009, p. 557, fig. 8O, S]). However, given the obvious similarity of all exoskeletal features except the size of the genal spine and those associated with enrolment, we now elect to include *P. newmani* within *Psalikelopsis*, avoiding contributing to the problem of an unnatural grade group (*Peltabellia*, which will be revised and restricted to a clade as work on bathyurid phylogeny progresses) or the proliferation of monotypic genera. This means that the prominent modifications of the derived group are excluded from the genus diagnosis, as they support an internal node within the genus.

Psalikelopsis is now known from three of

the lower Tulean zones of Adrain *et al.* (2009) and is distributed across the Great Basin region. With the expanded knowledge of the taxon herein, its occurrence in eastern Laurentia can be recognised with certainty. Brett & Westrop (1996, fig. 16.9, 16.10) illustrated a pygidium they assigned with question to *Acidiphorus* from the Fort Cassin Formation of New York State. The pygidium belongs to a derived species of *Psalikelopsis*, as it has the pleural bands and furrows bounded distally by a narrow ridge and underlain by a vertical “wall”, with a short pointed median spine posteriorly. We have also recovered pygidia representing two species of *Psalikelopsis*, one of which is very similar to the Fort Cassin

Figure 2 (opposite). *Psalikelopsis cuspidicauda* Ross, 1953, from Sections HC5 195.7 m, east side of Hillyard Canyon, and HC6 189.3 m, west side of Hillyard Canyon, Garden City Formation (lower Floian; Tulean; low *Psalikelopsis cuspidicauda* Zone), Bear River Range, Franklin County, southeastern Idaho, USA. **A, D, G, J,** cranium, SUI 128779, dorsal, right lateral, anterior, and ventral views, x10 (HC5 195.7 m). **B, E, H,** cranium, SUI 128780, dorsal, right lateral, and anterior views, x10 (HC5 195.7 m). **C, F, I,** cranium, SUI 128781, dorsal, anterior, and left lateral views, x12 (HC5 195.7 m). **K, L, P,** cranium, SUI 128782, left lateral, dorsal, and anterior views, x15 (HC5 195.7 m). **M, N, Q, S,** cranium, SUI 128783, dorsal, anterior, ventral, and right lateral views, x10 (HC5 195.7 m). **O, R, T,** cranium, SUI 128784, right lateral, anterior, and dorsal views, x7.5 (HC6 189.3 m).



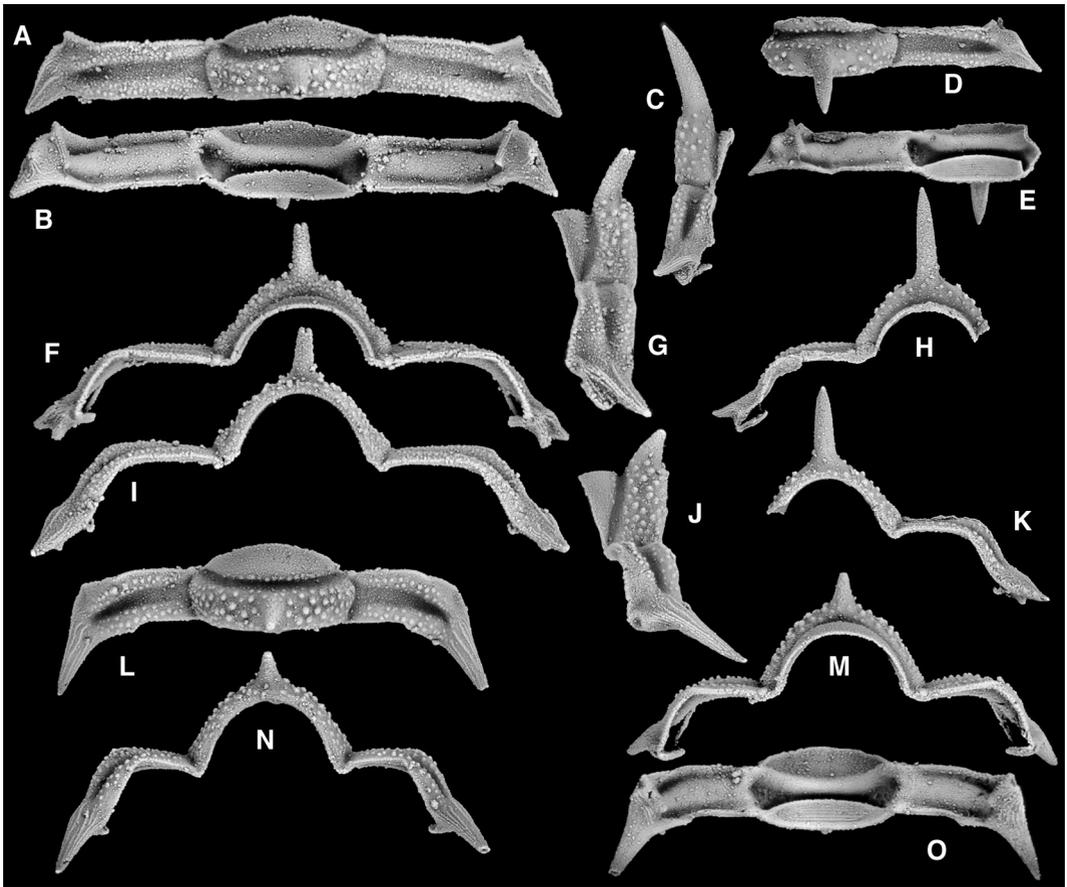


Figure 5. *Psalikelopsis cuspidicauda* Ross, 1953, from Sections HC5 203.7-204.2T m, east side of Hillyard Canyon, and HC6 189.3 m, west side of Hillyard Canyon, Garden City Formation (lower Floian; Tulean; low *Psalikelopsis cuspidicauda* Zone), Bear River Range, Franklin County, southeastern Idaho, USA. **A, B, F, G, I,** thoracic segment, SUI 128796, dorsal, ventral, anterior, left lateral, and posterior views, x12 (HC5 203.7-204.2T m). **C-E, H, K,** thoracic segment, SUI 128797, right lateral, dorsal, ventral, anterior, and posterior views, x7.5 (HC6 189.3 m). **J, L-O,** thoracic segment, SUI 128798, left lateral, dorsal, anterior, posterior, and ventral views, x12 (HC6 189.3 m).

species, from the Shallow Bay Formation of western Newfoundland. These occurrences are discussed below under *Psalikelopsis* sp. nov. 1 and *Psalikelopsis* sp. nov. 2.

At first glance, internal views of librigenae of species of *Psalikelopsis* show no sign of a Panderian notch, the prominent presence of which is a general feature of bathyurids. However, silicified material reveals that a distinct Panderian

notch is present in all species (Fig. 1). It is generally very small and is set nearly adjacent to the posterior facial suture. It is definitely distinguished from this suture, however, and is a distinct opening in the inner edge of the doublure. In some species (Fig. 1D-F) it is bounded by a small rim separating it from the raised line sculpture.

Figure 4 (opposite). *Psalikelopsis cuspidicauda* Ross, 1953, from Sections HC5 195.7 m and 203.7-204.2T m, east side of Hillyard Canyon, and HC6 189.3 m, west side of Hillyard Canyon, Garden City Formation (lower Floian; Tulean; low *Psalikelopsis cuspidicauda* Zone), Bear River Range, Franklin County, southeastern Idaho, USA. **A, C, F,** left librigena, SUI 128786, external, ventrolateral, and interval views, x12 (HC5 195.7 m). **B, E,** right librigena, SUI 128787, external and ventrolateral views, x12 (HC5 195.7 m). **D,** right librigena, SUI 128788, external view, x12 (HC5 203.7-204.2T m). **G, I, J,** right librigena, SUI 128789, ventrolateral, internal, and external views, x10 (HC6 189.3 m). **H, K,** left librigena, SUI 128790, external and ventrolateral views, x7.5 (HC6 189.3 m). **L,** left librigena, SUI 128791, external view, x10 (HC5 203.7-204.2T m). **M, O, P,** right librigena, SUI 128792, external, internal, and ventrolateral views, x10 (HC5 195.7 m). **N,** left librigena, SUI 128793, external view, x7.5 (HC6 189.3 m). **Q, S, U,** right librigena, SUI 128794, ventrolateral, internal, and external views, x5 (HC5 203.7-204.2T m). **T,** right librigena, SUI 128795, external view, x7.5 (HC6 189.3 m).

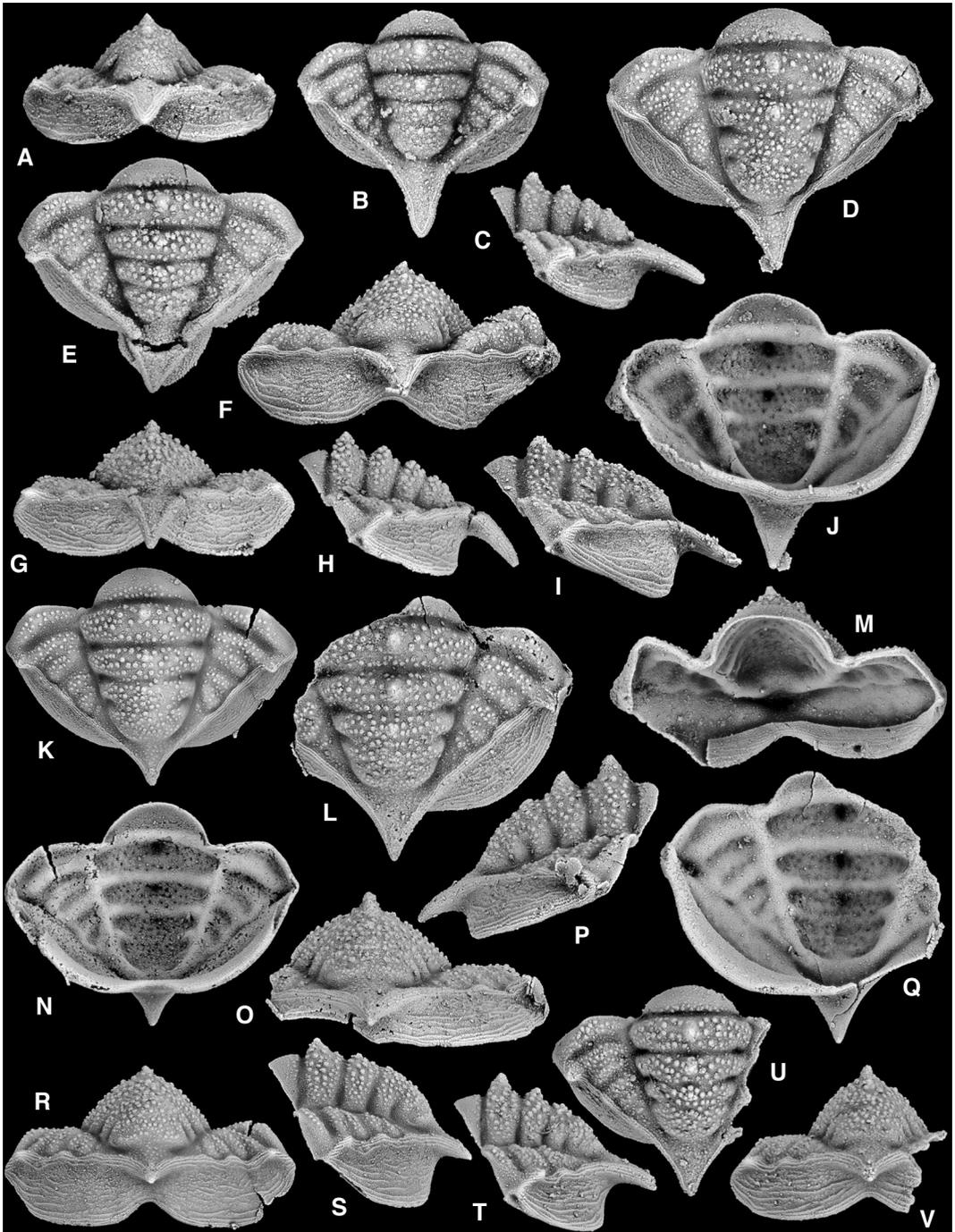


Figure 6. *Psalikilopsis cuspidicauda* Ross, 1953, from Sections HC5 195.7 m and 203.7-204.2T m, east side of Hillyard Canyon, and HC6 189.3 m, west side of Hillyard Canyon, Garden City Formation (lower Floian; Tulean; low *Psalikilopsis cuspidicauda* Zone), Bear River Range, Franklin County, southeastern Idaho, USA. **A-C**, pygidium, SUI 128799, posterior, dorsal, and left lateral views, x15 (HC5 195.7 m). **D, F, I, J, M**, pygidium, SUI 128800, dorsal, posterior, left lateral, ventral, and anterior views, x9 (HC5 195.7 m). **E, G, H**, pygidium, SUI 128801, dorsal, posterior, and left lateral views, x10 (HC5 203.7-204.2T m). **K, N, R, S**, pygidium, SUI 115172, dorsal, ventral, posterior, and left lateral views, x7.5 (HC6 189.3 m). **L, O, P, Q**, pygidium, SUI 128802, dorsal, posterior, right lateral, and ventral views, x9 (HC5 203.7-204.2T m). **T-V**, pygidium, SUI 128803, left lateral, dorsal, and posterior views, x12 (HC6 189.3 m).

Psalikilopsis cuspidicauda Ross, 1953 (Figs 1D, 2-10)

- 1951 *Psalikilus* ? sp.; Ross, p. 63, pl. 13, figs 28, 29, 33, 34, pl. 30, figs 1-3.
 1953 *Psalikilopsis cuspidicauda*; Ross, p. 639, pl. 63, figs 2-9, 12.
 1959 *Psalikilopsis cuspidicauda* Ross; Berg & Ross, p. 117.
 1975 *Psalikilopsis cuspidicauda* [sic] Ross; Fortey & Owens, 1975.
 1997 *Psalikilopsis cuspidicauda* Ross; Ross *et al.*, p. 44.
 1998 *Psalikilopsis cuspidicauda* Ross; White & Lieberman, p. 109.
 2003 *Psalikilopsis cuspidicauda* Ross; Jell & Adrain, p. 432.
 2003 *Psalikilopsis cuspidicauda* [sic] Ross; Adrain *et al.*, p. 560.
 2009 *Psalikilopsis cuspidicauda* [sic] Ross; Adrain *et al.*, p. 559, fig. 10A, E.

Diagnosis. Pygidium with prominent median nodes on at least first two axial rings, usually also on third; fulcrum set about half distance distally on pleura; small but prominent posterior pleural spine on first pygidial segment.

Description. Given the close similarity of this species to *P. paracuspidauda*, extended written description of both is redundant. As a large sample of high quality material of *P. paracuspidauda* is available from a single horizon, and it is a new taxon, we have elected to describe it. All differences between *P. cuspidicauda* and *P. paracuspidauda* are discussed below.

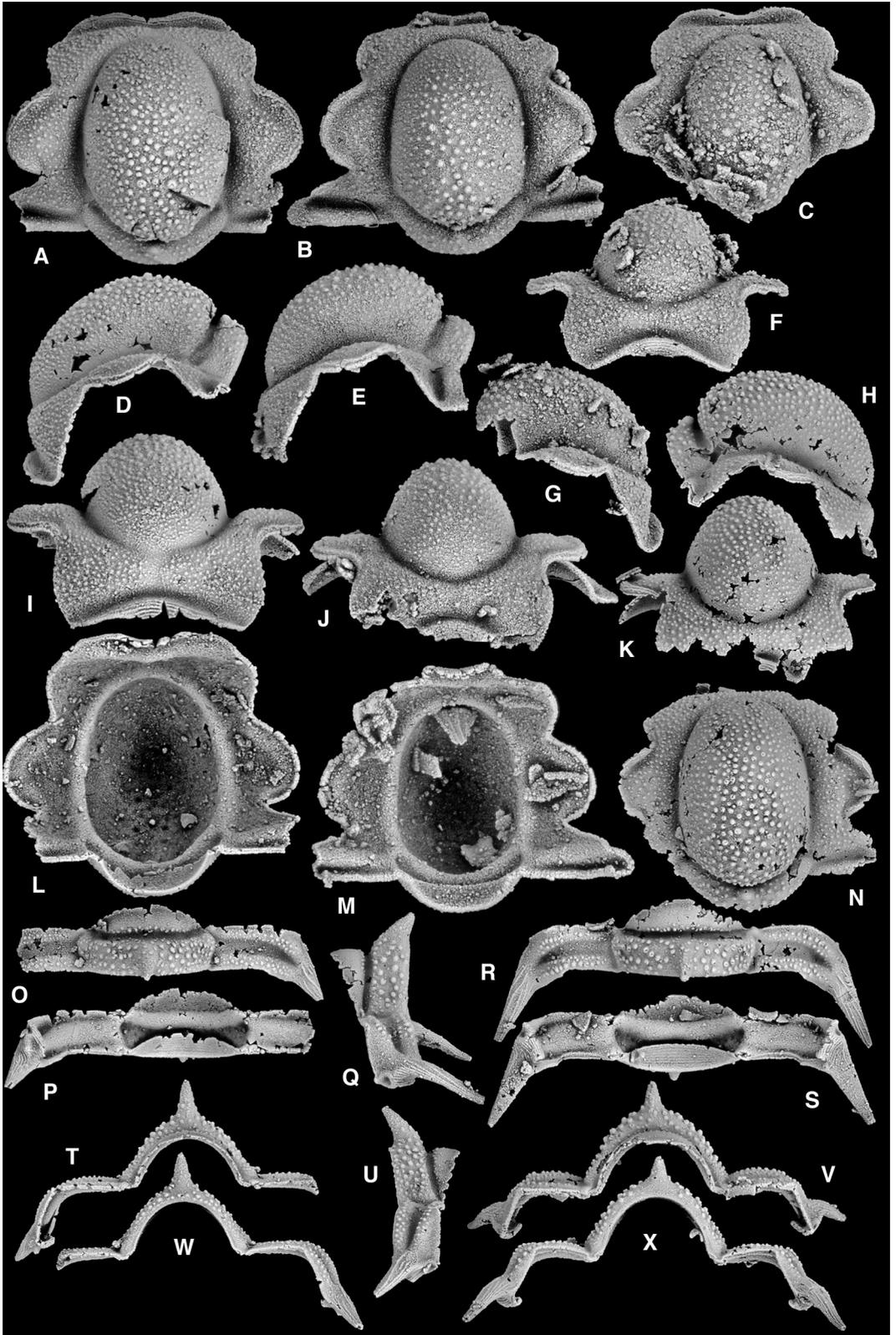
Material. Holotype is a cranidium, YPM 18774 (Ross 1953, pl. 63, figs. 4, 5, 9), exact horizon unknown ("Low zone 'G(2)'" [Ross 1953, p. 641]) but probably Section HC6 189.3 m. Assigned specimens SUI 115172, 128784, 128789, 128790, 128793, 128795, 128797, 128798, 128803, from Section HC6 189.3 m, west side of Hillyard Canyon; SUI 115171, 128779-128783, 128785-128787, 128792, 128799, 128800, from Section HC5 195.7 m, and SUI 128788, 128791, 128794, 128796, 128801, 128802, from Section HC5 203.7-204.2T m, east side of Hillyard Canyon, all Garden City Formation (lower Floian; Tulean; low *Psalikilopsis cuspidicauda* Zone), Bear River Range, Franklin County, southeastern Idaho, USA. Assigned specimens SUI 128886-128896, from Section G 162Tm, southern Confusion Range, and SUI 128804-128820, from Section D 88.9 m, southern House Range, all Fillmore Formation (lower Floian; Tulean; low *P. cuspidicauda* Zone), Ibex area, Tule Valley,

Millard County, western Utah.

Remarks. Ross (1951, p. 63, pl. 13, figs 28, 29, 33, 34, pl. 30, figs 1-3) correctly associated the cranidium, librigena, and pygidium of this species, referring it questionably in open nomenclature to *Psalikilus* Ross, 1951. However, when he later named the species, he was under the impression that the material he then described (Ross 1953, p. 639, pl. 63, figs 2-9, 12) represented a separate species, considering that the differing lengths of the pygidial terminal spine in the two available pygidia ruled out conspecificity. With the large sample sizes from multiple localities and horizons now available, it is clear that the length of the pygidial spine is variable within individual samples (e.g., Fig. 8A vs 8C). Although Ross's specimens represent end-members, they fall within the range of intrasample variation illustrated herein and there is little reason to doubt that they both represent *Psalikilopsis cuspidicauda*.

