

Affinities of the Lower Ordovician (Tulean; lower Floian) trilobite *Gladiatoria*, with species from the Great Basin, western United States

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Macropyge gladiator Ross, 1951a, is the type species of the previously monotypic *Gladiatoria* Hupé, 1955. It has been regarded as the only known post-Tremadocian macropygine ceratopygid, and the only known ceratopygid from the Ordovician of Laurentia. Well preserved new material from western Utah and southern Idaho includes the first positively identified cephalic sclerites and demonstrates that *Gladiatoria* is a component of Bathyruridae, a family common in shallow water Lower Ordovician assemblages from Laurentia. *Gladiatoria* is closely related to and regarded as the sister taxon of *Bathyurellus* Billings, 1865, to which it is nearly identical in cephalic morphology. In addition to an extended revision of the type species, which is from the lower *Psalikilopsis cuspidicauda* Zone, new species described include *G. phoenixi* (*Hintzeia celsaora* Zone), *G. nielsenae* (*Psalikilopsis cuspidicauda* Zone and *Psalikilus typicum* Zone), *G. harrisi* (upper *Psalikilopsis cuspidicauda* Zone), *G. reedi* (*Psalikilus typicum* Zone and *Psalikilus hestoni* Zone) and *G. crowei* (*Protopliomerella contracta* Zone). All are from the Tulean Stage (lower Floian).

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THE PHYLOGENETIC affinity of the species *Macropyge gladiator* Ross, 1951a, has long been enigmatic. Ross (1951a) originally assigned the species to *Macropyge* Stubblefield in Stubblefield & Bulman, 1927. *Macropyge* was historically considered a remopleuridoidean (e.g., Moore 1959; Peng 1984), though Kobayashi (1937) erected a monotypic family for it. Owens *et al.* (1982, p. 14) assigned *Macropyge* with question to Ceratopygidae Linnarsson, 1869 (see also Fortey & Chatterton [1988, pp. 196-197]). Hupé (1955) erected a new monotypic genus, *Gladiatoria*, with *M. gladiator* as type. Whittington (in Moore 1959) placed *Gladiatoria* in junior subjective synonymy of *Macropyge*. Most subsequent authors (e.g., Dean in Özgül *et al.* 1973; Dean 1989; Ross *et al.* 1997) have accepted this, though Dean (in Özgül *et al.* 1973) noted that it was not closely comparable to his new species, *M. taurina*, from Turkey. Shergold & Sdzuy (1984, p. 94) rejected the synonymy of *Gladiatoria* and *Macropyge*.

Understanding of the species has been hampered by the fact that it has been known only from pygidia and posterior thoracic segments (Ross 1951a, pl. 30, figs. 14, 22; Ross 1951b, pl. 84, figs 1-10). Ross (1951a, pl. 27, figs. 8-10) tentatively assigned a cranidium, but as recognized by Dean (1989, pp. 13, 38) this represents a species of the asaphid *Aulacoparia* Hintze & Jaanusson, 1956.

Ceratopygidae is a diverse family of Asaphina (*sensu* Fortey & Chatterton 1988). Forty-six genera have been proposed, of which 16 are presently considered subjective synonyms, two are homonyms, one is an objective synonym, and 29 are valid genera. Most of the family's diversity is Upper Cambrian, but twelve genera represented by some 58 valid species occur in the Tremadocian. The family has a wide distribution on other palaeocontinents, including Gondwana and associated terranes, North and South China, and Baltica. Although 44 species occur in the