Psalikilopsis cuspidicauda is extremely similar to the overlying species *P. paracuspidauda*, and there are no obvious differences apart from the pygidia. Pygidia of the species, however, are quite strongly differentiated in several not obviously related features. The first and second axial rings in *P. cuspidicauda* in the type area and at Section D 88.9 m in western Utah always bear a prominent median node, and the third usually does (though it is absent in a single specimen, Fig. 6D). The axial rings of *P. paracuspidauda* universally lack any expression of a median node. The position of the fulcrum in *P. cuspidicauda* is approximately half the distance distally on the pleura. The pleural bands and furrows are generally posterolaterally directed, and deflect only slightly at the fulcrum. In *P. paracuspidauda*, the fulcrum is set far distally and the bands and furrows run nearly transversely to the fulcrum, where they are deflected strongly posteriorly. Finally, the first segment in *P. cuspidicauda* has a prominent posterior spine, smaller than that in *P. redfordi*, but in most specimens clearly expressed (an exception is Fig. 7D). In *P. paracuspidauda* this spine is either reduced to a tiny nubbin (Fig. 18V) or not expressed at all (Fig. 18U).

A sample from Section G 162T m (Fig. 10 J, K, Y) includes pygidia which have the fulcrum set at half distance on the pleura and prominent first segment spines, and seem clearly to represent *P. cuspidicauda*. The axial nodes are only very prominent on one specimen from this sample, however (Fig. 10Y). On the others (Fig. 10J, K), they are plainly discernible but considerably reduced in expression. It is possible that this sample is stratigraphically intermediate



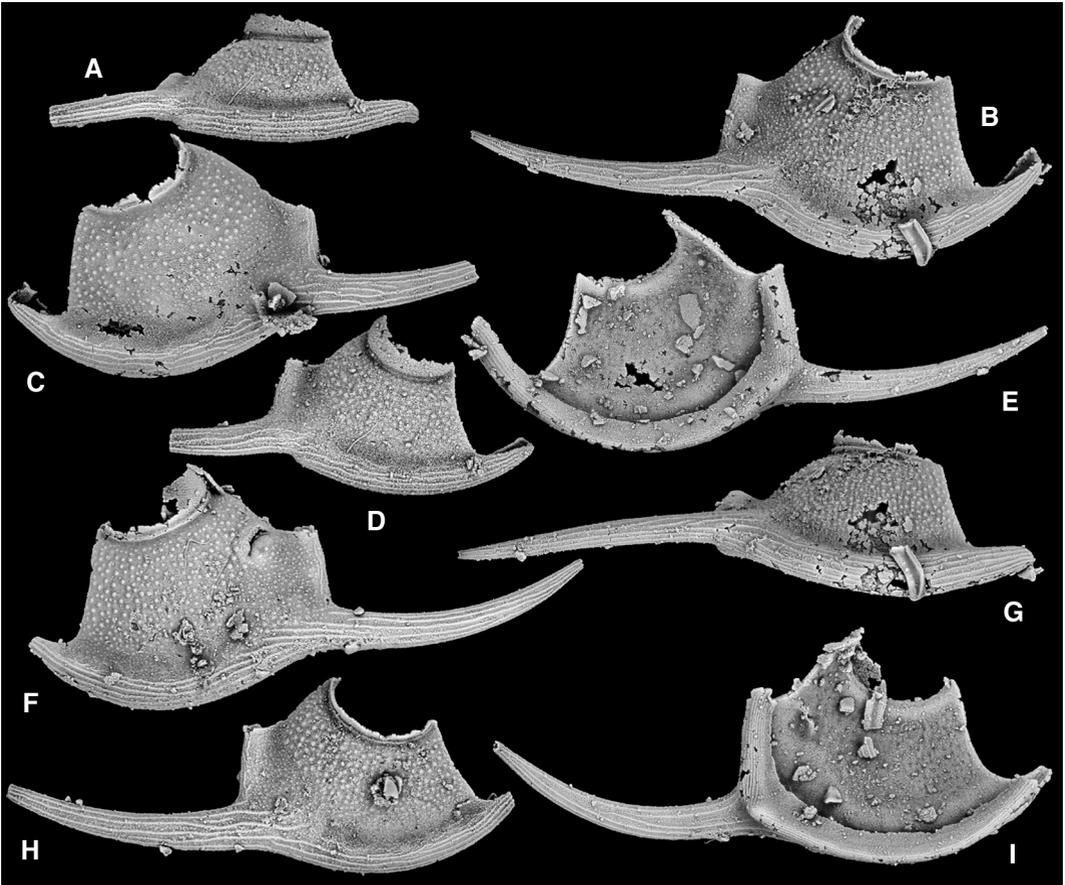
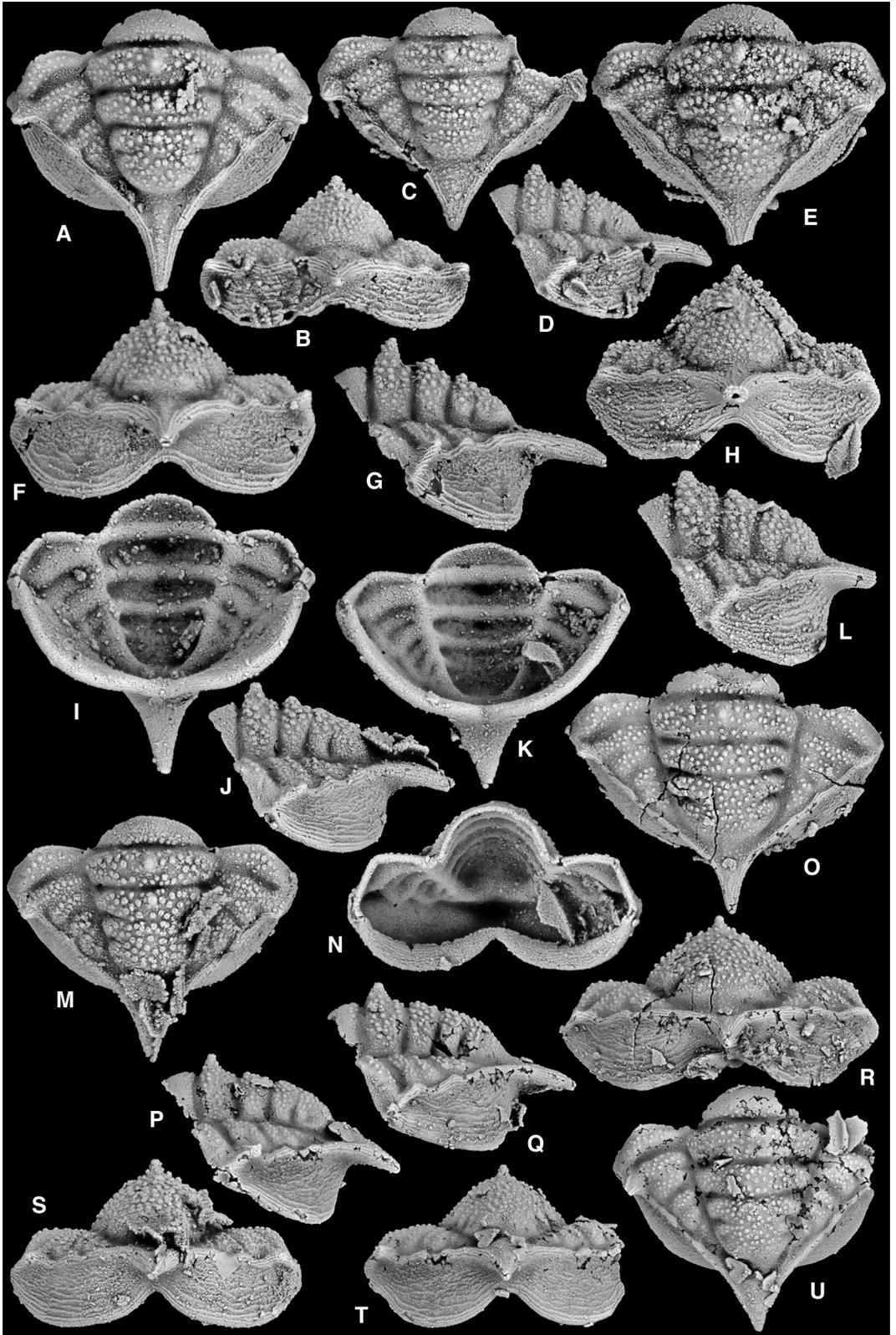


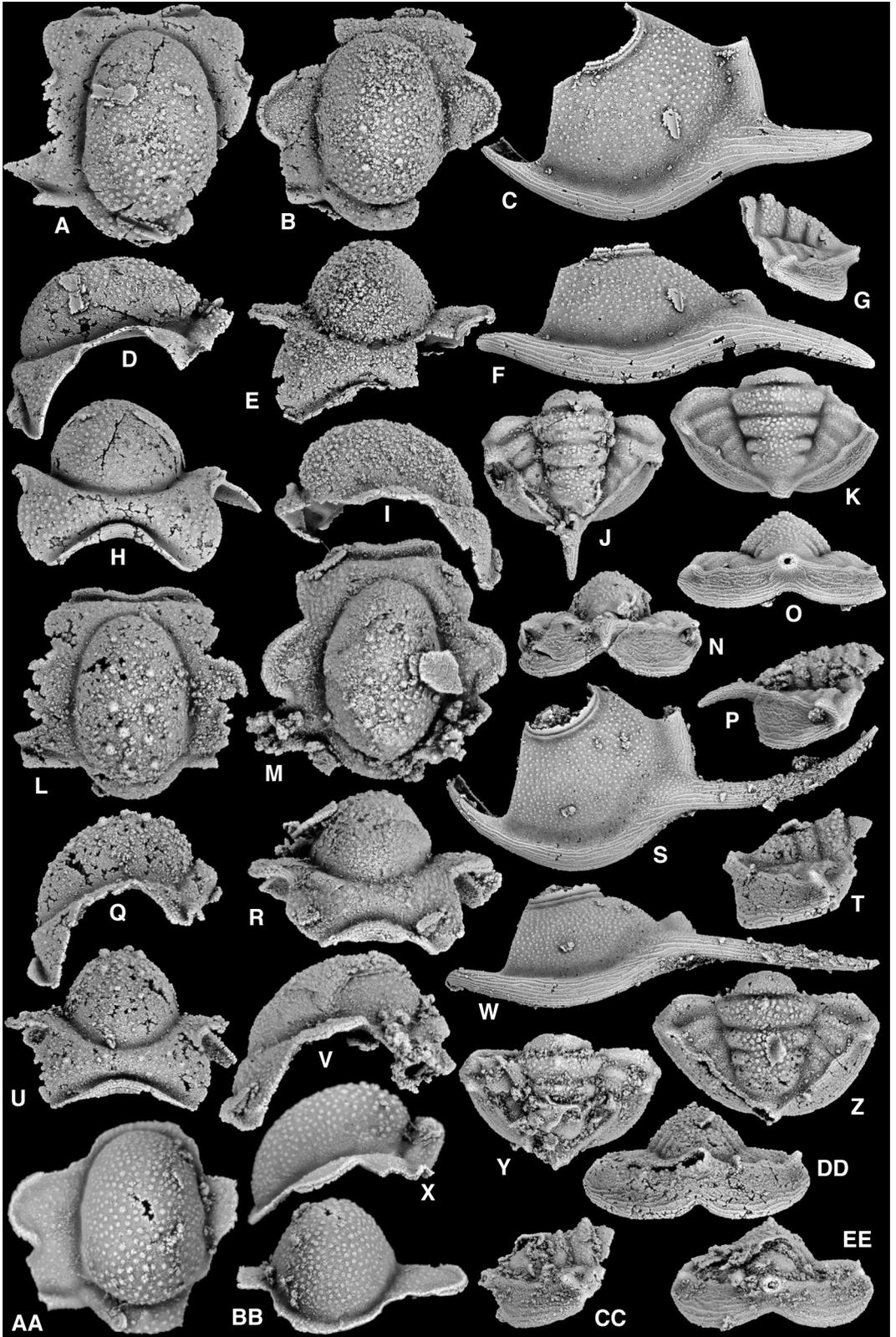
Figure 8. *Psalikelopsis cuspidicauda* Ross, 1953, from section D 88.9 m, Fillmore Formation (early Floian; Tulean; low *Psalikelopsis cuspidicauda* Zone), southern House Range. **A, D**, right librigena, SUI 128810, ventrolateral and external views, x12. **B, E, G**, right librigena, SUI 128811, external, internal, and ventrolateral views, x8. **C**, left librigena, SUI 128812, external view, x9. **F, I**, left librigena, SUI 128813, external and internal views, x9. **H**, right librigena, SUI 128814, external view, x12.

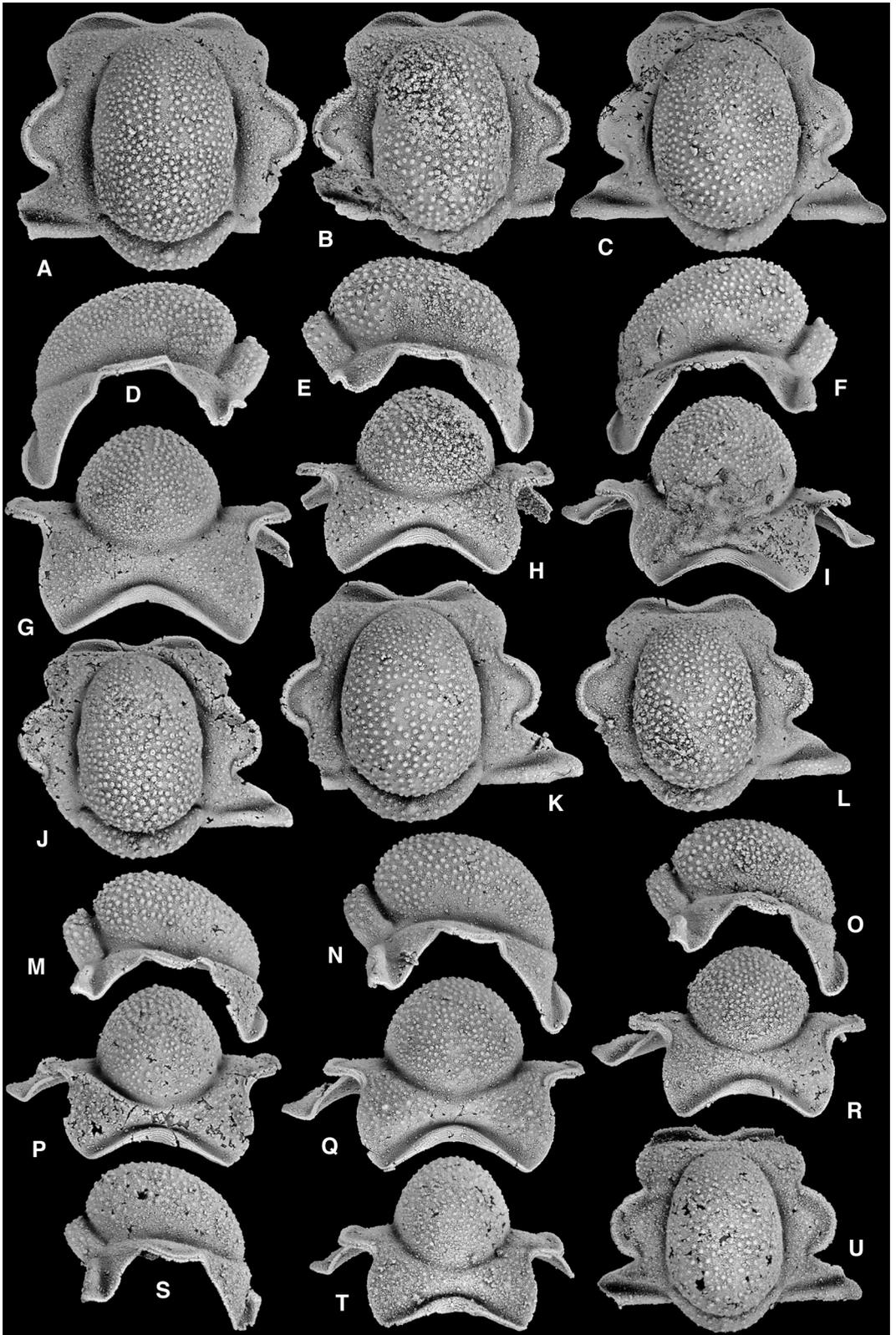
Figure 7 (opposite). *Psalikelopsis cuspidicauda* Ross, 1953, from section D 88.9 m, Fillmore Formation (early Floian; Tulean; low *Psalikelopsis cuspidicauda* Zone), southern House Range. **A, D, I, L**, cranium, SUI 128804, dorsal, left lateral, anterior, and ventral views, x15. **B, E, J, M**, cranium, SUI 128805, dorsal, left lateral, anterior, and ventral views, x15. **C, F, G**, cranium, SUI 128806, dorsal, anterior, and right lateral views, x12. **H, K, N**, cranium, SUI 128807, right lateral, anterior, and dorsal views, x10. **O, P, T, U, W**, thoracic segment, SUI 128808, dorsal, ventral, anterior, right lateral, and posterior views, x10. **Q-S, V, X**, thoracic segment, SUI 128809, left lateral, dorsal, ventral, anterior, and posterior views, x10.

Figure 9 (overleaf). *Psalikelopsis cuspidicauda* Ross, 1953, from section D 88.9 m, Fillmore Formation (early Floian; Tulean; low *Psalikelopsis cuspidicauda* Zone), southern House Range. **A, F, G, I**, pygidium, SUI 128815, dorsal, posterior, left lateral, and ventral views, x15. **B-D**, pygidium, SUI 128816, posterior, dorsal, and left lateral views, x15. **E, H, L**, pygidium, SUI 128817, dorsal, posterior, and left lateral views, x12. **J, K, M, N, S**, pygidium, SUI 128818, left lateral, ventral, dorsal, anterior, and posterior views, x12. **O, Q, R**, pygidium, SUI 128819, dorsal, left lateral, and posterior views, x10. **P, T, U**, pygidium, SUI 128820, left lateral, posterior, and dorsal views, x10.

Figure 10 (page 383). *Psalikelopsis cuspidicauda* Ross, 1953, from Section G 155.6-162T m, Fillmore Formation (lower Floian; Tulean; low *Psalikelopsis cuspidicauda* Zone), southern Confusion Range. **A, D, H**, cranium, SUI 128886, dorsal, left lateral, and anterior views, x7.5 (G 155.6 m). **B, E, I**, cranium, SUI 128887, dorsal, anterior, and right lateral views, x10 (G 155.6 m). **C, F**, left librigena, SUI 128888, external and ventrolateral views, x7.5 (G 162T m). **G, K, O**, pygidium, SUI 128889, left lateral, dorsal, and posterior views, x10 (G 162T m). **J, N, P**, pygidium, SUI 128890, dorsal, posterior, and right lateral views, x10 (G 162T m). **L, Q, U**, cranium, SUI 128891, dorsal, left lateral, and anterior views, x12 (G 155.6 m). **M, R, V**, cranium, SUI 128892, dorsal, anterior, and left lateral views, x15 (G 155.6 m). **S, W**, left librigena, SUI 128893, external and ventrolateral views, x7.5 (G 162T m). **T, Z, DD**, pygidium, SUI 128894, right lateral, dorsal, and posterior views, x10 (G 155.6 m). **X, AA, BB**, cranium, SUI 128895, left lateral, dorsal, and anterior views, x12 (G 162T m). **Y, CC, EE**, pygidium, SUI 128896, dorsal, right lateral, and posterior views, x10 (G 162T m).







between the samples from other sections with large, prominent, tubercles, and samples of the overlying *P. paracuspidauda*, and that the pygidia are in morphological transition to loss of the nodes. However, lower and higher samples of *Psalikilopsis* have not been found at Section G, nor have pygidia with these variably expressed nodes been found in other sections.

***Psalikilopsis paracuspidauda* sp. nov.** (Figs 1E, F, 11-19)

Diagnosis. Pygidium with fulcrum set far distally; pygidial axial rings lacking prominent median nodes; posterior pleural spine on first pygidial segment reduced to small node or not expressed.