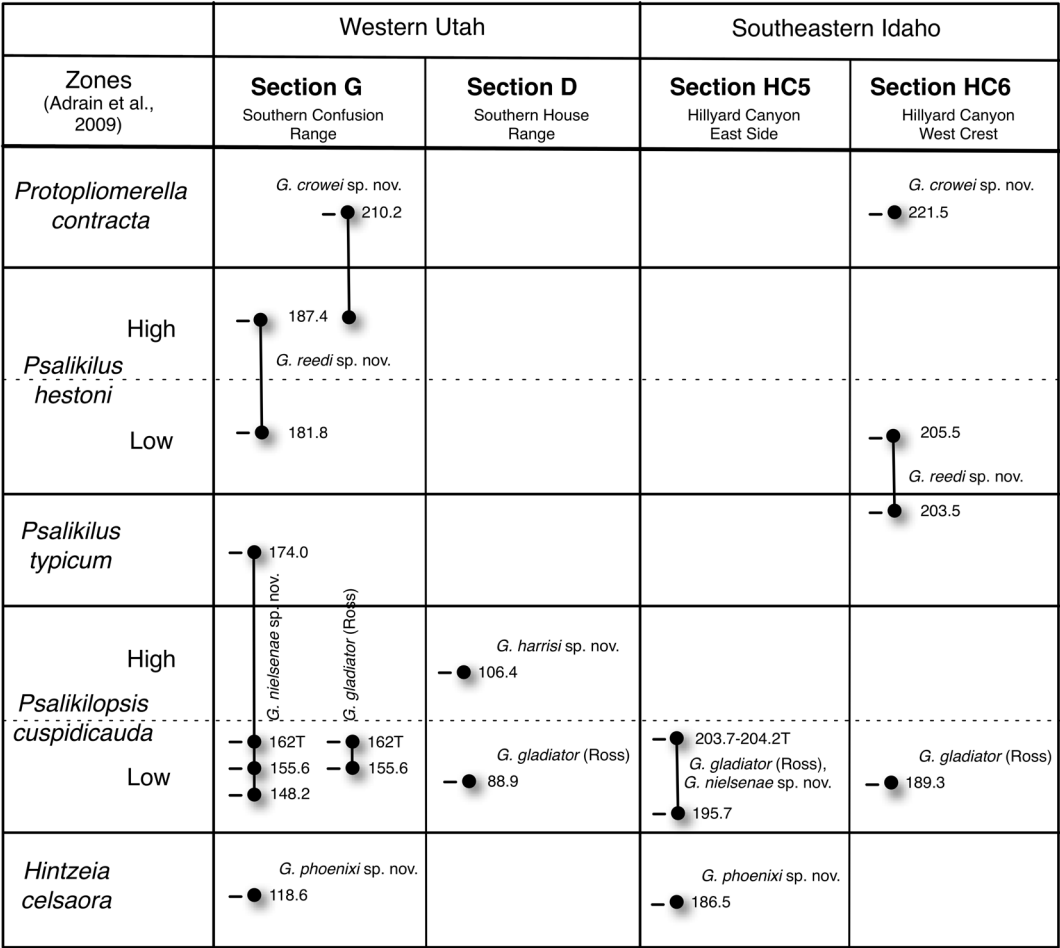


Figure 1. Schematic diagram of stratigraphic distribution of species of *Gladiatoria* in Tulean (lower Floian) sections of the Fillmore Formation in western Utah (Sections G, D) and the Garden City Formation in southeastern Idaho (Sections HC5, HC6). Measurements are in metres. Metreages are not to scale. Zonation is that established by Adrain *et al.* (2009). The “T” designation stands for a talus sample, almost all of which are weathering essentially *in situ*.

lower Tremadocian, only 12 are known from upper Tremadocian strata, and none from younger rocks. Hence, if *Gladiatoria gladiator* really was a ceratopygid, it would be the youngest member of the family, and the only example known from the Ordovician of Laurentia.

The present paper is based on new material collected in the course of a comprehensive field-based revision (Adrain *et al.* 2001, 2003, 2009; Adrain & Westrop 2006a, b, 2007a, b; McAdams & Adrain 2009a, b, 2010, 2011) of the silicified Lower Ordovician trilobite faunas described by Ross (1951a) and Hintze (1953). New collections have yielded the first knowledge of unambiguously associated cephalic sclerites of the type species, along with material of five new species referable to *Gladiatoria*. This new material demonstrates that the taxon should be assigned to Bathyruridae Walcott, 1886, a group

which is common in Laurentian shallow water faunas of this age.

LOCALITIES AND STRATIGRAPHY

Material described is from the type Ibexian sections in the Ibex area of western Utah (Hintze 1951, 1953, 1973; Ross *et al.* 1997) and from Ross’ (1949, 1951a) sections through the Garden City Formation in southeastern Idaho. We remeasured and logged the sections, and sampled them in detail. Full locality data, including maps and a graphical section log for Section G at Ibex, were presented by Adrain *et al.* (2009) and are not repeated herein. The horizons, sections, and zones from which species were recovered are shown schematically in Figure 1.