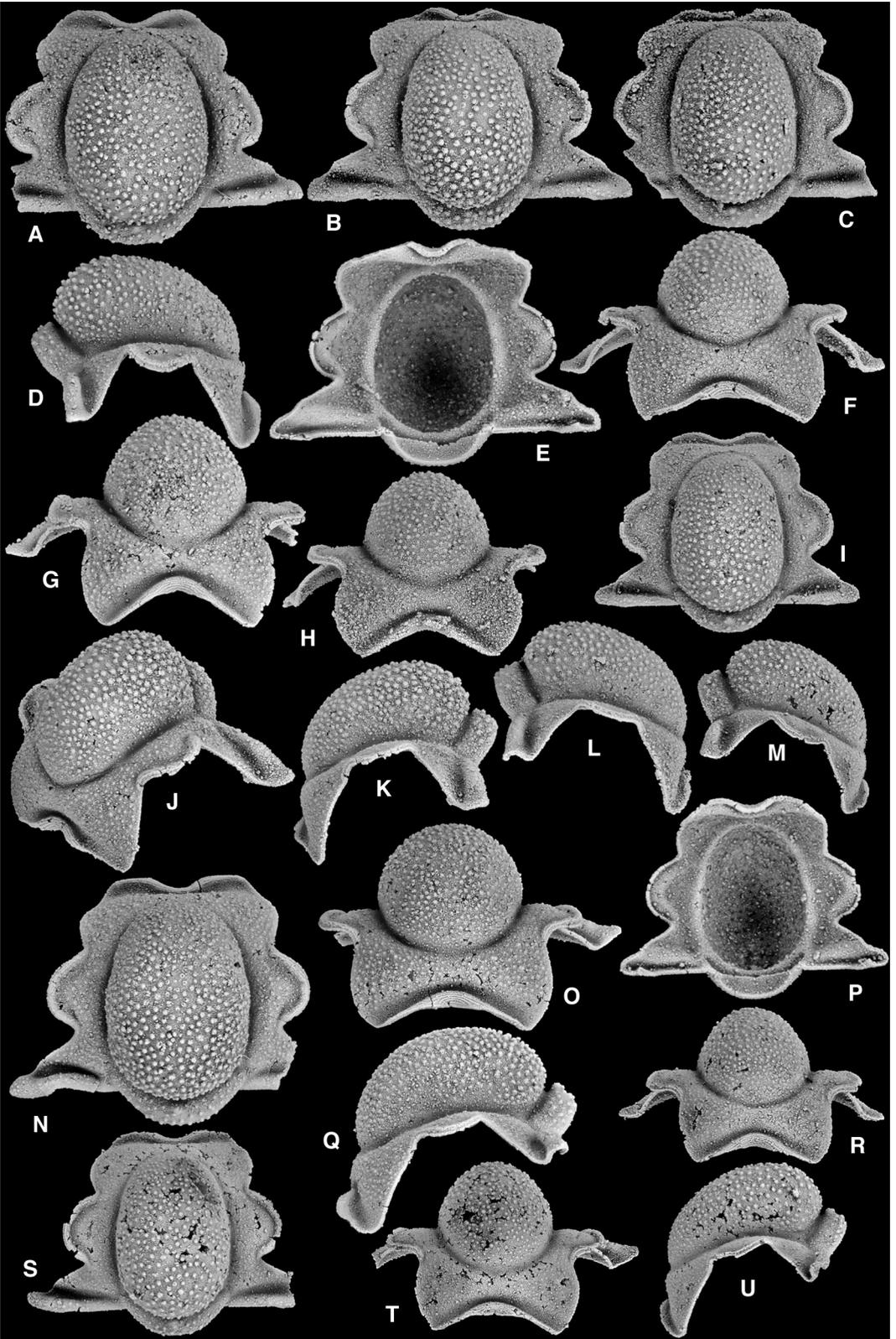
Description. Cranial measurements were made on the largest and most intact specimens (Figs 11A, C, K, L, U, 12A, B, I, N, S, 13J, 14A, C, H). For measurement of the distance across the posterior projections, where the projection was preserved only on one side, the distance to the sagittal line from this side was doubled. Cranium strongly vaulted and convex; sculpture of densely distributed, moderately sized tubercles on LO and glabella, tubercles finer on anterior part of glabella; sculpture of much finer tubercles on preglabellar field, frontal area, interocular fixigena, and posterior fixigena; maximum cranial width across posterior projections 146.0% (137.2-154.1) sagittal length; width across midlength of palpebral lobes 114.7% (111.3-117.3) sagittal length; anterior border about as long (exsag.) abaxially as LO, in lateral

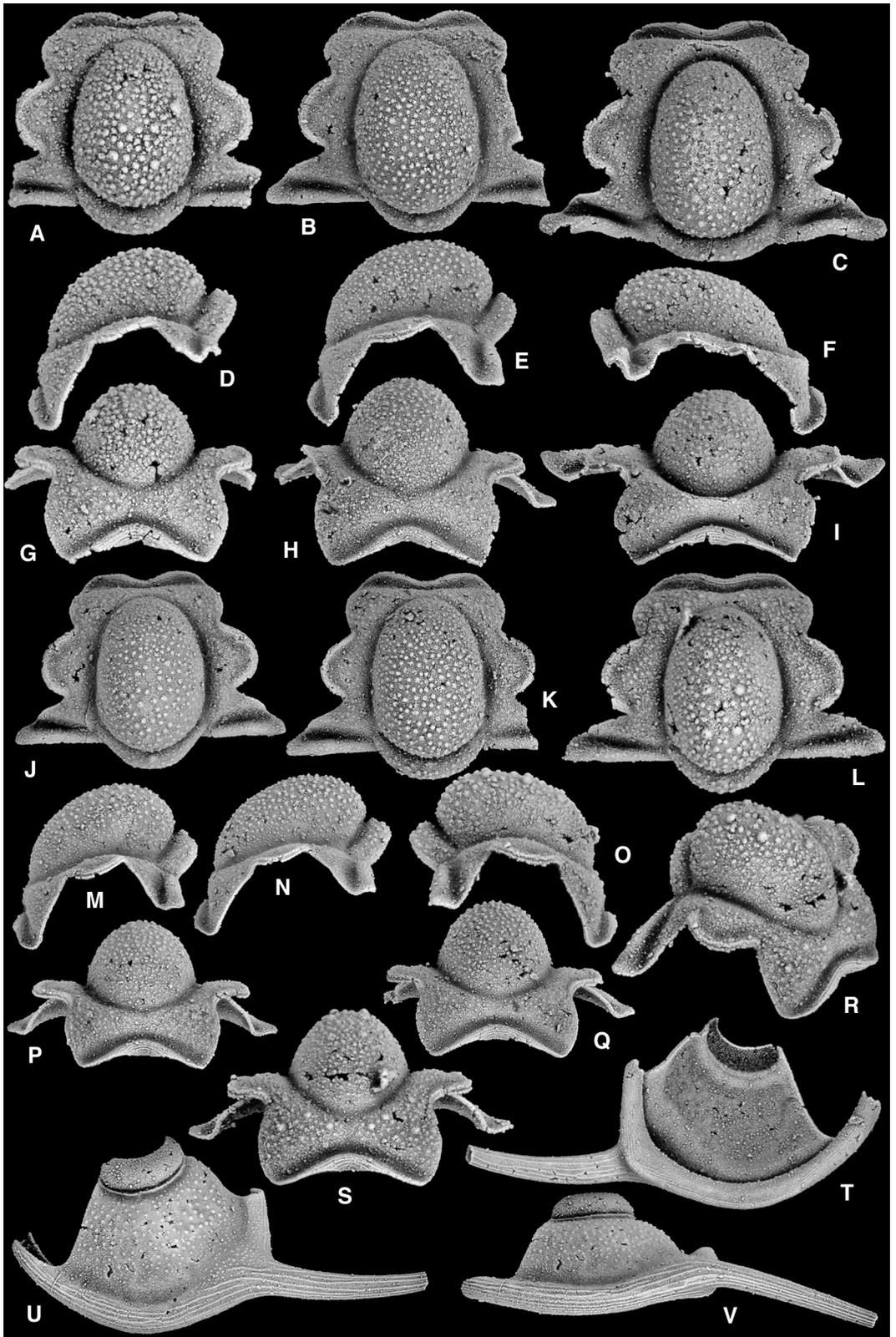
regions border is formed of short, inflated rim with one or two raised lines on forward face; anterior border furrow is long, dorsally concave, and shallow in lateral areas, with gradational slope to rear of border anteriorly and sharper and more distinct break to frontal areas and preglabellar field posteriorly; anterior border transversely dorsally arched in transverse profile, more strongly bowed medially; anterior border is bowed strongly posteriorly medially, to crowd out border furrow and abut medial part of preglabellar field; this medial bow creates a taller anterior face on which is set eight or nine fine raised lines set more or less subparallel to dorsal margin; anterior sections of facial sutures laterally convex opposite anterior border, laterally concave opposite rear of anterior border furrow, and strongly laterally bowed opposite frontal areas, width across maximum point of divergence (β) 85.1% (78.8-90.2) cranial sagittal length; frontal areas moderately inflated, sloped strongly downward from interocular fixigena and mostly facing obliquely anterolaterally; preglabellar field strongly inflated in sagittal profile, forming distinct bulge which overhangs medially withdrawn area of anterior border and anterior border furrow; palpebral lobes moderately large, distance across γ 80.5% (77.7-85.0) cranial sagittal length, distance across ϵ 92.0% (87.4-96.6) cranial sagittal length; lobe strongly but unevenly laterally bowed, anterior curve shallower than posterior curve, so lobe slung slightly posteriorly; lobe with strong, narrow, inflated border around margin with sculpture of several raised lines set subparallel to margin; shallow, narrow, but

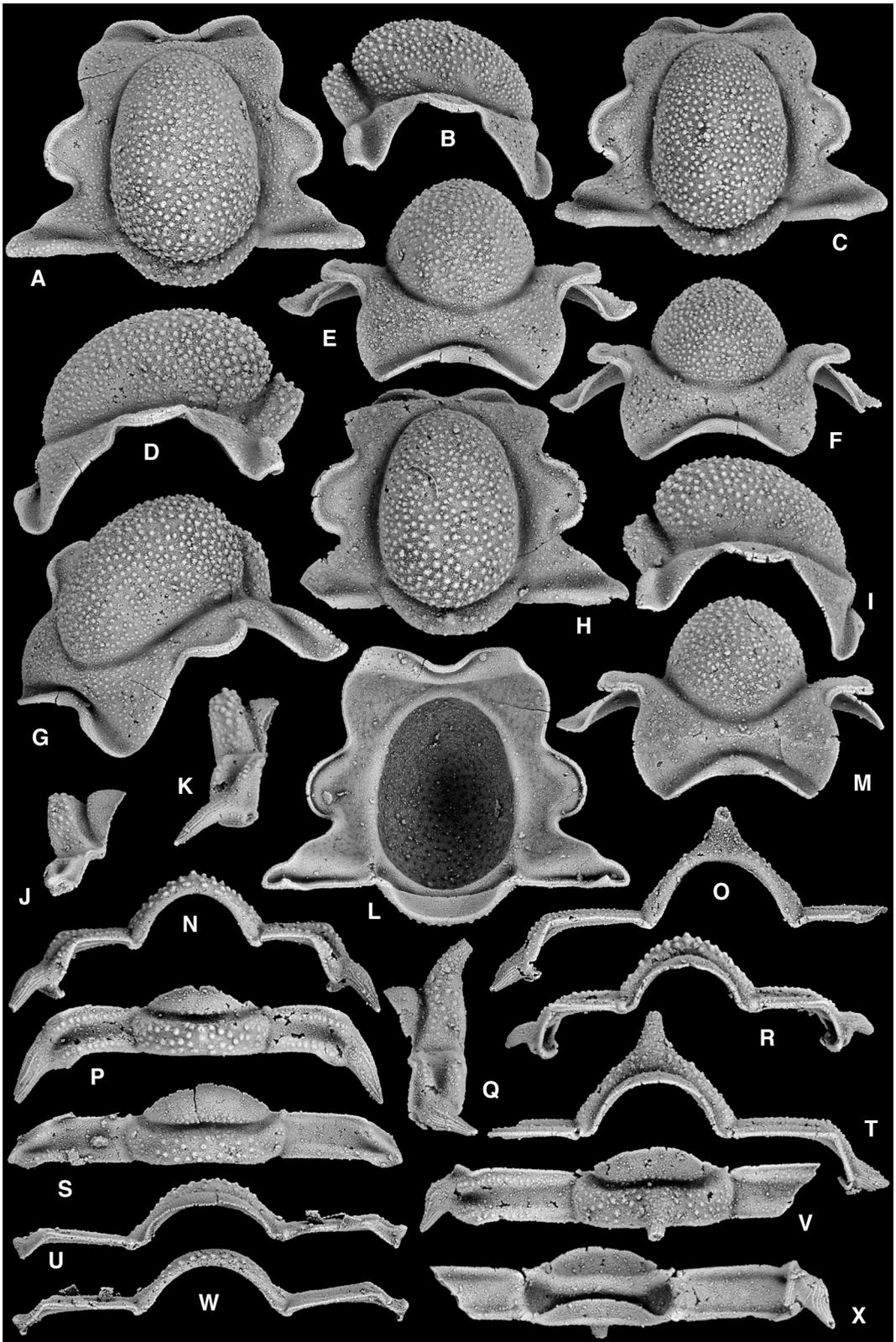
Figure 11 (opposite). *Psalikilopsis paracuspidauda* sp. nov., from Section D 106.4 m, Fillmore Formation (lower Floian; Tulean; high *Psalikilopsis cuspidicauda* Zone), southern House Range, Ibex area, Millard County, western Utah, USA. **A, D, G,** cranium, SUI 128821, dorsal, left lateral, and anterior views, x8. **B, E, H,** cranium, SUI 128822, dorsal, right lateral, and anterior views, x9. **C, F, I,** cranium, SUI 128823, dorsal, left lateral, and anterior views, x8. **J, M, P,** cranium, SUI 128824, dorsal, right lateral, and anterior views, x9. **K, N, Q,** cranium, SUI 128825, dorsal, right lateral, and anterior views, x9. **L, O, R,** cranium, SUI 128826, dorsal, right lateral, and anterior views, x8. **S-U,** cranium, SUI 128827, right lateral, anterior, and dorsal views, x12.

Figure 12 (overleaf). *Psalikilopsis paracuspidauda* sp. nov., from Section D 106.4 m, Fillmore Formation (lower Floian; Tulean; high *Psalikilopsis cuspidicauda* Zone), southern House Range, Ibex area, Millard County, western Utah, USA. All magnifications are x10. **A, D, G,** cranium, SUI 128828, dorsal, right lateral, and anterior views. **B, E, F, J, K,** cranium, SUI 128829, dorsal, ventral, anterior, oblique, and left lateral views. **C, H, L,** cranium, SUI 128830, dorsal, anterior, and right lateral views. **I, M, P, R,** cranium, SUI 128831, dorsal, right lateral, ventral, and anterior views. **N, O, Q,** cranium, SUI 128832, dorsal, anterior, and left lateral views. **S-U,** cranium, SUI 128833, dorsal, anterior, and left lateral views.

Figure 13 (page 387). *Psalikilopsis paracuspidauda* sp. nov., from Section D 106.4 m, Fillmore Formation (lower Floian; Tulean; high *Psalikilopsis cuspidicauda* Zone), southern House Range, Ibex area, Millard County, western Utah, USA. **A, D, G,** cranium, SUI 128834, dorsal, left lateral, and anterior views, x15. **G, E, H,** cranium, SUI 128835, dorsal, left lateral, and anterior views, x12. **C, F, I,** cranium, SUI 128836, dorsal, right lateral, and anterior views, x12. **J, M, P,** cranium, SUI 128837, dorsal, left lateral, and anterior views, x12. **K, N, Q,** cranium, SUI 128838, dorsal, left lateral, and anterior views, x10. **L, O, R, S,** cranium, SUI 128839, dorsal, right lateral, oblique, and anterior views, x15. **T-V,** left librigena, SUI 128840, internal, external, and ventrolateral views, x9.







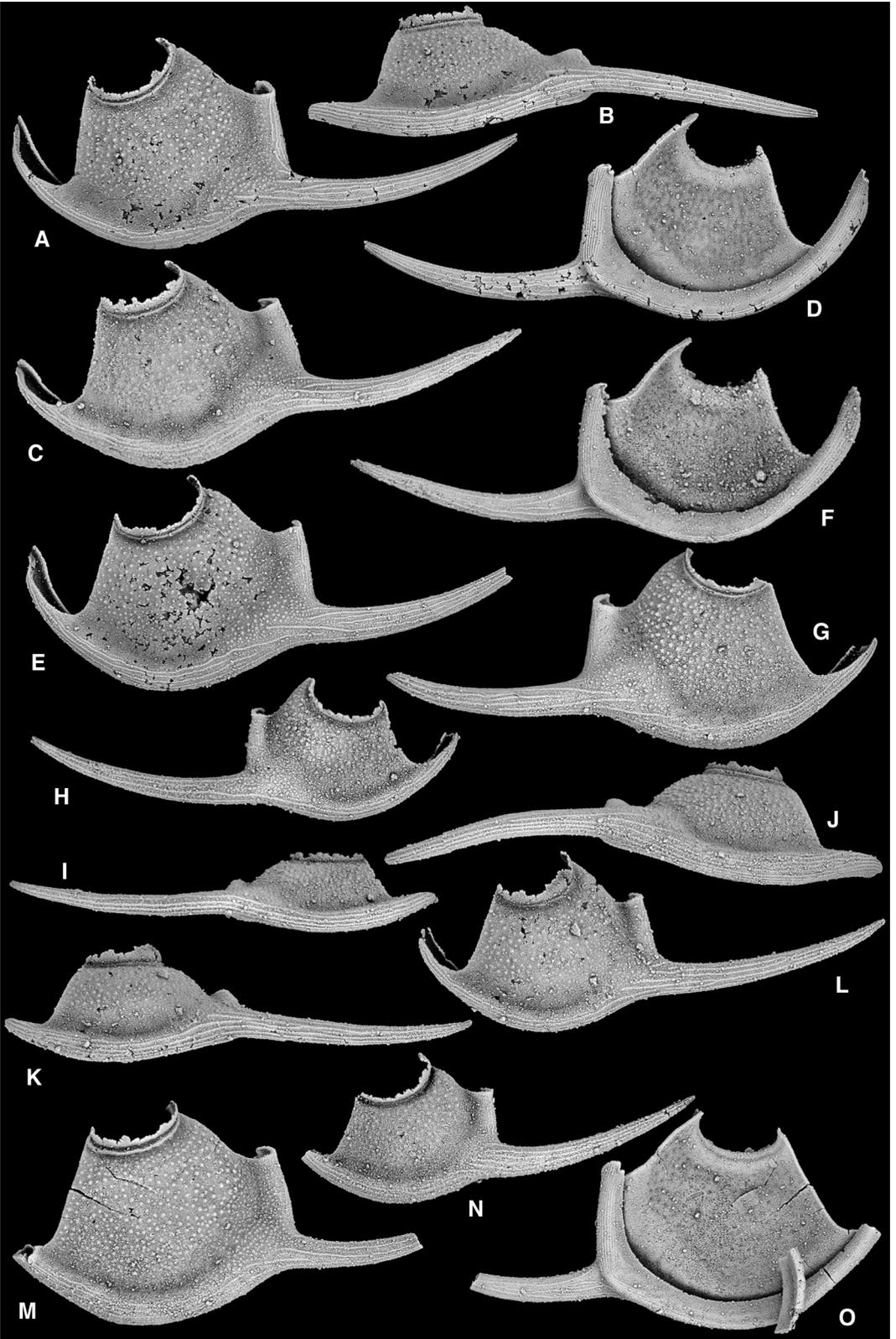
distinct palpebral lobe running inside inflated rim, deeper and slightly narrower opposite anterior and posterior edges of lobe; interocular fixigena held nearly horizontal, with very slight dorsal inflation, sloping slightly toward palpebral furrow and axial furrow in transverse profile; eye ridge very faintly expressed dorsally, indiscernible in some specimens, running obliquely from anterior of palpebral lobe forward to L3, faint anterior bounding furrow usually clearly visible ventrally (e.g., Fig. 14L); posterior fixigena slightly more inflated than frontal area, sloped down toward posterior border furrow; posterior section of facial suture with significant anterolateral bow, so posterior fixigena extended laterally; posterior border furrow quite long (exsag.) and shallow, lengthened abaxially, with nearly gradational contact anteriorly with posterior facial suture and sharper contact posteriorly with posterior border, deepest posteriorly at fulcrum; posterior border dorsally inflated, quite short (exsag.) proximally, lengthened distally, forming laterally sharp, relatively short (exsag.), only partially lobate distal tip; entire border with crowded fine tubercles, slightly larger than and more densely distributed than those on adjacent posterior fixigena; posterior margin of posterior border transversely straight to fulcrum, projected posteriorly at fulcrum in shallow triangle, directed anterolaterally distal to fulcrum; glabella with maximum width across anterior part of L1 71.8% (63.8-75.9) sagittal length excluding LO; glabella broadly oviform in plan view, sagittal length (excluding LO) 84.5% (82.5-91.3) that of cranidium, tall, strongly dorsally inflated, rising high above fixigena in sagittal profile; sagittal

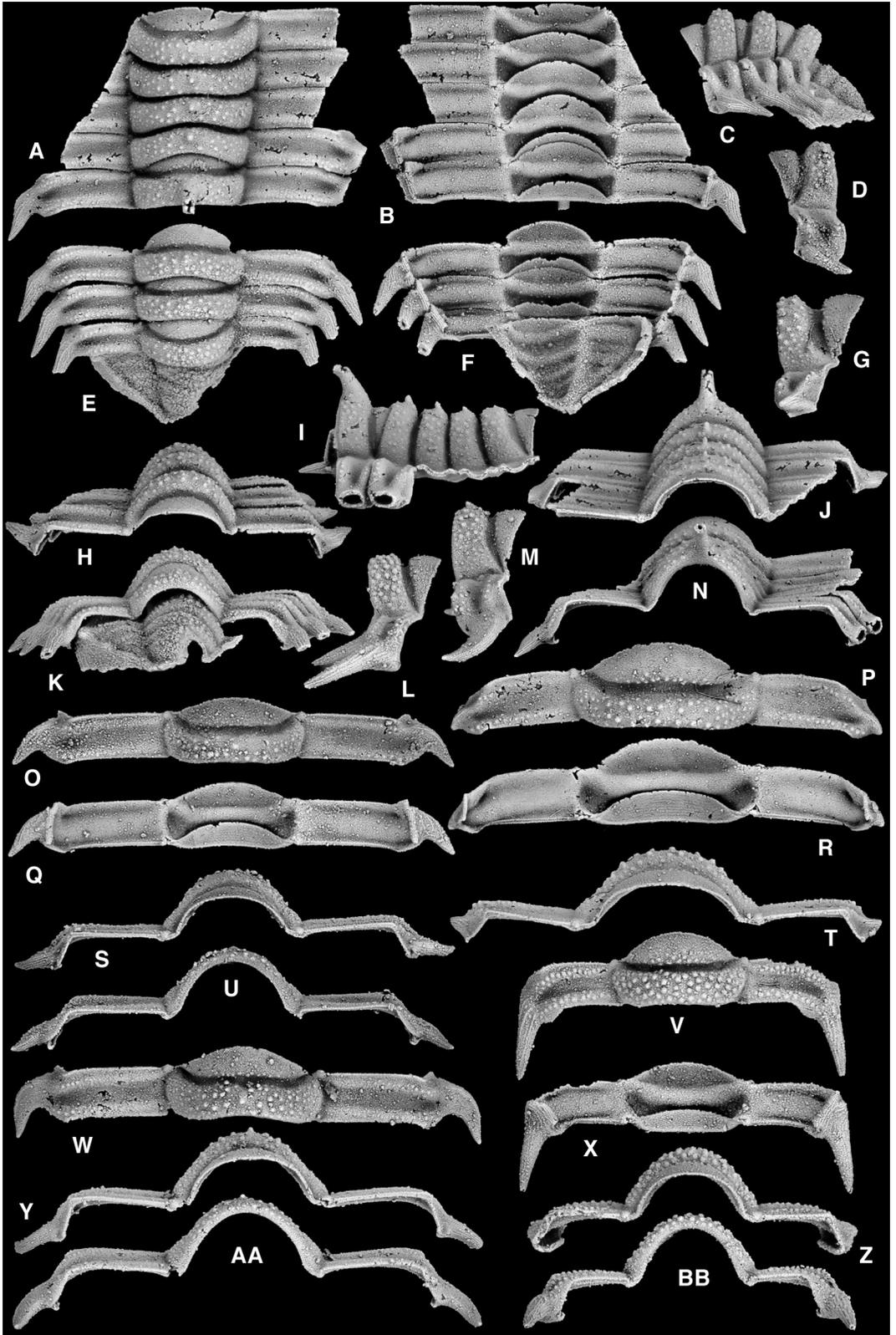
profile strongly curved, curve tighter posteriorly than anteriorly, so that slight hump is formed in front of SO; axial furrows very narrow, faintly impressed and laterally bowed around LO, width across posterior contact of furrows with posterior margin 53.5% (50.3-58.1) cranidial sagittal length; axial furrows laterally confluent with posterior border furrow; axial furrows much deeper in front of LO and around main portion of glabella, wider in middle part of course opposite palpebral lobes, narrower anteriorly, running without obvious distinction or change in course into preglabellar furrow; preglabellar furrow slightly shallower medially (best seen in anterior view); S1 and S2 visible in lateral view in most specimens (see especially Fig. 14B) as oblique, posteriorly swept smooth areas; L1 and L2 not prominent, but each with distinct independent inflation, seen dorsally as slight lateral bulges in the lateral margin of glabella; L3 with very slight independent inflation, not visible in all specimens; uniformly strong tubercles on dorsal part of glabella give way to much finer tubercles on lower, lateral-facing parts along axial and preglabellar furrows; LO short, sagittal length 10.0% (8.1-11.8) that of cranidium, longer sagittally than exsagittally, strongly posteriorly bowed, with sculpture of scattered prominent tubercles slightly smaller and more sparsely distributed than those on main glabella; median node prominent, set anteriorly near anterior margin; SO deep, anterior edge with sharp contact with rear of main glabella, posterior edge with sharp but slightly more gradational contact with LO, bowed posteriorly slightly less than posterior margin of LO, joining axial furrow in smooth

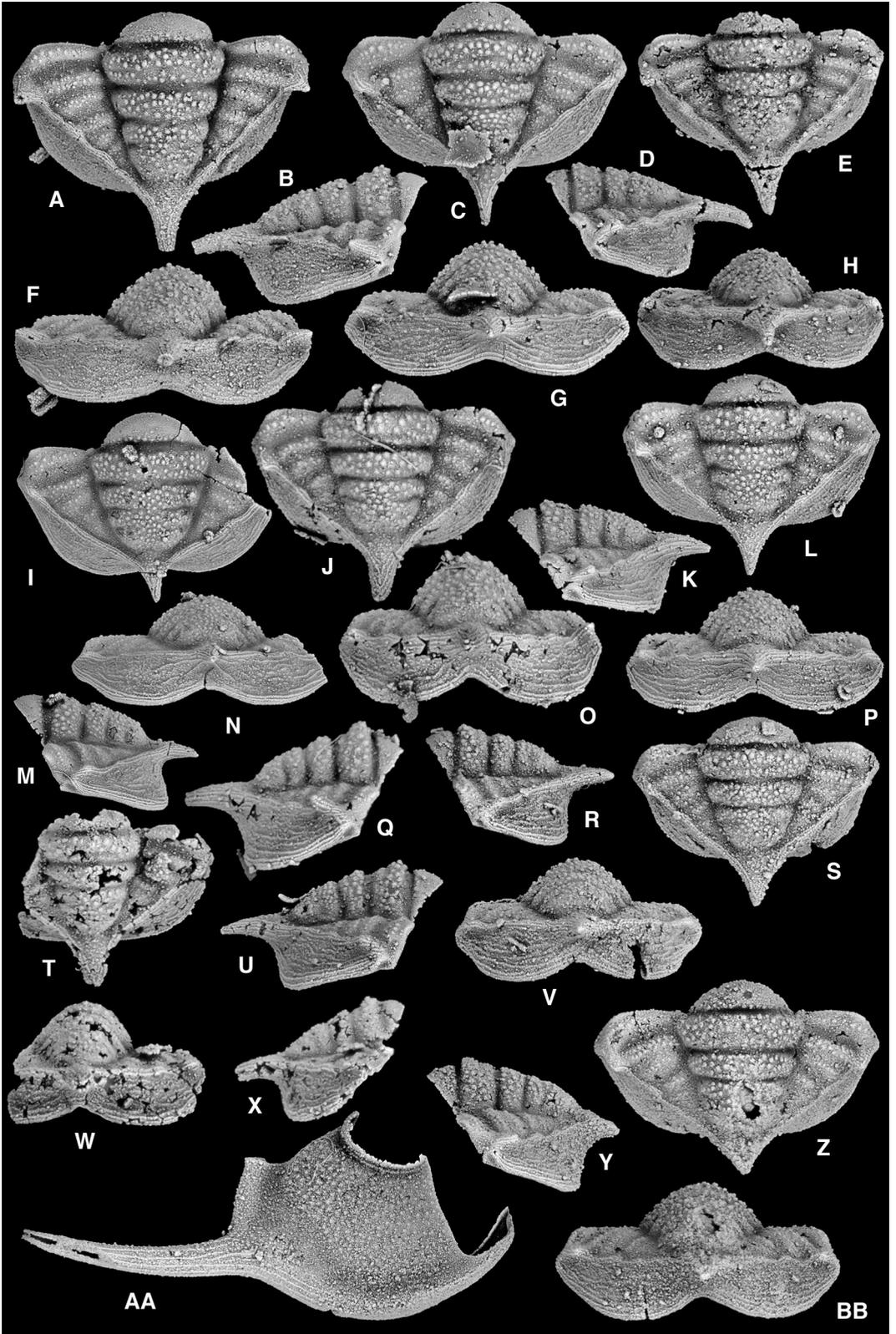
Figure 14 (opposite). *Psalikelopsis paracuspidauda* sp. nov., from Section D 106.4 m, Fillmore Formation (lower Floian; Tulean; high *Psalikelopsis cuspidicauda* Zone), southern House Range, Ibex area, Millard County, western Utah, USA. **A, D, E, G, L**, cranidium, SUI 128841, dorsal, left lateral, anterior, oblique, and ventral views, x8. **B, C, F**, cranidium, SUI 128842, right lateral, dorsal, and anterior views, x8. **H, I, M**, cranidium, SUI 128843, dorsal, right lateral, and anterior views, x10. **J, S, U, W**, thoracic segment, SUI 128844, right lateral, dorsal, anterior, and posterior views, x10. **K, N, P, R**, thoracic segment, SUI 128845, right lateral, posterior, dorsal, and anterior views, x12. **O, Q, T, V, X**, thoracic segment, SUI 128846, posterior, left lateral, anterior, dorsal, and ventral views, x10.

Figure 15 (overleaf). *Psalikelopsis paracuspidauda* sp. nov., from Section D 106.4 m, Fillmore Formation (lower Floian; Tulean; high *Psalikelopsis cuspidicauda* Zone), southern House Range, Ibex area, Millard County, western Utah, USA. **A, B, D**, left librigena, SUI 128847, external, ventrolateral, and internal views, x9. **C, F**, left librigena, SUI 128848, external and internal views, x10. **E**, left librigena, SUI 128849, external view, x9. **G, J**, right librigena, SUI 128850, external and ventrolateral views, x9. **H, I**, right librigena, SUI 128851, external and ventrolateral views, x12. **K, L**, left librigena, SUI 128852, ventrolateral and external views, x10. **M, O**, left librigena, SUI 128853, external and internal views, x8. **N**, left librigena, SUI 128854, external view, x12.

Figure 16 (page 391). *Psalikelopsis paracuspidauda* sp. nov., from Section D 106.4 m, Fillmore Formation (lower Floian; Tulean; *Psalikelopsis cuspidicauda* Zone), southern House Range, Ibex area, Millard County, western Utah, USA. All magnifications are x10. **A, B, I, J, N**, thoracic segments, SUI 128855, dorsal, ventral, right lateral, anterior, and posterior views. **C, E, F, H, K**, thoracic segments and pygidium, SUI 128856, left lateral, dorsal, ventral, anterior, and posterior views. **D, O, Q, S, U**, thoracic segment, SUI 128857, left lateral, dorsal, ventral, anterior, and posterior views. **G, P, R, T**, thoracic segment, SUI 128858, right lateral, dorsal, ventral, and anterior views. **L, V, X, Z, BB**, thoracic segment, SUI 128859, right lateral, dorsal, ventral, anterior, and posterior views. **M, W, Y, ZZ**, thoracic segment, SUI 128860, right lateral, dorsal, anterior, and posterior views.







curve so that it resembles confluent continuation of axial furrow, which is much shallower to the rear of this contact; doublure of broad, crescentic articulating surface underlying LO, with sculpture of fine, closely spaced raised lines set mainly transversely; lateral rear corners of LO with small ventrally directed processes; rear margin of posterior border with ventral transverse groove to receive anterior edge of first thoracic segment; small triangle of doublure distal to fulcrum; fossulae not expressed.

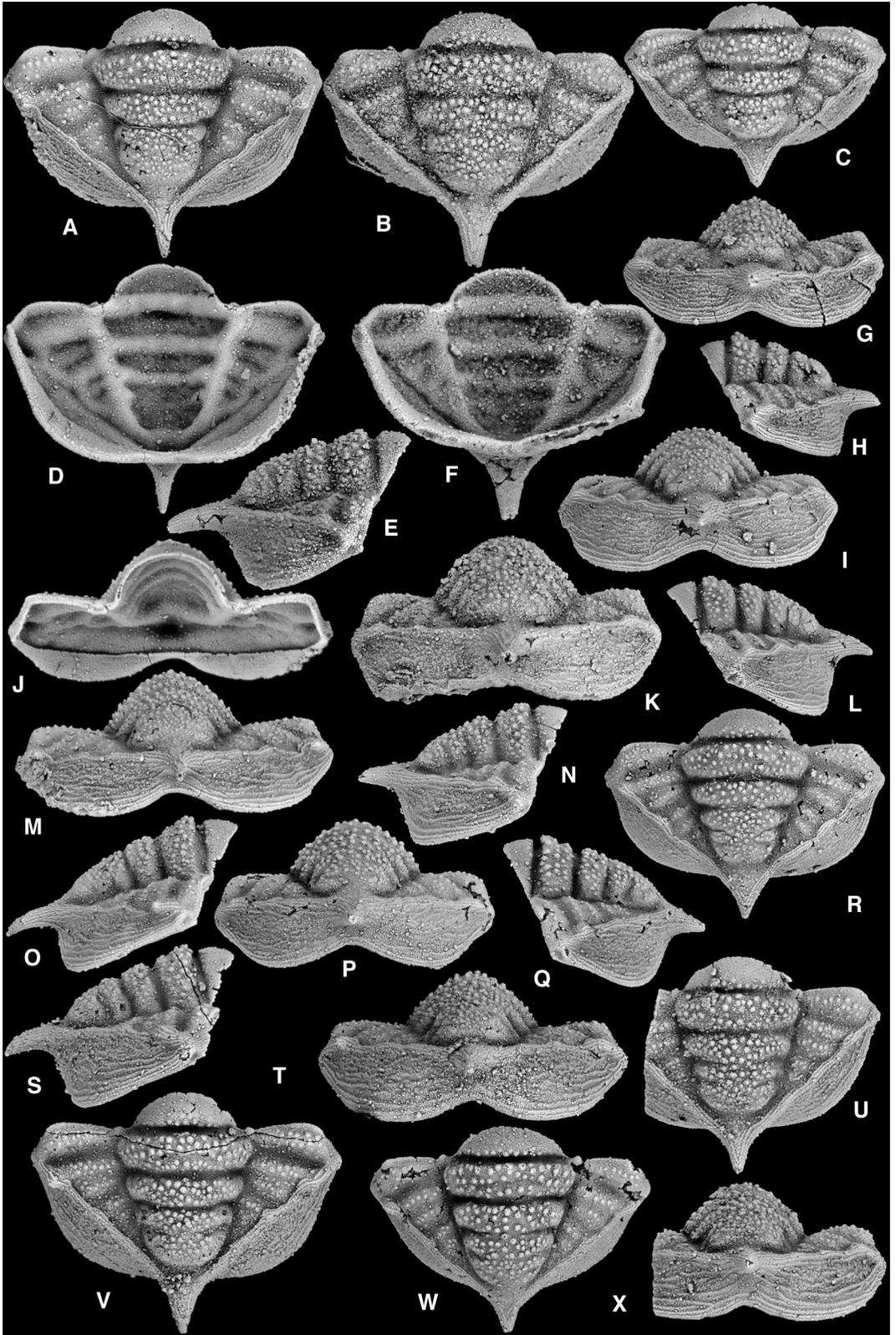
Librigenal measurements were made on the two largest, nearly intact specimens (Fig. 15A, C). Main body of librigena (excluding anterior projection and genal spine) with maximum width behind eye 86.5% (83.8-89.2) exsagittal length; main body with exsagittal length 46.2% (45.3-47.1) total librigenal length (from tip of anterior projection to tip of genal spine); anterior section of facial suture with length 42.9% (41.6-44.2) exsagittal length of main body and posterior section of facial suture with length 39.2% (35.5-42.8) exsagittal length of main body; anterior section with slight anterior bow opposite field, curved strongly across lateral border; posterior section slightly sinuous, with posterior bow proximally and slight anterior bow distally, curved only gently across posterior border; visual surface rarely preserved, but long, relatively narrow, and bulbous, bounded by narrow furrow separating very narrow, ridge-like socle; socle separated from field by shallow furrow; field with background faint caecal sculpture, including radiating structures aligned approximately

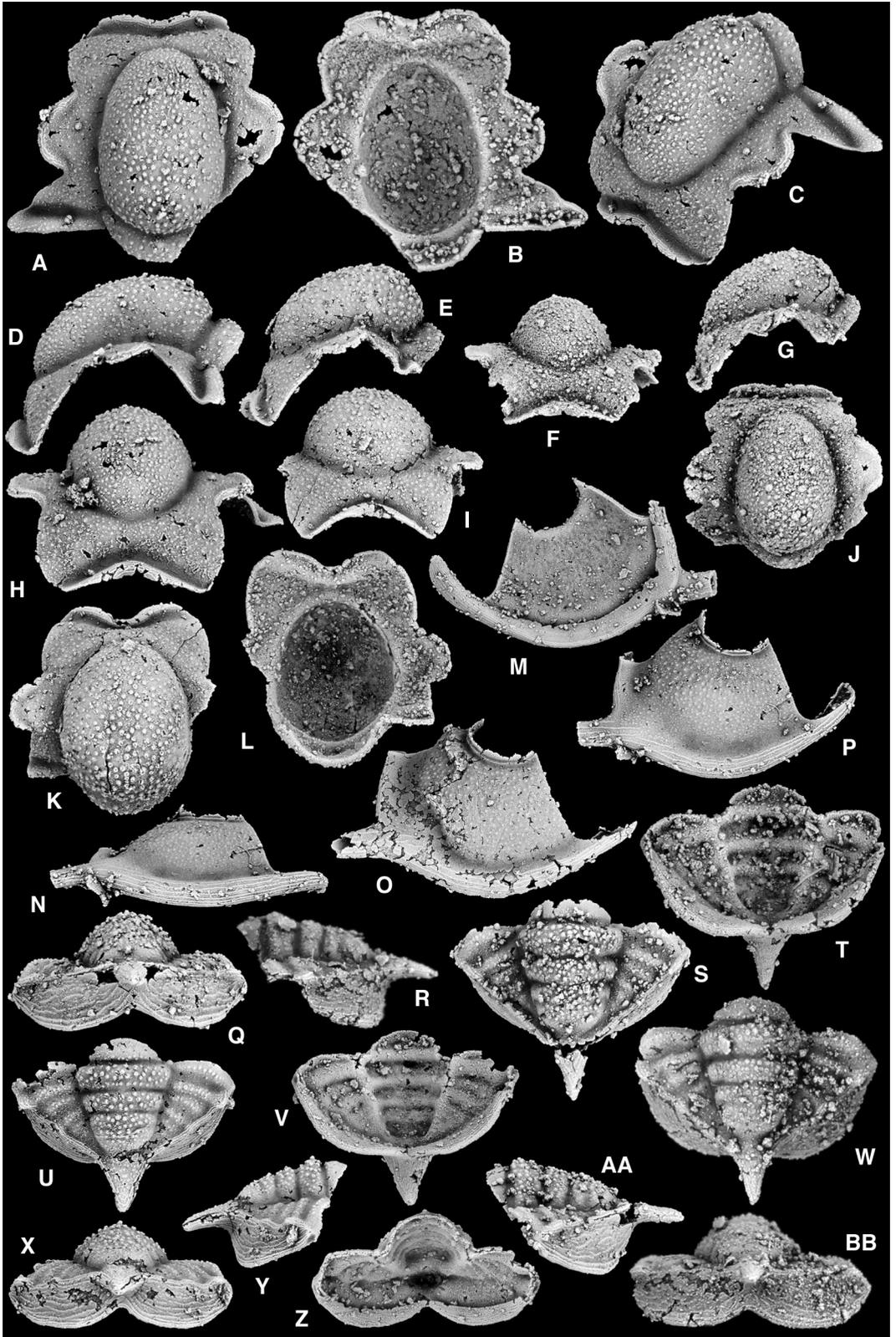
transversely, and faint pits; sculpture of fine to moderate tubercles of medium density, subdued in some specimens (e.g., Fig. 15C) set atop caecal sculpture; lateral border furrow very broad and shallow, expressed mainly as concave region lacking tubercles; posterior border slightly narrower than lateral border but otherwise similar; lateral border with lateral margin strongly but not evenly arcuate, curve strongest at midlength; border semicylindrical in section, moderately inflated, wider posteriorly than anteriorly, with sculpture of prominent raised lines running subparallel with margin, more closely spaced and linear anteriorly, more widely spaced and irregular posteriorly, lines finer and more closely spaced on lateral and ventrolateral aspects of border; posterior border with raised line sculpture similar to anterior part of lateral border; genal spine long, length 44.4% (43.2-45.5) total librigenal length, curved, subcylindrical in section, tapered evenly to sharp distal point, with sculpture of raised lines running down length of spine on all aspects, more closely spaced ventrolaterally than dorsally or ventrally, ventrolateral lines contiguous with those on lateral border, a few ventromedial lines contiguous with those on posterior aspect of posterior border; area in front of base of genal spine (confluence of lateral and posterior borders) somewhat swollen, with independent sculpture of fine tubercles distinct from that on field; anterior projection with length 14.5% (12.9-16.0) librigenal length, raised lines contiguous from lateral border on anterior aspect; doublure flat posteriorly, differentiated into

Figure 17 (opposite). *Psalikilopsis paracuspida* sp. nov., from Section D 106.4 m, Fillmore Formation (lower Floian; Tulean; high *Psalikilopsis cuspidicauda* Zone), southern House Range, Ibex area, Millard County, western Utah, USA. **A, B, F**, pygidium, SUI 128861, dorsal, right lateral, and posterior views, x10. **C, G, U**, pygidium, SUI 128862, dorsal, posterior, and right lateral views, x12. **D, E, H**, pygidium, SUI 128863, left lateral, dorsal, and posterior views, x12. **I, M, N**, pygidium, SUI 128864, dorsal, left lateral, and posterior views, x10. **J, O, Q**, pygidium, SUI 128865, dorsal, posterior, and right lateral views, x17. **K, L, P**, pygidium, SUI 128866, left lateral, dorsal, and posterior views, x12. **R, S, V**, pygidium, SUI 128867, left lateral, dorsal, and posterior views, x12. **T, W, X**, pygidium, SUI 128868, dorsal, posterior, and right lateral views, x17. **Y, Z, BB**, pygidium, SUI 128869, left lateral, dorsal, and posterior views, x12. **AA**, right librigena, SUI 128870, external view, x10.