SYSTEMATIC PALAEONTOLOGY

Repository. All type and figured material is housed

in the Paleontology Repository, Department of Geoscience, University of Iowa, Iowa City, with specimen number prefix SU1.

Note on terminology. The librigenae treated herein, and those of the closely related *Bathyuirellus*, have generally featureless fields which give the impression of extending nearly to the lateral margin. This margin is typically developed into a sharp, distinctly inflated rim, bounded adaxially by a narrow furrow. It is important to note that this rim is not in itself the true lateral border, and the furrow is not the lateral border furrow. Reference to other bathyurid librigenae (e.g., Loch 2007, pl. 20, fig. 7) shows that true posterior and lateral border furrows matching the inner extent of the doublure are present and are almost certainly secondarily effaced in *Gladiatoria* and *Bathyuirellus*. Presumptively plesiomorphic librigenae like that illustrated by Loch also have a sharp inflated lateral rim with associated narrow furrow identical to that retained in *Bathyuirellus* and *Gladiatoria*. Hence these structures are not termed the “lateral border” and “lateral border furrow” herein as they are both secondary modifications of part of the true lateral border.

Family BATHYURIDAE Walcott, 1886

***Gladiatoria* Hupé, 1955**

Type species. Macropyge gladiator Ross, 1951a, from the Garden City Formation (lower Floian; Tulean; lower *Psalikilopsis cuspidicauda* Zone), Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho, USA.

Other species. Gladiatoria crowei sp. nov.; *G. harrisi* sp. nov.; *G. nielsenae* sp. nov.; *G. phoenixi* sp. nov.; *G. reedi* sp. nov.; *Gladiatoria* sp. 1.

Diagnosis. External surfaces of all sclerites with either very fine anastomosing raised lines or completely smooth and lacking sculpture, tubercles never developed; glabellar furrows visible only as shallow indentations in lateral glabellar margin or entirely effaced; glabella long, gently waisted; preglabellar field short (sag.) or absent in mature specimens; eye socle absent, eye separated from field by narrow, incised furrow; librigenal posterior and lateral border furrows extremely shallow or completely effaced; librigenal lateral margin with pronounced, sharp rim; genal spine moderately long and tapering rapidly to a sharp point; pygidium elongate, axis extended posteriorly into large, inflated spine with sharp posterior tip; two pygidial axial rings; two segments expressed on pygidial

pleurae, posteriormost expressed more weakly and variably; pygidial doublure broad beneath spine, anterior margin marked by raised ridge interrupted medially, short portion of doublure turned dorsally anterior to ridge.

Remarks. Now that cephalic material has been properly associated and additional species described, the affinity of *Gladiatoria* is obvious. It is very similar to the bathyurid genus *Bathyuirellus* Billings, 1865. Either the genera are sister groups, or possibly *Gladiatoria* creates paraphyly in *Bathyuirellus*. *Bathyuirellus* as recognised herein consists only of two eastern Laurentian species, both from the Floian Catoche Formation of western Newfoundland, Canada. Fortey (1979) revised the type species, *B. abruptus*, and described his new *B. platypus*. Fortey also transferred other species which had previously been assigned to *Bathyuirellus*, which have a fan-shaped pygidium, to his new genus *Punka*. Apart from the Catoche Formation species, Fortey included *Bathyuirellus* (?) *teretus* Young, 1973, but this species is not closely related. We are in the process of revising it on the basis of extensive new collections, and it is clearly a member of the *Acidiphorus* group (*sensu* McAdams & Adrain 2007). Fortey (1979, p. 90) also considered that a pygidium from the *Strigigenalis plicolabeona* Zone illustrated in open nomenclature by Hintze (1953, pl. 9, fig. 16) and one illustrated by Young (1973, pl. 6, figs 17, 20) from the same horizon (H 191.7 m in our section) belonged to *Bathyuirellus* and that the correct cranidial assignment for Young's pygidium was the holotype of *Bathyuirellus* (?) *teretus* (Young, 1973, pl. 2, figs 5, 8, 13). In fact, new collections indicate without question that these pygidia belong to *Benthamaspis distincta* Young, 1973. The pygidia of *Acidiphorus teretus* are actually Young's (1973, figs 10, 11, 13) “Unassigned pygidium 6” which bear long posterior spines.