Figure 18 (overleaf). *Psalikilopsis paracuspida* sp. nov., from Section D 106.4 m, Fillmore Formation (lower Floian; Tulean; high *Psalikilopsis cuspidicauda* Zone), southern House Range, Ibex area, Millard County, western Utah, USA. All magnifications are x12. **A, D, J, M, O**, pygidium, **holotype**, SUI 128871, dorsal, ventral, anterior, posterior, and right lateral views. **B, E, F, K**, pygidium, SUI 128872, dorsal, right lateral, ventral, and posterior views. **C, G, H**, pygidium, SUI 128873, dorsal, posterior, and left lateral views. **I, L, R**, pygidium, SUI 128874, posterior, left lateral, and dorsal views. **N, U, X**, pygidium, SUI 128875, right lateral, dorsal, and posterior views. **P, Q, W**, pygidium, SUI 128876, posterior, left lateral, and dorsal views. **S, T, V**, pygidium, SUI 128877, right lateral, posterior, and dorsal views.

Figure 19 (page 395). *Psalikilopsis paracuspida* sp. nov., from Locality YH-E, Yellow Hill Limestone (lower Floian; Tulean; high *Psalikilopsis cuspidicauda* Zone), Yellow Hill, near Pioche, Lincoln County, eastern Nevada. **A-D, H**, cranidium, SUI 128878, dorsal, ventral, oblique, left lateral, and anterior views, x12. **E, I, K, L**, cranidium, SUI 128879, left lateral anterior, dorsal, and ventral views, x9. **F, G, J**, cranidium, SUI 128880, anterior, left lateral, and dorsal views, x12. **M, N, P**, right librigena, SUI 128881, internal, ventrolateral, and external views, x8. **O**, right librigena, SUI 128882, external view, x8. **Q-T**, pygidium, SUI 128883, posterior, left lateral, dorsal, and ventral views, x12. **U, V, X-Z**, pygidium, SUI 128884, dorsal, ventral, posterior, right lateral, and anterior views, x10. **W, ZZ, BB**, pygidium, SUI 128885, dorsal, left lateral, and posterior views, x12.





ventrally curved sector and flat slightly upturned adaxial sector anteriorly beneath anterior part of lateral border and anterior projection; doublure beneath posterior border with prominent, nearly straight, fine raised lines set subparallel with posterior margin, occupying most of doublure near posterior facial suture, doublure wider toward base of genal spine, extra width composed of inner concave strip lacking sculpture; inner margin of doublure describes continuous arc, lacking angular change in course between posterior border and lateral border; beneath genal spine base doublure forms distinct genal angle, independent of and below base of genal spine; raised lines contiguous with those beneath posterior border but much finer and closer spaces are crowded around the "corner" of this angle, whereas the broad doublural area anterior to this, beneath the genal spine base, lacks sculpture; raised lines subparallel with lateral margin run along lateral part of doublure beneath lateral border furrow, occupying no more than a quarter to a third of width posteriorly, but progressively encroaching on unsculptured region anteriorly, to dominate by the tip of the anterior projection; tiny Panderian notch (Fig. 1E, F) developed nearly adjacent to posterior facial suture.

Hypostome and rostral plate not identified.

Thorax with axial lobe widest anteriorly, progressively narrower posteriorly; general construction of segments is a tuberculate axial ring, a long, deep ring furrow, a very large articulating half ring, usually with a scattering of small tubercles on its posteromedian region, shallow axial furrows, a very long (exsag.) pleural furrow occupying at least half the exsagittal length of the segment, anterior and posterior pleural bands reduced to transverse inflated strips of similar length, with generally transversely aligned tuberculate sculpture of varying size depending on position in thorax, faint transverse furrows set anterior to anterior band and posterior to posterior band, a pleural spine derived mainly from the anterior pleural band but connected also to the posterior band, shorter in anterior segments, longer in posterior segments, set posterolaterally, turned more posteriorly in posterior segments, curved and slightly sinuous, with prominent raised line sculpture; the anterior edge of the pleural region forms a transverse tongue which articulates with a narrow ventral transverse groove beneath the posterior edge of the pleurae of the next segment anteriorly (or the posterior border of the cranidium); a peg-like process is set at the anterior end of the axial furrow which articulates with a small socket in the posterior end of the next segment anteriorly (or the posterior of the cranidium); ventrally, the doublure forms a

crescentic articulating surface beneath the axial ring with sculpture of fine, very subdued, closely spaced raised lines; the only other doublure is set far distally at the base of the pleural spine, where there is a small region bounded adaxially by an inflated, slightly obliquely set ridge; the front of this ridge terminates at an anterior process; this articulates with a notch set at the rear of the ridge in the next anterior segment; the fulcrum is set quite far distally, and the portion of the pleura distal to the fulcrum is narrow and turned down from about 45° to about 60° from horizontal depending on position in the thorax. The main variation from anterior to posterior along the thorax is as follows: the pleural spine is smaller anteriorly for coaptative reasons, and there is a fairly large anteriorly facing articulating facet in front of it which is greatly reduced posteriorly; the pleural spine is progressively larger posteriorly, and becomes more posteriorly turned; the pleural furrow is longest anteriorly and is progressively shorter posteriorly; the tuberculate sculpture on the axial ring and the pleural bands becomes progressively more dense posteriorly; the axial region becomes progressively, but not radically, narrower relative to the overall width posteriorly; the overall segment width becomes narrower over the last three segments; anteriormost and posteriormost segments lack median axial nodes or spines; however, three segments in the middle part of the thorax have prominent median nodes and a fourth, behind them, has a prominent, short, median spine, slightly sagittally curved, running posterodorsally.

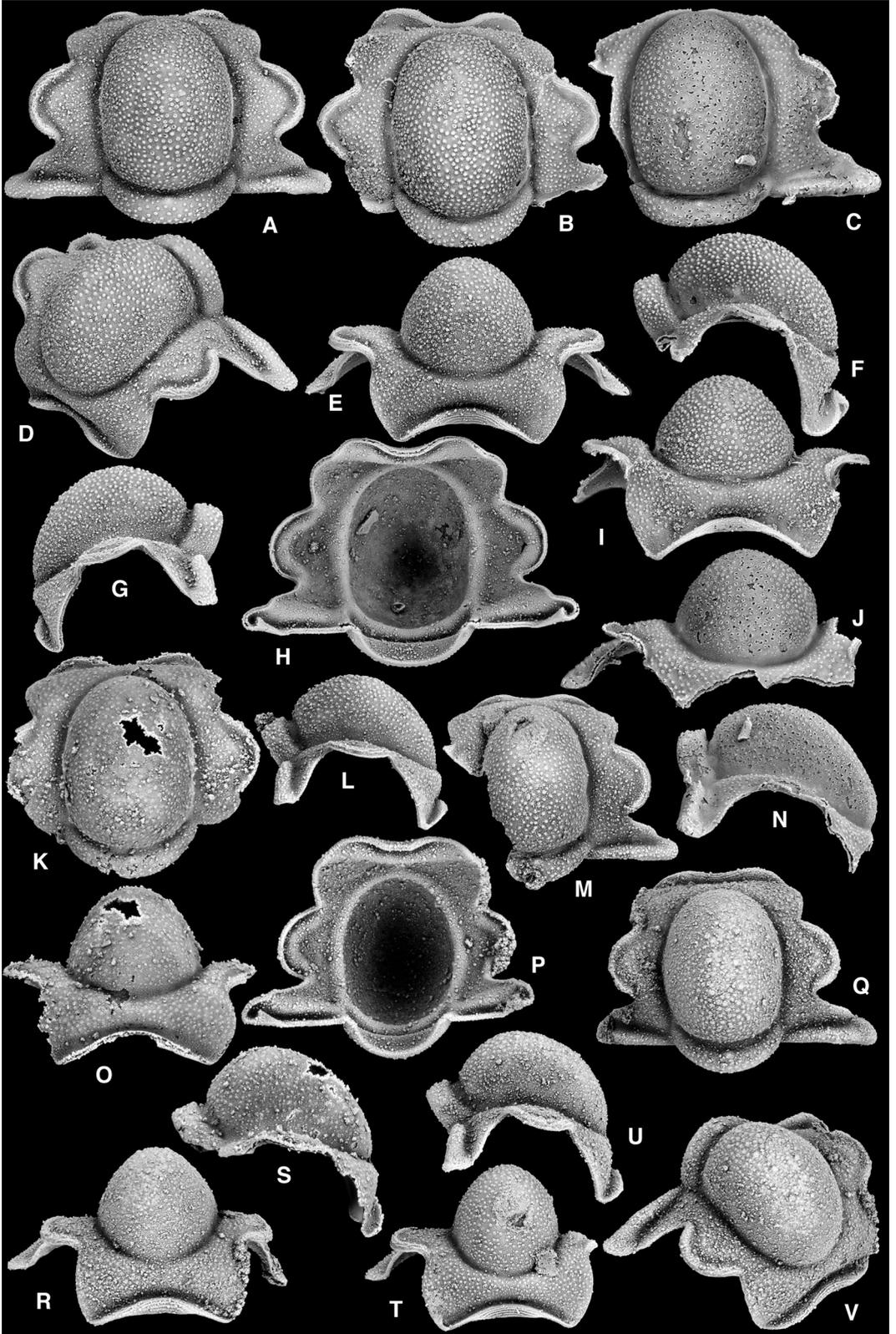
Pygidial measurements were made on the large, nearly or completely intact specimens (Figs 17A, C, L, S, 18A-C, R, V). Pygidium with maximum width across first segment 128.9% (120.3-142.8) sagittal length; axis of four segments, maximum axial width across first segment 43.9% (41.2-45.9) maximum pygidial width; width across fourth segment 54.5% (46.5-59.6) width across first segment; length of axis excluding articulating half ring 56.6% (55.1-58.3) total sagittal length of pygidium; articulating half ring large and medially long, sagittal length 13.3% (11.9-14.8) total pygidial length, anterior margin subsemicircular, slightly more strongly curved sagittally, ring sloped forward and down from general sagittal profile of axis, gently dorsally convex in sagittal profile, almost exactly semicircular in transverse profile (along with rest of axis), lacking sculpture on most of surface but with scattering of small tubercles along rear edge, slightly more prominent medially in some specimens; first ring furrow deep and either exactly transverse or slightly anteriorly bowed; second ring furrow nearly as deep as first; third

ring furrow slightly shorter (sag.; exsag.) than second but still prominent, partially effaced medially in some specimens; fourth ring furrow much less well expressed, effaced medially in most specimens; pseudo-articulating half ring of second specimen prominent and tuberculate; pseudo-articulating half ring of third segment discernible but small; that of fourth segment not clearly differentiated; first axial ring slightly longer sagittally than exsagittally (including partially merged second pseudo-articulating half ring), with sculpture of small to medium, densely crowded tubercles, tubercles somewhat larger medially, no distinct median tubercle; posterior rings progressively smaller, but with essentially the same morphology; axis terminated by broad terminal piece, rear rounded; some specimens have a very distinctly terminated axis (e.g., Fig. 18C, U, V), others are less distinct medially and more gradational (e.g., Fig. 17A, J), and some have a subdued but clearly independently swollen post-axial ridge running onto the posterior spine (e.g., Figs 17E, 18A); first segment with maximum exsagittal pleural length 46.1% (40.0-48.9) sagittal axial length, anterior margin almost exactly transversely straight to fulcrum, which is set far distally, margin turned sharply posterolaterally distal to fulcrum; anterior pleural band set off from margin by faint transverse accessory furrow, well inflated, with sculpture of scattered small tubercles arranged in irregular transverse row or rows, band is progressively longer (exsag.) distally; posterior pleural band shorter than anterior band, with similar scattering of slightly finer tubercles; pleural furrow long (exsag.) and trough-like, terminated just past fulcrum where anterior and posterior pleural bands merge to form subtrapezoidal tip sculptured with small raised lines, with small, stubby spine at posterolateral corner; interpleural furrows similar to pleural furrows in long, trough-like morphology, but slightly (Fig. 17A) to substantially (Fig. 18A) shallower and distinctly shorter (exsag.) at any given point; interpleural furrows progressively longer (exsag.) distally, similar to pleural furrows; morphology of pleural region of segments two and three generally similar to segment one, but progressively narrower, more weakly expressed, and turned more posterolaterally; pleura of third segment barely expressed on some specimens (e.g., Fig. 17I, L); fourth segment with no associated expression of inflated pleural bands, pleural region adjacent to fourth ring is narrow and depressed; pleural bands and furrows terminated by inflated, ridge-like border, with sculpture of three or four very fine, somewhat irregular, raised lines; border runs from rear of

small spine opposite first posterior pleural band to posterior spine and continues along abaxial edge of median posterior spine; border runs generally straight, opposing borders forming slightly acute angle, but course is deflected slightly around the terminus of each segment's pleurae; border set off from pleura by narrow furrow, deeper opposite pleural and interpleural furrows than opposite pleural bands; posterior median spine of variable length and width, but generally short, ranging from squat and subtriangular (Figs 17S, 18C) to more narrow and elongate (Fig. 18A), sides formed from continuation of border, median part sculptureless and slightly depressed except in specimens where post-axial ridge is more prominent, spine tapers to sharp posterior point in most specimens; posterolateral faces of pygidium formed by more or less vertical "wall," slightly concave, and broadly bilobate, ventral margin describing broad "W" in posterior view, with strong median embayment; wall is bounded dorsally by border and ventrally by a second, less well defined, inflated border-like structure with more prominent raised lines; main surface of wall with sculpture of sparse, in many specimens irregular, raised lines; anterior corner of wall beneath anterior pleural band of first segment with small pit-like articular facet; in ventral view, no doublure visible; small doublure sector visible in anterior view (Fig. 18J), set vertically and tucked up opposite ventral region of the wall, slightly taller laterally than medially, lacking sculpture.

Ontogeny. The smallest recovered cranidia (e.g., Fig. 13L) are very similar in proportions to large specimens, with the main difference being the plain expression of three primary pairs of glabellar tubercles. Fixigenal paired tubercles are not expressed on the posterior fixigena or interocular fixigena, but two anterior pairs are expressed on the frontal area. Aside from loss of distinction of these tubercles, the only significant cranidial change with size is a relative expansion in the size of the glabella. Librigenal changes involve considerable expansion of the width and area of the field, and reduction in the relative length of the genal spine (though it is retained as a very long spine in large specimens). The only observable change across the size range of sampled pygidia is a slight reduction in the prominence of the posterior spine.

Material. Holotype, pygidium, SUI 128871 (Fig. 18A, D, J, M, O), and assigned specimens SUI 128821-128870, 128872-128877, from Section D 106.4 m, Fillmore Formation (lower Floian; Tulean; high *Psalikilopsis cuspidicauda*



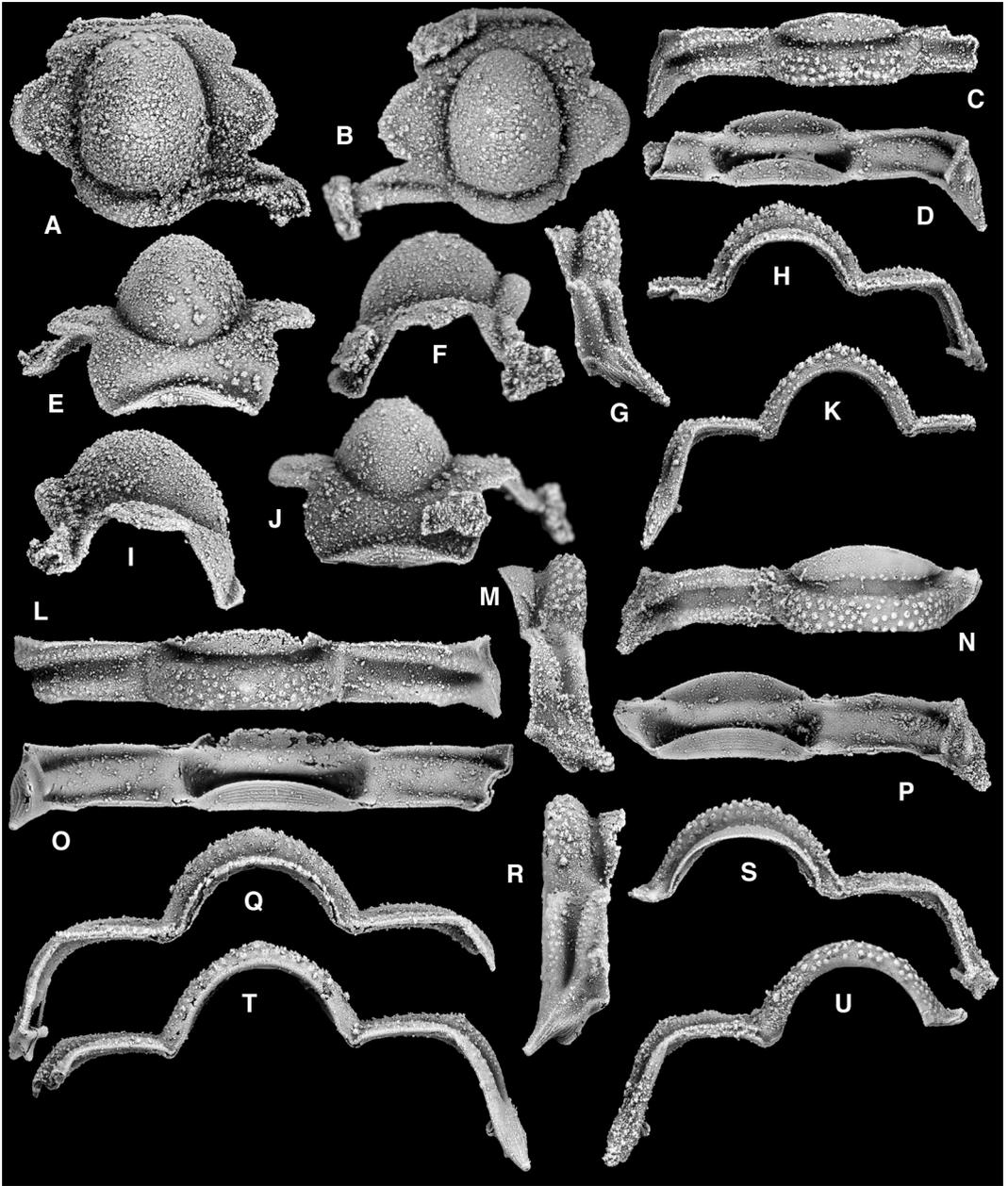


Figure 21. *Psalikilopsis redfordi* sp. nov., from Section HC5 186.5 m, Garden City Formation (lower Floian; Tulean; *Hintzeia celsaora* Zone), east side of Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho, USA. **A, D, E, I,** cranium, SUI 128902, dorsal, anterior, and right lateral views, x12. **B, F, J,** cranium, SUI 128903, dorsal, left lateral, and anterior views, x15. **C, D, G, H, K,** thoracic segment, SUI 128904, dorsal, ventral, left lateral, anterior, and posterior views, x10. **L, O, Q, R, T,** thoracic segment, SUI 128905, dorsal, ventral, anterior, right lateral, and posterior views, x10. **M, N, P, S, U,** thoracic segment, SUI 128906, left lateral, dorsal, ventral, anterior, and posterior views, x7.5.