Recently, Loch (2007) described two new species from the Floian Kindblade Formation of Oklahoma which he assigned to *Bathyuirellus*, *B. arbucklensis* and *B. inflatus*. The species *B. arbucklensis* does not appear to be a member of the clade, as it has strongly anteriorly divergent facial sutures, a broad frontal area, and an extremely long anterior border, and a pygidium with the pleural region dorsally concave and crossed proximally by furrows. Loch (2007) made comparisons with the Dapingian (Whiterockian) *Bathyuirellus pogonipensis* Hintze, 1953. In the present state of knowledge, this species, with its broad, fan-shaped pygidium with the pleurae crossed by furrows, would presumably be among those assigned to *Punka*. Loch also

compared *arbucklensis* to *Bathyuirellus? teretus* Young, 1973, but, as noted above, this species is not closely related to *Bathyuirellus* or other “bathyuirellines”. Loch’s second species, *B. inflatus*, also exhibits many significant differences with the Catoche species which indicate it is probably not a member of *Bathyuirellus*. The Oklahoma species has assigned librigenae with a very distinct and well impressed lateral border furrow, whereas those of the Catoche species (and those of all species of *Gladiatoria*) have the lateral border furrow completely or almost completely effaced. The anterior border of the two illustrated cranidia of *B. inflatus* is sharply upturned, forming a strong anterior rim, whereas those of the Catoche species (and *Gladiatoria*) are flat, with a shallow border furrow. The preglabellar furrow of *B. inflatus* is deep and well impressed medially, whereas those of the Catoche species (and *Gladiatoria*) are very shallow medially. The pygidium assigned to *B. inflatus* is very unlike those of the Catoche species (and *Gladiatoria*), which have the first segment strongly deflected posteriorly at the fulcrum, to run almost posteriorly in the distal part. That of *B. inflatus* runs nearly transversely and only slightly posteriorly distally. The pygidium is very similar to those of some species of *Benthamaaspis* Poulsen, 1946, but does not closely resemble those of *Bathyuirellus*. If *B. inflatus* is phylogenetically related to *Bathyuirellus*, it definitely lies outside the clade of *Bathyuirellus*+*Gladiatoria*, as it lacks all of its synapomorphies. We regard neither of Loch’s (2007) species as members of *Bathyuirellus*.