Figure 20 (opposite). *Psalikilopsis redfordi* sp. nov., from Section HC5 186.5 m, Garden City Formation (lower Floian; Tulean; *Hintzeia celsaora* Zone), east side of Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho, USA. **A, D, E, G, H,** cranium, SUI 115146, dorsal, oblique, anterior, left lateral, and posterior views, x8. **B, F, I,** cranium, SUI 128897, dorsal, right lateral, and anterior views, x6. **C, J, N,** cranium, SUI 128898, dorsal, anterior, and right lateral views, x6. **K, O, S,** cranium, SUI 128899, dorsal, anterior, and right lateral views, x10. **L, M, T,** cranium, SUI 128900, right lateral, dorsal, and anterior views, x10. **P, Q, R, U, V,** cranium, SUI 128901, ventral, dorsal, anterior, right lateral, and oblique views, x12.



Zone), southern House Range, Ibex area, Millard County, western Utah; assigned specimens SUI 128878-128885 from Locality YH E, Yellow Hill Limestone (lower Floian; Tulean; high *Psalikilopsis cuspidicauda* Zone), Yellow Hill, near Pioche, Lincoln County, eastern Nevada.

Etymology. Latin *para*, against, and the specific epithet *cuspidicauda*.

Remarks. *Psalikilopsis paracuspidauda* was differentiated from the very similar but slightly older *P. cuspidicauda* above. It is compared at length with *P. redfordi* below. The three derived species were distinguished from the oldest species, *P. newmani*, in the genus discussion above.

The thoracic parts (one with attached pygidium) illustrated in Fig. 16A, E were recovered from the same sample and are likely from the same individual. They articulate directly with one another, and it does not seem likely that an intervening segment (or segments) is missing. This combined specimen includes eight thoracic segments. Most known bathyurid thoraces have nine segments (e.g., Whittington 1953, pl. 65, figs 7, 16, pl. 67, fig. 10; Whittington 1963, pl. 10, fig. 9, pl. 11, fig. 11, pl. 14, fig. 1), though some have ten (e.g., Whittington 1965, pl. 14, fig. 4). Assuming *Psalikilopsis* had the more common nine segmented thorax, then most likely the anteriormost segment is missing from this specimen, and the segment bearing the median axial spine is the sixth.

Psalikilopsis redfordi sp. nov. (Figs 1B, C, 20-24)

1953 *Psalikilus spinosum* Hintze, *partim*, p. 212, pl. 9, fig. 7a-c (only; pl. 9, figs 3a-c, 6 = *Psalikilus spinosum*).

2009 *Psalikilopsis* sp. nov. 1; Adrain *et al.*, p. 557, fig. 9C, G.

Material. Holotype, pygidium, SUI 115147, and assigned specimens SUI 115146, 128897-128925 from Section HC5 186.5 m Garden City Formation (lower Floian; Tulean; *Hintzeia*

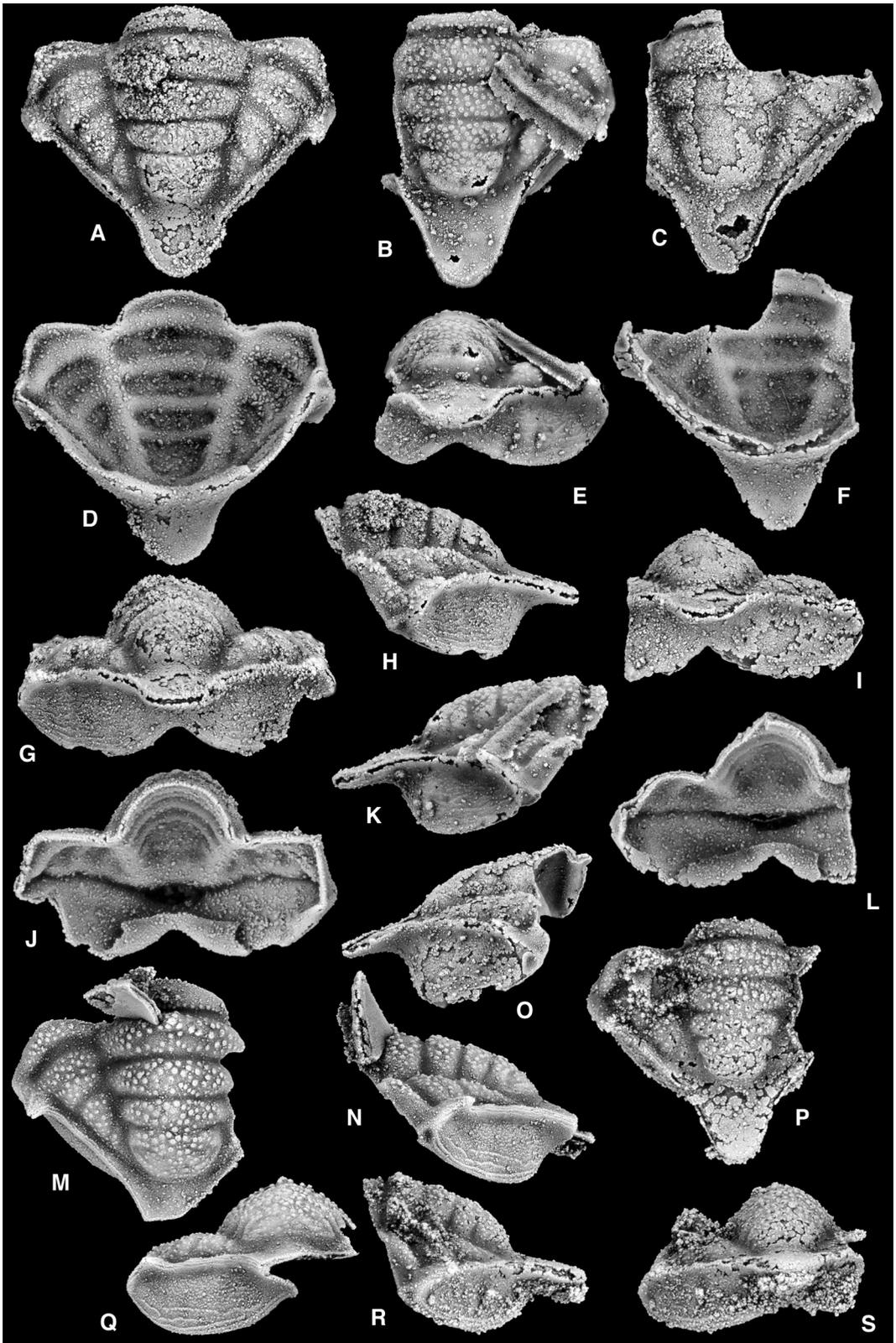
celsaora Zone), east side of Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho; assigned specimens SUI 128926-128930 from Section G 118.6 m, Fillmore Formation (lower Floian; Tulean; *Hintzeia celsaora* Zone), southern Confusion Range, Ibex area, Tule Valley, Millard County, western Utah.

Etymology. After Robert Redford.

Diagnosis. Librigena with lateral border broad posteriorly, inflated area behind genal spine base prominent, genal spine reduced in large specimens to short spike; pygidium subtriangular, with prominent pleural spine on first segment and broad, shelf-like, lobate median posterior spine.

Description. *Psalikilopsis redfordi* shares the prominent coaptative modifications of *P. cuspidicauda* and *P. paracuspidauda* and extended written description is redundant. Instead, this differential description notes all observable differences with *P. paracuspidauda*. Most of these distinctions apply also to *P. cuspidicauda*. Cranidium with frontal areas and preglabellar field more steeply downturned from glabella, so that preglabellar field may not be visible in standard dorsal view; this results in a relatively shorter sagittal cranial length which affects all of the ratios using this measurement given in the *P. paracuspidauda* description, but the various width dimensions (across β , etc.) are very similar between the species; sculpture on main glabellar lobe and LO slightly finer; librigena with lateral border much more prominent, broad, and forming adaxial ridge along border furrow, with many more, finer, more closely set raised lines; lateral border furrow much deeper and more prominent; field somewhat narrower, with much more prominent tuberculate sculpture; posterior border much narrower (tr.), about half the course of the border in *P. paracuspidauda*; inflated region in front of genal spine base very prominent; genal spine in large specimens very short, a fraction of the length of the long spine of *P. paracuspidauda*; pygidium with fulcrum not set as far distally, and bands and furrows expressed distal to fulcrum on both first

Figure 22. *Psalikilopsis redfordi* sp. nov., from Section HC5 186.5 m, Garden City Formation (lower Floian; Tulean; *Hintzeia celsaora* Zone), east side of Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho, USA. **A**, right librigena, SUI 128907, external view, x7.5. **B**, left librigena, SUI 128908, external view, x10. **C, F, H**, left librigena, SUI 128909, external, ventrolateral, and internal views, x10. **D**, left librigena, SUI 128910, external view, x8. **E**, left librigena, SUI 128911, external view, x10. **R**, right librigena, SUI 128912, external view, x12. **I**, left librigena, SUI 128913, external view, x10. **J, K**, right librigena, SUI 128914, internal and external views, x10. **L**, left librigena, SUI 128915, external view, x15. **M**, right librigena, SUI 128916, external view, x12. **N**, right librigena, SUI 128917, external view, x12. **O**, right librigena, SUI 128918, external view, x15. **P**, left librigena, SUI 128919, external view, x10. **Q**, left librigena, SUI 128920, external view, x10. **R, S**, left librigena, SUI 128921, external and internal views, x10.



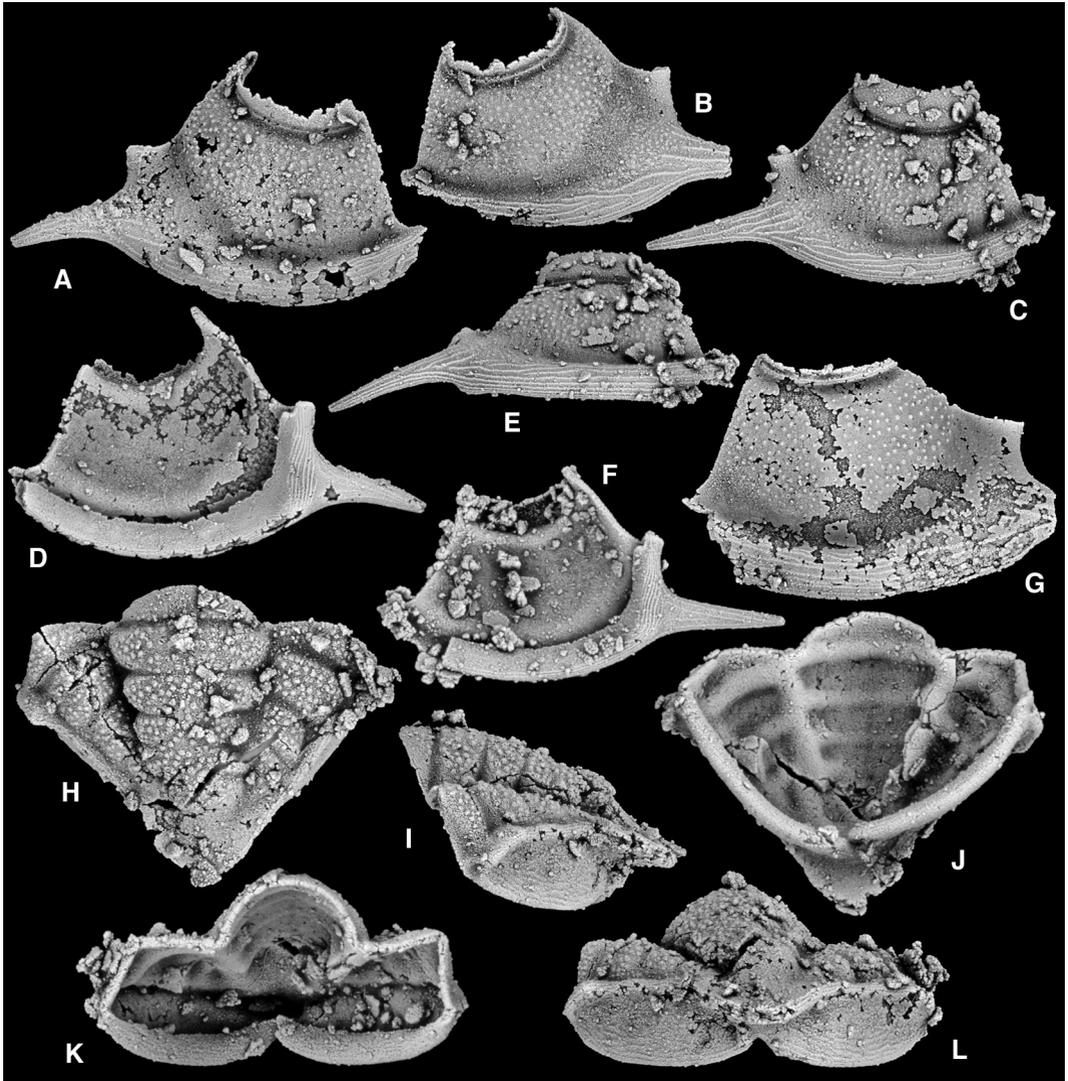
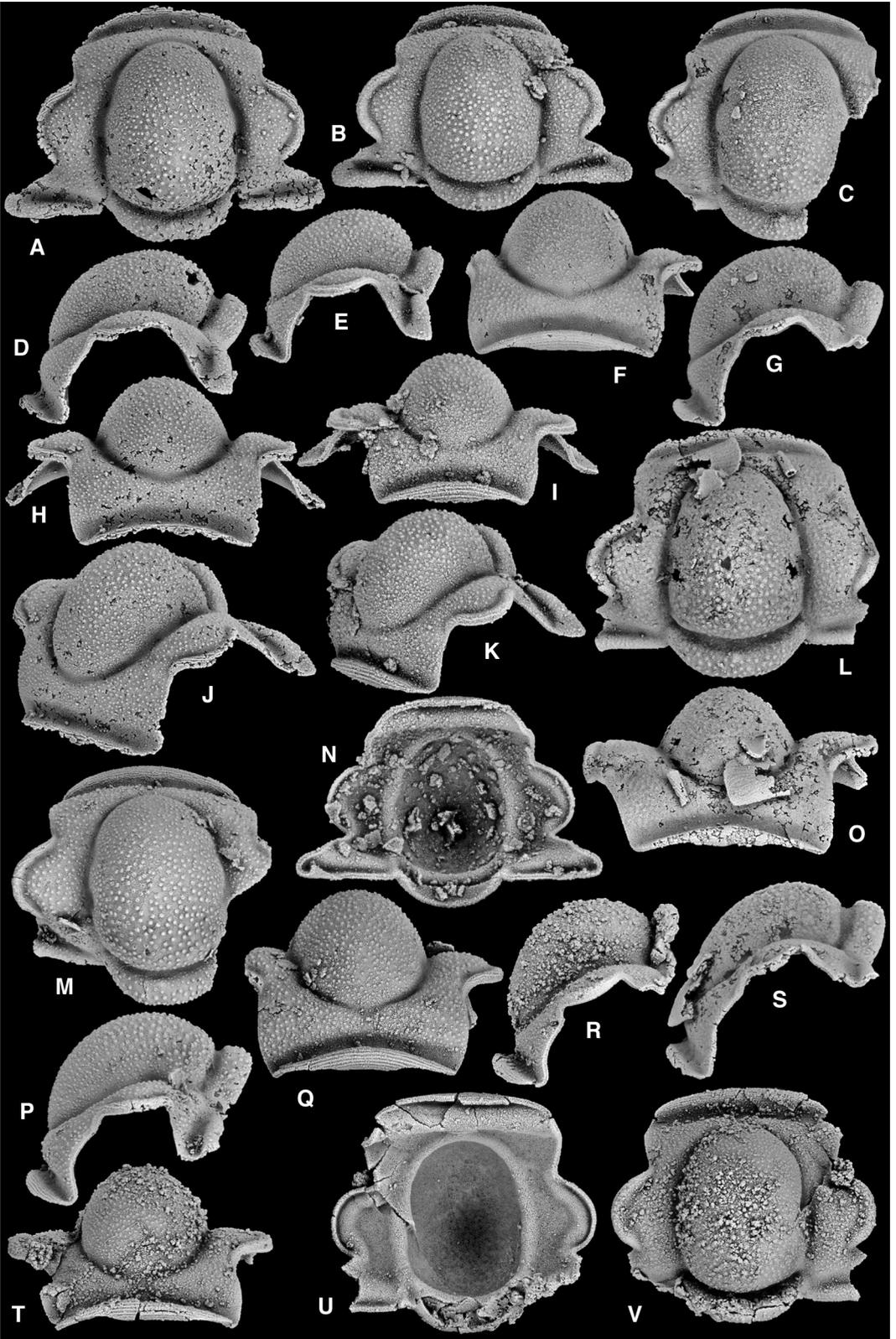


Figure 24. *Psalikelopsis redfordi* sp. nov., from Section G 118.6 m, Fillmore Formation (lower Floian; Tulean; *Hintzeia celsaora* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. **A, D**, right librigena, SUI 128926, external and internal views, x10. **B**, left librigena, SUI 128927, external view, x12. **C**, **E, F**, right librigena, SUI 128928, external, ventrolateral, and internal views, x12. **G**, left librigena, SUI 128929, external view, x7.5. **H-L**, pygidium, SUI 128930, dorsal, left lateral, ventral, anterior, and posterior views, x12.

Figure 23 (opposite). *Psalikelopsis redfordi* sp. nov., from Section HC5 186.5 m, Garden City Formation (lower Floian; Tulean; *Hintzeia celsaora* Zone), east side of Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho, USA. **A, D, G, H, J**, pygidium, **holotype**, SUI 115147, dorsal, ventral, posterior, left lateral, and anterior views, x12. **B, E, K**, pygidium, SUI 128922, dorsal, posterior, and right lateral views, x12. **C, F, I, L, O**, pygidium, SUI 128923, dorsal, ventral, posterior, anterior, and right lateral views, x12. **M, N, Q**, pygidium, SUI 128924, dorsal, left lateral, and posterior views, x15. **P, R, S**, pygidium, SUI 128925, dorsal, left lateral, and posterior views, x17.

and second segments; third axial furrow well expressed versus medially shallowed; furrow separating fourth segment from terminal piece clearly expressed as transverse furrow laterally versus almost obsolete; pleural bands relatively larger and more dorsally inflated; pleural furrows relatively shorter (exsag.); posterior pleural

spine on first segment large and prominent versus reduced or nearly not expressed; furrow separating pleurae from bounding ridge wider; “wall” beneath pleurae held at different attitude to general plane of pleurae, such that it is not visible or barely visible versus clearly visible in standard dorsal view; posterior spine broad and



lobate, shelf-like dorsally, versus narrow and pointed; median embayment in “wall” stronger in posterior view.

Ontogeny. Smaller cranidia have been recovered for this species than any other (Fig. 21B). They show evidence of paired cranial primary tubercles, though they are much less prominent than in small specimens of *P. paracuspida* (see above). Importantly, they show an unmodified anterior border, demonstrating that the coaptive modifications appeared fairly late in ontogeny. Other differences from larger specimens include a much smaller glabella, less downsloped frontal areas, and weaker palpebral furrow. The smallest librigenae (e.g., Fig. 22O) are quite unlike large specimens, as they have a narrow field, relatively larger eye, much less inflated lateral border, much narrower field, and much longer genal spine. In isolation one might doubt that they are conspecific, but all of these features are gradually transformed with size. The pygidial sample is small, and includes no small specimens.

Remarks. *Psalikilopsis redfordi* is distinguished collectively from *P. cuspidicauda* and *P. paracuspida* by the above differential description and was distinguished from the oldest species, *P. newmani*, in the genus discussion. *Psalikilopsis redfordi* is fairly common in the *Hintzeia celsa* Zone of the Garden City Formation of southeastern Idaho, but rare in the small sample available from the zone in the Fillmore Formation of western Utah.

***Psalikilopsis newmani* sp. nov.** (Figs 1A, 25-30)

1953 *Jeffersonia* ? sp. B; Hintze, p. 175, pl. 9, figs 8, 11, 12.

1975 *Peltabellia* sp. B of Hintze; Fortey & Owens, p. 228.

2009 *Peltabellia* sp. nov. 3; Adrain *et al.*, p. 557, fig. 8O, S.

Diagnosis. Anterior border of simple construction, anterior border furrow deep medially; S1 and S2 strongly impressed (for genus); median occipital node very small, set on anterior edge of LO; librigenal field broad versus exsagittal length of main body of librigena; genal spine reduced

to very short, broadly triangular point in large specimens; all four pygidial segments usually with pleural bands expressed, even if faintly.