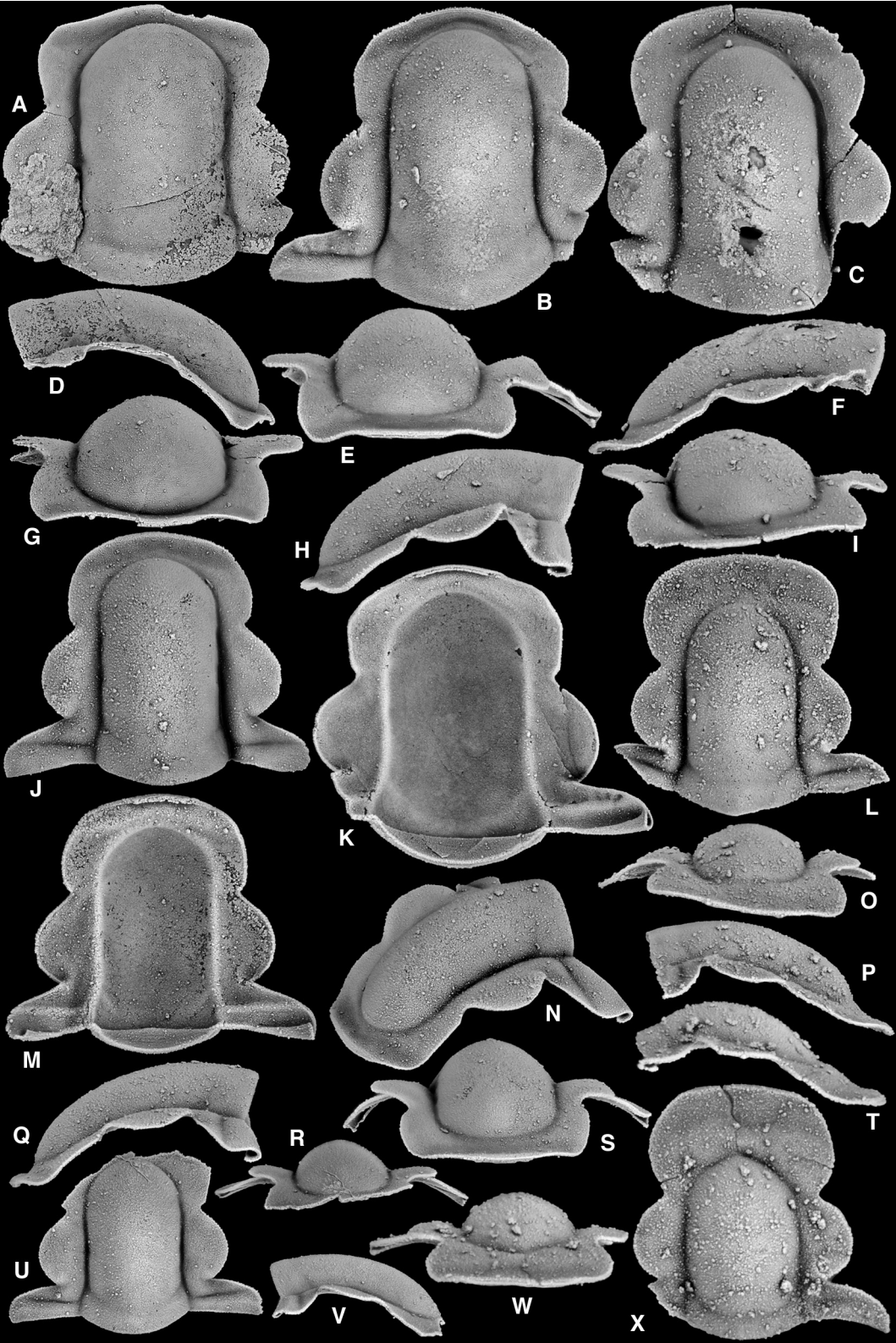
The two Catoche Formation species of *Bathyuirellus* have striking pygidial morphology, which together with distinctive cranial morphology was the basis of Fortey’s (1979) restriction and diagnosis of the genus. Now that the type and other species of *Gladiatoria* are known from abundant material, it is clear that the stratigraphically lower species *G. phoenixi* and *G. nielsenae* have cephalic morphology nearly identical with that of *Bathyuirellus*, including the same low, unvaulted glabella, relatively short and subdued anterior border, and librigenae with the true posterior and lateral border furrows effaced but retaining identical sharp, inflated lateral rims bounded by narrow furrows. The only substantial

cranial difference between the two species of *Bathyuirellus* and these two species of *Gladiatoria* is that the occipital furrow is well impressed in *Bathyuirellus* but largely dorsally effaced in *G. phoenixi* and *G. nielsenae* (which is interpreted as a synapomorphy shared by them and *G. crowei*; the other small clade within *Gladiatoria*, including the type species, retains a better impressed occipital furrow; see discussion below). The hypostome of *B. platypus* (Fortey 1979, pl. 31, figs 9, 11) differs only in minor proportion (it is narrower and has a medially longer posterior border) from those assigned to species of *Gladiatoria* (Fig. 14). At first glance, the pygidia of the two genera appear radically different. However this is entirely due to the large posterior spine developed in *Gladiatoria*. Apart from this structure, pygidia of *Bathyuirellus* and *Gladiatoria* share several apparent synapomorphies. They are each relatively small for a bathyurid, with very narrow pleurae. The structure of the first segment is directly comparable between the genera, with a very narrow proximal part, a sharp posterior deflection at the fulcrum, and a longer nearly posteriorly directed distal part. In transverse profile, the proximal part is nearly horizontal as part of a strongly vaulted axial/proximal region, and the distal part is steeply sloping (cf. Fig. 26N with Fortey 1979, pl. 32, fig. 8). Ventrally, the pygidia also share nearly identical, apparently uniquely derived morphology, as they each have the doublure developed into a broad shelf underlying all but a small anterior triangle of the dorsal pygidium. This shelf is bounded in both genera by a distinct ventral rim along its anterior margin (illustrated for *B. platypus* in negative as a prepared internal mold by Fortey [1979, pl. 31, figs. 12, 14] and for *B. abruptus* as a ventrally preserved specimen [Fortey 1979, pl. 32, fig. 12]), which is interrupted by a median slit-like depression.