Description. Cranial measurements were based on the specimens of Figures 25A, B and 26H. In the case of the latter, width across posterior projections was calculated by doubling the width from the intact right one to the sagittal line. Cranidium with maximum width across posterior projections 142.2% (137.7-147.1) sagittal length; anterior border with anterior margin gently anteriorly arcuate, cut laterally by oblique connective suture; border forming inflated anterior rim with sculpture of transverse raised lines on dorsal and anterior aspect, longer sagittally than exsagittally (disregarding truncation by connective suture); anterior border furrow long, relatively shallow, and trough-like, contact with rear of anterior border gradational, contact with preglabellar field and frontal area along a distinct break in slope, slightly less marked at lateral extremes; preglabellar field long, nearly as long sagittally as combined anterior border and border furrow, dorsally inflated to slightly overhanging border furrow; preglabellar field and frontal areas steeply sloped from interocular fixigenae; frontal areas markedly convex; preglabellar field and frontal areas with sculpture of dense, even, very fine tubercles; anterior branches of facial suture only moderately anteriorly bowed (in anterior view; they appear more strongly bowed in dorsal view), width across β 82.2% (82.0-82.7) cranial sagittal length; palpebral lobe large, long, and moderately wide, distance across lobes 118.8% (116.1-120.7) cranial sagittal length, distance across γ 81.1 % (80.5-81.7) and that across ϵ 99.0% (96.1-101.9) cranial sagittal length; lateral margin of lobe nearly semicircular, widest point only slightly posterior to midlength; edge of lobe developed into strongly inflated narrow rim with sculpture of raised lines set subparallel with margin; rim bounded adaxially by narrow but strongly incised palpebral furrow, of similar depth all along course, terminated at anterior and posterior extent of rim, not extending onto posterior fixigena; interocular fixigena quite strongly swollen and dorsally inflated in transverse profile, wide, with sculpture of fine tubercles similar to that on frontal area; eye ridge

Figure 25. *Psalikilopsis newmani* sp. nov., from Section G 99.3 m and 99T m, Fillmore Formation (lower Floian; Tulean; *Psalikilus spinosum* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. **A, D, H, J,** cranidium, SUI 128931, dorsal, left lateral, anterior, and oblique views, x10 (G 99T m). **B, E, I, K, N,** cranidium, SUI 115131, dorsal, left lateral, anterior, oblique, and ventral views, x10 (G 99.3 m). **C, F, G,** cranidium, SUI 128932, dorsal, anterior, and left lateral views, x8 (G 99T m). **L, O, S,** cranidium, SUI 128933, dorsal, anterior, and left lateral views, x8 (G 99T m). **M, P, Q,** cranidium, SUI 128934, dorsal, left lateral, and anterior views, x8 (G 99T m). **R, T-V,** cranidium, SUI 128935, left lateral, anterior, ventral, and dorsal views, x8 (G 99.3 m).

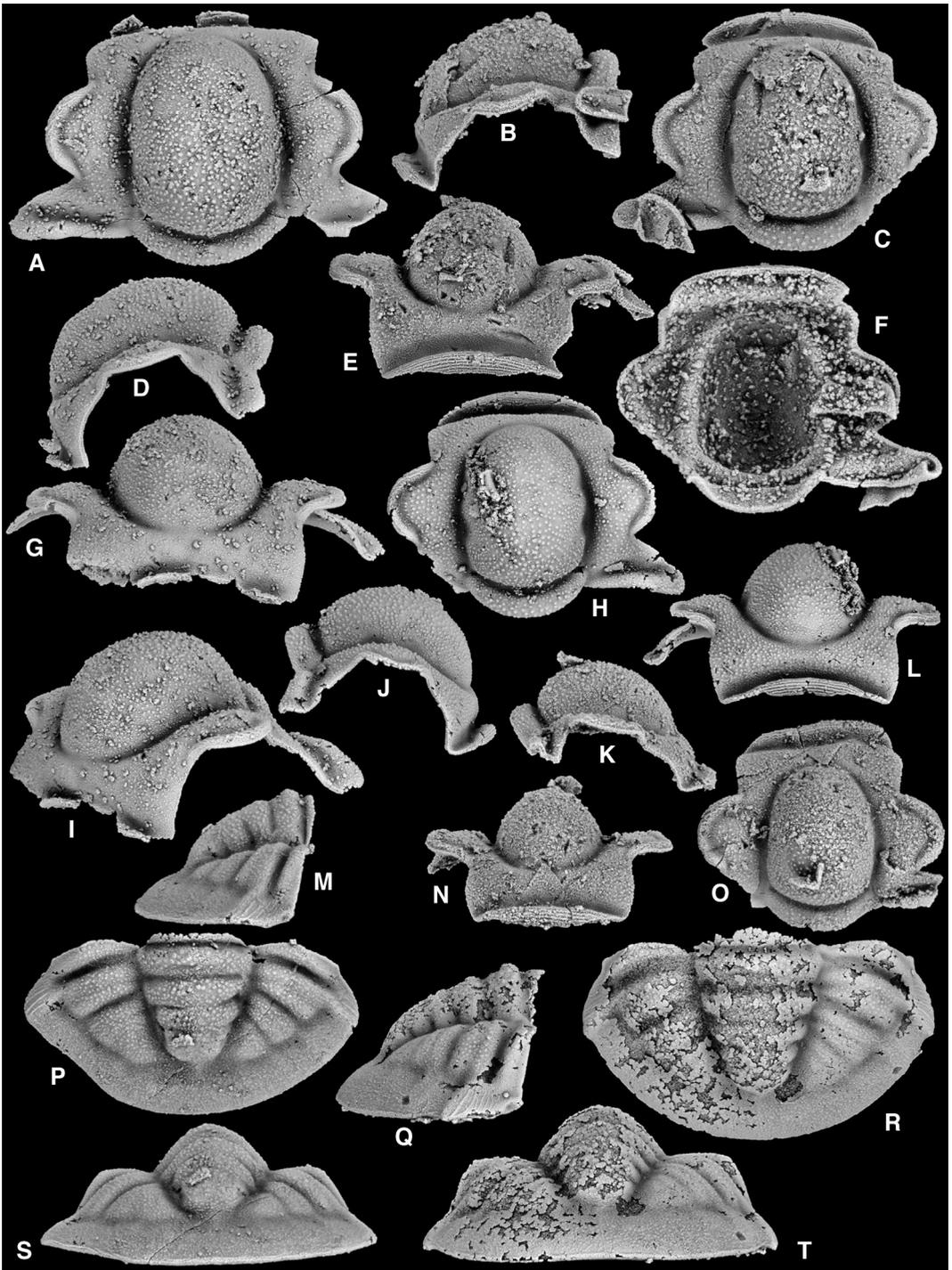


Figure 26. *Psalikilopsis newmani* sp. nov., from Section G 99.3 m and 99T m, Fillmore Formation (lower Floian; Tulean; *Psalikilus spinosum* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. **A, D, G, I**, cranidium, SUI 128936, dorsal, left lateral, anterior, and oblique views, x7.5 (G 99.3 m). **B, C, E, F**, cranidium, SUI 128937, left lateral, dorsal, anterior, and ventral views, x9 (G 99.3 m). **H, J, L**, cranidium, SUI 128938, dorsal, right lateral, and anterior views, x10 (G 99T m). **K, N, O**, cranidium, SUI 128939, right lateral, anterior, and dorsal views, x10 (G 99.3 m). **M, P, S**, pygidium, SUI 128940, right lateral, dorsal, and posterior views, x12 (G 99T m). **Q, R, T**, pygidium, SUI 128941, right lateral, dorsal and posterior views, x9 (G 99T m).

faintly discernible dorsally on some specimens (e.g., Fig. 25A, C), obscure on others (e.g., Fig. 26A), anterior bounding furrow obvious ventrally (Fig. 25U), ridge running obliquely from anterior terminus of palpebral rim to L3; posterior fixigena sloped steeply posteriorly from interocular fixigena, with moderate inflation, sculpture of fine tubercles distinctly smaller and less well expressed than those on interocular fixigena, fading out along posterior projection; posterior section of facial suture with anterior bulge at fulcrum; posterior border furrow long (exsag.) and trough-like, proximal end not in contact with axial furrow, deep furrow begins some distance distally, furrow longer distally, shallowed out prior to contact with facial suture; posterior border moderately inflated, with sculpture of very fine tubercles, finer than those on posterior fixigena, short proximally, progressively longer distally, forming relatively small lobe-like terminus distally; glabella with maximum width across L2 79.1% (77.1-82.5) sagittal length excluding LO; glabella dorsally inflated, with strong sagittal dorsal convexity, stronger posteriorly than anteriorly, so glabella with gentle posterior "hump," with strongly arcuate transverse profile, and with slightly straighter sides and more convex top; axial furrows moderately broad and deep, laterally bowed, deflected individually around L1-L3; axial furrow very shallow opposite LO, so that general anterior course of furrow communicates posteriorly more directly with SO than posterior course of furrow; axial furrow grading into preglabellar furrow with more or less distinct deflection in course at adaxial end of eye ridge; preglabellar furrow narrower than axial furrow, not evenly arcuate but reaching subtle angle at median point, shallowed but still impressed medially; main part of glabella with small to medium sized tubercles on median and rear part, largest of any developed on cranium, grading into much finer tubercles anteriorly and laterally, similar in size to those on frontal areas; L1, L2 and L3 all weakly but distinctly independently inflated; S1 and S2 visible dorsally as distinct notches between weakly swollen lobes, visible laterally as obliquely set regions of reduced tuberculate sculpture, variably well expressed; SO deep, laterally bowed, slightly longer sagittally than exsagittally, with sharper change in slope anteriorly than posteriorly; LO with width 53.4% (50.6-56.3) sagittal cranial length and sagittal length 10.3% (9.8-11.1) that of cranium, slightly longer sagittally than exsagittally, distal end gently swollen near axial furrow, sculpture of scattered small tubercles similar to that on rear of main glabellar lobe; median node subdued but distinct, set near anterior margin of LO;

doublure consisting of crescentic articulating surface beneath LO, slightly concave and lacking sculpture, and very small triangle underlying rear of distalmost part of posterior projection.

Librigenal measurements were not made owing to a lack of intact large specimens and the considerable changes in proportions that take place from smaller specimens. Librigena very wide, about as wide as long in largest specimens; anterior section of facial suture strongly anteriorly bowed; posterior section of facial suture more gently posteriorly bowed; eye moderately large, long and low, separated from socle by narrow furrow; socle very narrow, about as wide as furrow separating it from visual surface, appearing as linear raised ridge in smaller specimens (Fig. 27G, M), slightly broader in larger specimens (Fig. 27A, O); socle separated from field by furrow about twice as broad as that separating it from the visual surface, furrow slightly shallower anteriorly, wider and shallower in large specimens; field with substantial inflation and convexity, sculpture of fine, fairly densely distributed tubercles, in some specimens arranged in loose radial rows reflecting underlying caecal sculpture; lateral border furrow broad, deeper and narrower anteriorly than posteriorly, connecting posteriorly with posterior border furrow; in most specimens the furrows form a contiguous, uninterrupted structure but in some (Fig. 27H, O) there is a slight constriction and interruption in front of swollen base of genal spine; anterior part of lateral border furrow lacking sculpture, but posterior border furrow and area of junction in front of genal spine base bears very fine tuberculate sculpture in many specimens; lateral border wide and prominently inflated, lateral margin strongly bowed in larger specimens, narrower anteriorly than posteriorly, with sculpture of coarse raised lines, crowded and subparallel with margin anteriorly, more widely spaced and irregular posteriorly, rear adaxial part lacking raised lines but with sculpture of very fine scattered tubercles; anterior projection long, turned slightly ventrally distally, with raised line sculpture continued from lateral border; posterior border with limited course, narrow, lacking sculpture or with very sparse very fine tubercles; posterior margin strongly curved from facial suture to adaxial edge of genal spine; genal spine in largest specimens blunt, posteriorly directed triangle, smaller specimens with short, cylindrical spine; region in front of base of genal spine swollen, interrupting raised line sculpture and in some specimens encroaching on junction of lateral and posterior border furrows; outer edge of doublure below lateral border and region beneath genal spine and base with raised line sculpture;



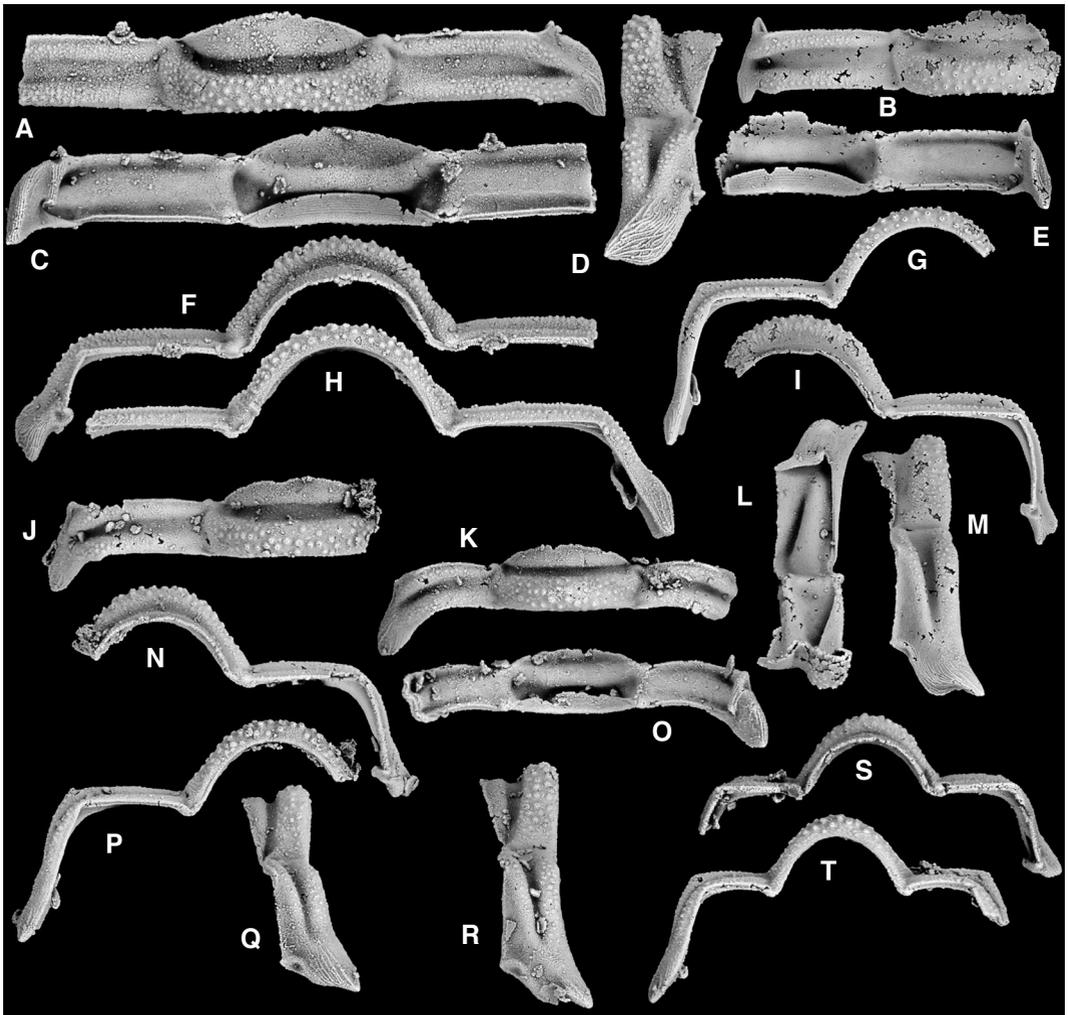


Figure 28. *Psalikelopsis newmani* sp. nov., from Section G 99.3 m and 99T m, Fillmore Formation (lower Floian; Tulean; *Psalikelus spinosum* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. **A, C, D, F, H,** thoracic segment, SUI 128953, dorsal, ventral, right lateral, anterior, and posterior views, x10 (G 99.3 m). **B, E, G, I, L, M,** thoracic segment, SUI 128954, dorsal, ventral, anterior, posterior, ventral articulating facet, and left lateral views, x7.5 (G 99T m). **J, N, P, R,** thoracic segment, SUI 128955, dorsal, anterior, posterior, and left lateral views, x10 (G 99T m). **K, O, Q, S, T,** thoracic segment, SUI 128956, dorsal, ventral, left lateral, anterior, and posterior views, x12 (G 99T m).

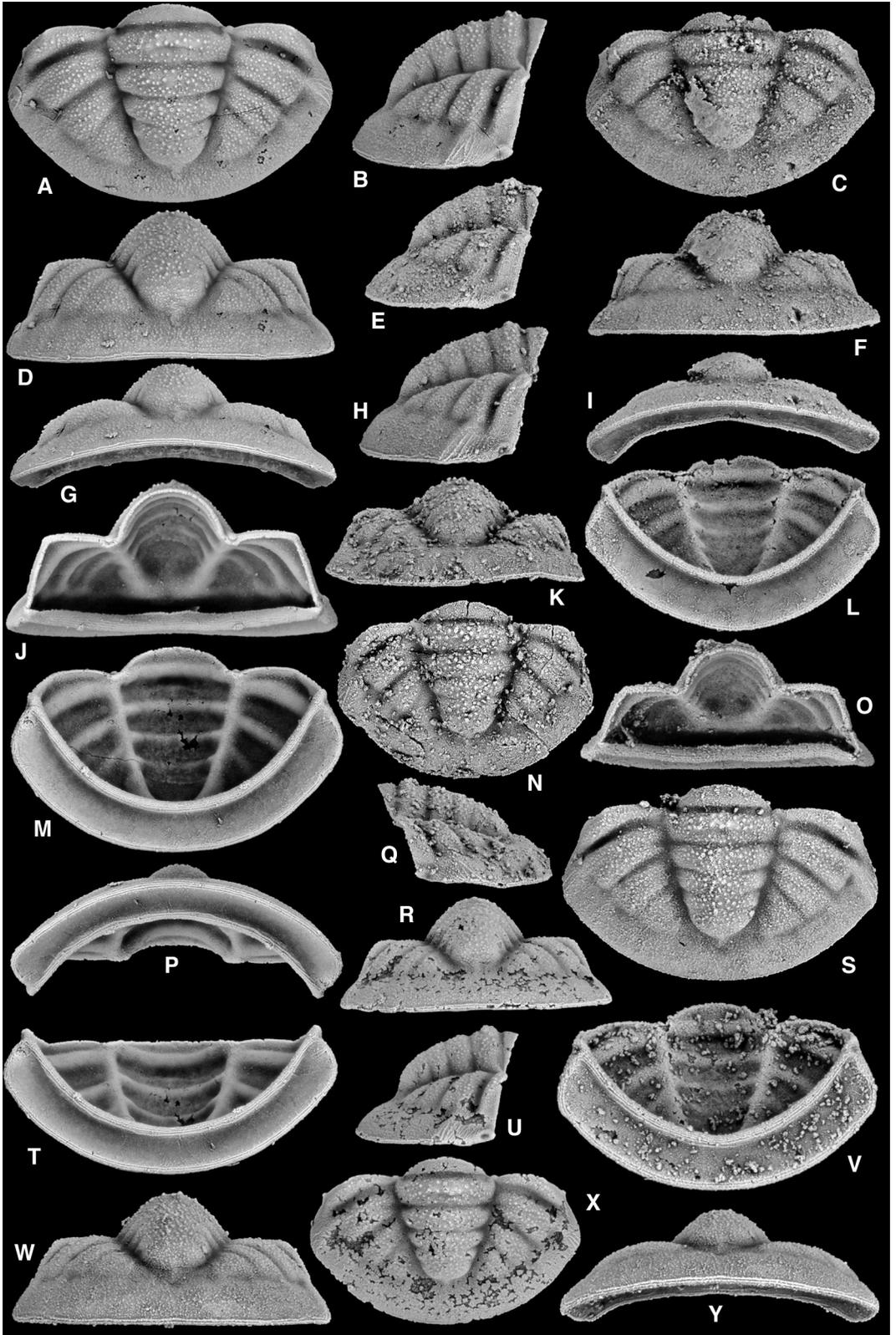
Figure 27 (opposite). *Psalikelopsis newmani* sp. nov., from Section G 99.3 m and 99T m, Fillmore Formation (lower Floian; Tulean; *Psalikelus spinosum* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. **A, D,** left librigena, SUI 128942, external and ventrolateral views, x9 (G 99T m). **B,** left librigena, SUI 128943, external view, x15 (G 99T m). **C,** right librigena, SUI 128944, external view, x10 (G 99.3 m). **E,** right librigena, SUI 128945, external view, x10 (G 99T m). **F,** right librigena, SUI 128946, external view, x10 (G 99.3 m). **G, J, K,** right librigena, SUI 128947, external, internal, and ventrolateral views, x10 (G 99T m). **H,** left librigena, SUI 128948, external view, x10 (G 99T m). **I,** left librigena, SUI 128949, external view, x9 (G 99T m). **L, Q,** left librigena, SUI 128950, external and ventrolateral views, x9 (G 99.3 m). **M, N, P,** right librigena, SUI 128951, external, internal, and ventrolateral views, x10 (G 99.3 m). **O,** right librigena, SUI 128952, external view, x9 (G 99.3 m).

inner part of doublure turned up along distinct break in slope from sculptured region, smooth, terminating in sharp edge along inner bound of lateral and posterior border furrows; distinct Panderian notch set almost adjacent to posterior

facial suture (Fig. 1A).

Hypostome and rostral plate not identified.

Thoracic segments with large articulating half ring lacking sculpture, rear margin describing very shallow W shape in anterior segments,



nearly transverse in posterior segments; ring furrow long and deep, shorter (exsag.) distally; axial ring shortest sagittally, longest along axial furrow, with sculpture of medium sized tubercles on middle region and much smaller fine tubercles above axial furrow; rear of ring gently anteriorly bowed; lateral regions of ring with distinct independent inflation (Fig. 28F, H); axial furrow shallow, interrupted anteriorly by short, anteriorly-turned extension of anterior pleural band, bowed laterally around ring and not clearly distinguished from pleural furrow, distinct and very narrow posteriorly where it cuts across posterior pleural band; anterior pleural band slightly shorter (exsag.) than posterior pleural band, inflated, semicylindrical, with sculpture of very fine tubercles, set back from anterior margin by short (exsag.), shallow furrow, broadened distally into triangular articulating facet with small distal socket; posterior pleural band with slightly larger tubercles than anterior band; pleural furrow very long (exsag.) and trough-like, shorter distal to fulcrum and pinched out distally; anterior and posterior bands fuse distally to form pleural spine, short and posteriorly turned, with sculpture of fine, anastomosing raised lines; anterior pleural margin forms transverse articular ridge; transverse groove beneath posterior pleural margin articulates with this ridge; doublure forms crescentic articular surface beneath axial ring with sculpture of densely crowded, transverse raised lines; doublure under distal portion of pleura underlies spine and forms notch with posteriorly directed peg which articulates with distal pleural socket.

Pygidial measurements based on specimens of Figures 29A, C, S, X and 30A, G, M, Q. Pygidium with maximum width 160.3% (156.2-164.4) sagittal length; axis with maximum width across first ring 37.6% (35.2-38.9) maximum pygidial width and sagittal length 64.4% (61.1-69.6) that of pygidium; articulating half ring large, sagittal length 10.3% (9.1-11.7) that of pygidium, unsculptured; ring furrow transverse, moderately long, deep; first ring with pseudo-articulating half ring of second segment prominently expressed, taking up nearly half of sagittal length; first ring longer (exsag.) distally, gently inflated into lateral lobes near axial furrow; ring with sculpture of small to medium tubercles, expressed also on area

of pseudo-articulating half ring; anterior bound of pseudo-articulating half ring forming anteriorly arched furrow, well expressed only medially; axial furrow deep and well expressed all along course, nearly straight and not prominently deflected around rings, running out into flattened posterior area, but rear of axis clearly circumscribed; faint post-axial ridge discernible on all specimens; first and second axial furrows transverse and typically well impressed, third much more weakly expressed; second and third rings similar in morphology to first, but pseudo-articulating half ring progressively less well expressed; fourth ring differentiated from transverse terminal piece; width across fourth ring 63.9% (60.4-67.6) that across first ring; anterior and posterior pleural bands of first segment subequal in length (exsag.), with sculpture of fine tubercles, turned posteriorly at fulcrum and merged distally into articulating facet with socket similar in morphology to thorax, rear part of merged area extended posteriorly to form anterior face of border, sculptured with raised lines, exsagittal length of first segment 72.3% (59.4-79.8) sagittal length of axis; first pleural furrow very long and deep, pinched off proximal to distal articulating surface; pleura of second segment well expressed, anterior pleural band distinctly longer (exsag.) than posterior band, sculpture similar to first segment, pleural furrow still prominent but not as deep as that of first segment, bands and furrow terminated at broad, flat, unsculptured, steeply downturned region bounding pygidium posteriorly, set off from proximal pleura by shallow, narrow bounding furrow; first interpleural furrow very short (exsag.) and shallow, but course discernible on all specimens; second interpleural furrow about as well expressed as first; pleura of third segment expressed in all specimens as complete complement of bands and pleural furrow, but crowded, posteriorly turned, narrow, and much less well defined than first two segments; pleura of fourth segment small and weakly defined, fourth pleural furrow clear in most specimens (e.g., Figs 29S, 30G), not expressed in a few (e.g., Fig. 30I); posterior margin of pygidium almost semicircular; posterolateral rim sharp, with sculpture of subparallel raised lines; ventral region beneath flattened posterior area forming broad, ventrally concave shelf lacking sculpture; inner extent of

Figure 29. *Psalikilopsis newmani* sp. nov., from Section G 99.3 m and 99T m, Fillmore Formation (lower Floian; Tulean; *Psalikilus spinosum* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. **A, B, D, G, J, M, P, T**, pygidium, **holotype**, SUI 128957, dorsal, posterior, slightly posteroventral, anterior, ventral, extreme posteroventral, and moderate posteroventral views, x10 (G 99T m). **C, E, F, L, O**, pygidium, SUI 128958, dorsal, right lateral, posterior, slightly posteroventral, ventral, and anterior views, x10 (G 99.3 m). **H, S, V, W, Y**, pygidium, SUI 128959, right lateral, dorsal, ventral, posterior, and slightly posteroventral views, x12 (G 99.3 m). **K, N, Q**, pygidium, SUI 128960, posterior, dorsal, and left lateral views, x10 (G 99.3 m). **R, U, X**, pygidium, SUI 115132, posterior, right lateral, and dorsal view, x12 (G 99T m).

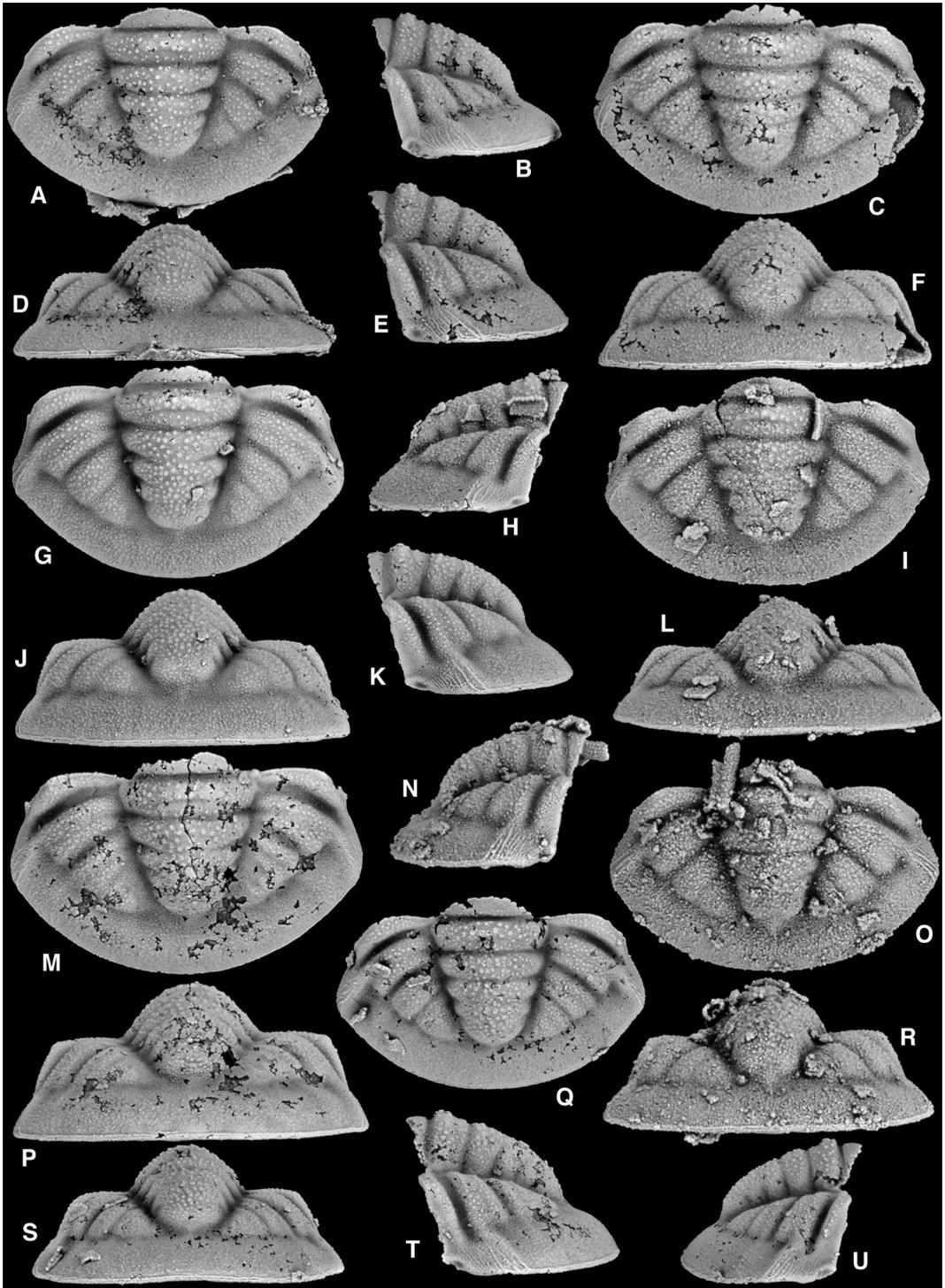


Figure 30. *Psalikilopsis newmani* sp. nov., from Section G 99T m, Fillmore Formation (lower Floian; Tulean; *Psalikilus spinosum* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. **A, B, D,** pygidium, SUI 128961, dorsal, left lateral, and posterior views, x12. **C, E, F,** pygidium, SUI 128962, dorsal, left lateral, and posterior views, x15. **G, J, K,** pygidium, SUI 128963, dorsal, posterior, and left lateral views, x10. **H, I, L,** pygidium, SUI 128964, right lateral, dorsal, and posterior views, x12. **M, P, T,** pygidium, SUI 128965, dorsal, posterior, and left lateral views, x10. **N, O, R,** pygidium, SUI 128966, right lateral, dorsal, and posterior views, x15. **Q, S, U,** pygidium, SUI 128967, dorsal, posterior, and right lateral views, x12.

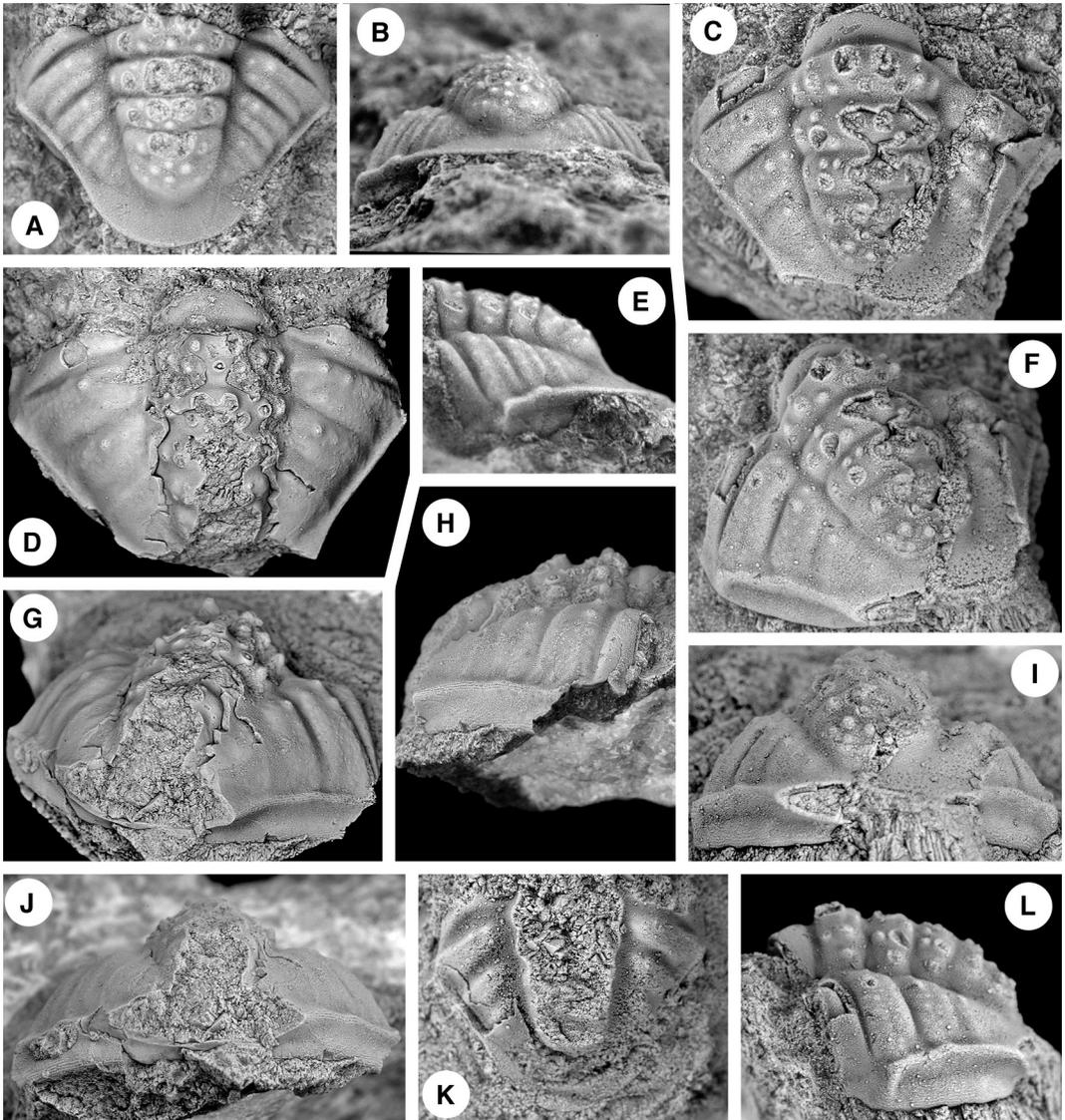


Figure 31. *Psalikelopsis* sp. nov. 1, from Back Cove Section, boulder 9.5/4, Shallow Bay Formation (Floian), Cow Head Peninsula, western Newfoundland, Canada. A, B, E, pygidium, GSC 134000, dorsal, posterior, and left lateral views, x10. C, F, I, L, pygidium, GSC 134001, dorsal, oblique, posterior, and left lateral views, x6. D, G, H, J, pygidium, GSC 134002, dorsal, oblique, right lateral, and posterior views, x2.5. K, pygidium, GSC 134003, dorsal view, x7.5.

shelf bounded by prominent inflated ridge with raised line sculpture, running beneath distal extent of dorsal expression of pleural bands and furrows; narrow doublural sector turned dorsally from inflated ridge and held vertically (Fig. 29J, O).

Ontogeny. The available sample of cranidia and pygidia includes no small specimens. The librigena undergoes substantial holaspid ontogenetic change. The genal spine is elongate and cylindrical in the smallest recovered specimen (Fig. 27B) and becomes first a sharp point (Fig.

27L) then a more bluntly rounded point (Fig. 27A) with increasing size. The rear of the lateral border furrow and the entire posterior border furrow become shallower in large specimens. The field becomes considerably broader with size. The eye socle and the furrow separating the socle from the field each become broader with size. The lateral margin becomes more laterally arcuate with increasing size.

Material. Holotype, pygidium, SUI 128957 (Fig. 29A, B, D, G, J, M, P, T), from Section G 99T

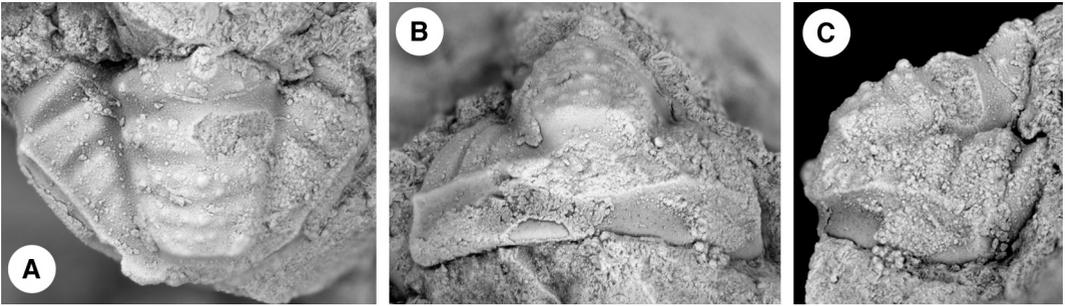


Figure 32. *Psalikelopsis* sp. nov. 2, from Back Cove Section, boulder 9.1/3, Shallow Bay Formation (Floian), Cow Head Peninsula, western Newfoundland, Canada. **A, B, C,** pygidium, GSC 134004, dorsal, posterior, and right lateral views, x12.

m, and assigned specimens SUI 115131, 115132, 128931-128956, 128958-128967, from Section G 99.3 m and G 99T m, Fillmore Formation (lower Floian; Tulean; *Psalikilus spinosum* Zone), southern Confusion Range, Ibex area, Millard County, western Utah.

Etymology. After Paul Newman.

Remarks. *Psalikelopsis newmani* was distinguished from all of the more derived species in the genus discussion. Although it is common in the *Psalikilus spinosum* Zone at Ibex, the species has not been recovered from this interval in the Garden City Formation in southeastern Idaho.

***Psalikelopsis* sp. nov. 1** (Fig. 31)

Material. Assigned specimens GSC 134000-134003, from Back Cove Section, boulder 9.5/4, Shallow Bay Formation (Floian), Cow Head Peninsula, western Newfoundland, Canada.

Remarks. Two boulders from conglomerates of the Shallow Bay Formation contain sparse material representing two species of *Psalikelopsis*. The beds from which the boulders were derived are dated as *Prioniodus elegans* Zone (Fåhraeus & Nowlan 1978), which indicates they are younger than all of the western Laurentian species treated herein. The *Prioniodus elegans* Zone is broadly equivalent to the *Oepikodus communis* Zone of the Midcontinent scheme. The western Laurentian species are from strata assigned to the underlying *Acodus deltatus/Oneotodus costatus* Zone (Ross *et al.* 1997).

Psalikelopsis sp. nov. 1 is represented by four pygidia, which are distinguished by their broad but short posterior projection. Whereas in the western Laurentian species this projection is in the form of a posteromedian spine, it is more of a broad shelf in *Psalikelopsis* sp. nov. 1. The condition is closest to that seen in *P. redfordi*, in

which the spine is somewhat broad, flattened, and lobate, but that of *Psalikelopsis* sp. nov. 1 is much wider and slightly shorter sagittally. The pleural regions are of approximately the same dimensions, but the axis of *Psalikelopsis* sp. nov. 1 is broader than that of *P. redfordi*, and has a sculpture of large and more widely spaced versus small and dense tubercles. The subquadrate pleural spine on the first segment (e.g., Fig. 31E) hardly protrudes laterally in *Psalikelopsis* sp. nov. 1, whereas it is quite broad in *P. redfordi*.

***Psalikelopsis* sp. nov. 2** (Fig. 32)

Material. Assigned specimen GSC 134004, from Back Cove Section, boulder 9.1/3, Shallow Bay Formation (Floian), Cow Head Peninsula, western Newfoundland, Canada.

Remarks. A second species in the Shallow Bay Formation is represented by a single pygidium. This is very similar to the single pygidium from the Fort Cassin Formation illustrated by Brett & Westrop (1996, fig. 16.9, 16.10) and they could possibly represent the same species. However this cannot be determined with confidence on the basis of two incomplete sclerites. The Fort Cassin pygidium has a narrower, apparently posteriorly pointed spine which is very different from the broad shield seen in *Psalikelopsis* sp. nov. 1. The pygidium of *Psalikelopsis* sp. nov. 2 has the spine broken off, but it appears similar in basal width to that of the Fort Cassin specimen. The specimens share a narrow pleural region and an axial sculpture of a few larger tubercles with scattered medium tubercles, with the axial sculpture in general less dense than in *Psalikelopsis* sp. nov. 1. Among the western Laurentian species, *Psalikelopsis* sp. nov. 2 compares most closely with *P. cuspidicauda*, as it does not have the fulcrum set far distally as in *P. paracuspicauda*.

Taken together, all of the eastern Laurentian species differ from the older western Laurentian

taxa in the possession of much coarser axial tuberculation and in apparently having an out-turned ventral rim to the “wall”.

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