In view of these multiple striking putative synapomorphies, we view *Bathyuirellus*+*Gladiatoria* as a well supported clade. At present *Bathyuirellus* is known only from eastern Laurentia while *Gladiatoria* is known only from western Laurentia. Eastern and western Laurentian shallow water benthic trilobites are well differentiated during the Floian, with no well documented species clearly shared

Figure 2. *Gladiatoria gladiator* (Ross, 1951). from Section HC5 195.7 m and HC5 203.7-204.2T m, both Garden City Formation (Tulean; lower *Psalikilopsis cuspidicauda* Zone), east side of Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho, USA. **A, D, F**, cranidium, SUI 126566, dorsal, left lateral, and anterior views, x8 (HC5 195.7 m). **B, C, E, G, H**, cranidium, SUI 115173, dorsal, ventral, anterior, right lateral, and oblique views, x8 (HC5 195.7 m). **I, J, L, M**, cranidium, SUI 126567, dorsal, ventral, right lateral, and anterior views, x9 (HC5 195.7 m). **K, N, O**, cranidium, SUI 126568, dorsal, right lateral, and anterior views, x9 (HC5 195.7 m). **P, S, V, W**, cranidium, SUI 126569, dorsal, anterior, right lateral, and oblique views, x7.5 (HC5 203.7-204.2T m). **Q, R, T**, cranidium, SUI 126570, dorsal, left lateral, and anterior views, x10 (HC5 195.7 m). **U, X, Y**, cranidium, SUI 126571, dorsal, anterior, and left lateral views, x10 (HC5 195.7 m).





(though several claims of wide distribution have been made in the literature). This is presumably due to the influence of the transcontinental arch. However, many genera are distributed in both regions. Given that *Gladiatoria* has only now been described on anything more than the posterior parts of a single species, and that *Bathyuirellus* is documented mainly from a single formation in Newfoundland (though Fortey [1979] noted its undescribed occurrence in Spitsbergen; Brett & Westrop [1996] also assigned material from the Fort Cassin Formation, New York State, to *B. platypus*), their geographic distributions should be interpreted with caution.

While the idea that the genera together form a clade seems very well supported, whether they are each monophyletic is a more difficult issue. The cephalic morphology of *Bathyuirellus* is virtually identical with that of the oldest and presumptively plesiomorphic species of *Gladiatoria*. The more “normal” (though still highly derived) pygidium of *Bathyuirellus* could be the plesiomorphic precursor to the large inflated spine developed in *Gladiatoria*. (If this is so, *Gladiatoria* sp. 1, described below, which lacks the long posterior spine, could conceivably represent a basal species of *Gladiatoria* transitional in morphology.) In this case, the species of *Bathyuirellus* might be basal members of the clade and *Bathyuirellus* might be rendered paraphyletic by *Gladiatoria*. *Bathyuirellus*, however, has pygidial modifications in addition to those shared with *Gladiatoria*, including a very well impressed proximal pleural furrow on the first segment and an inflated, vaulted, posterior pleural region covered with dense raised lines. If these features are synapomorphic then the Catoche species are sister taxa which are together the sister taxon of *Gladiatoria*. It is difficult to evaluate these alternatives given the available information. At present we regard the pygidial structures in *Bathyuirellus* as synapomorphic and the genera as monophyletic sister taxa.

Within *Gladiatoria* there appear to be two sister clades. *Gladiatoria phoenixi*, *G. nielsenae* and *G. crowei* share a long preglabellar field, generally subparallel-sided glabella, and a narrow librigenal field. All of these are probably symplesiomorphies, as they are shared also with both species of *Bathyuirellus*. However the three species uniquely share a nearly completely

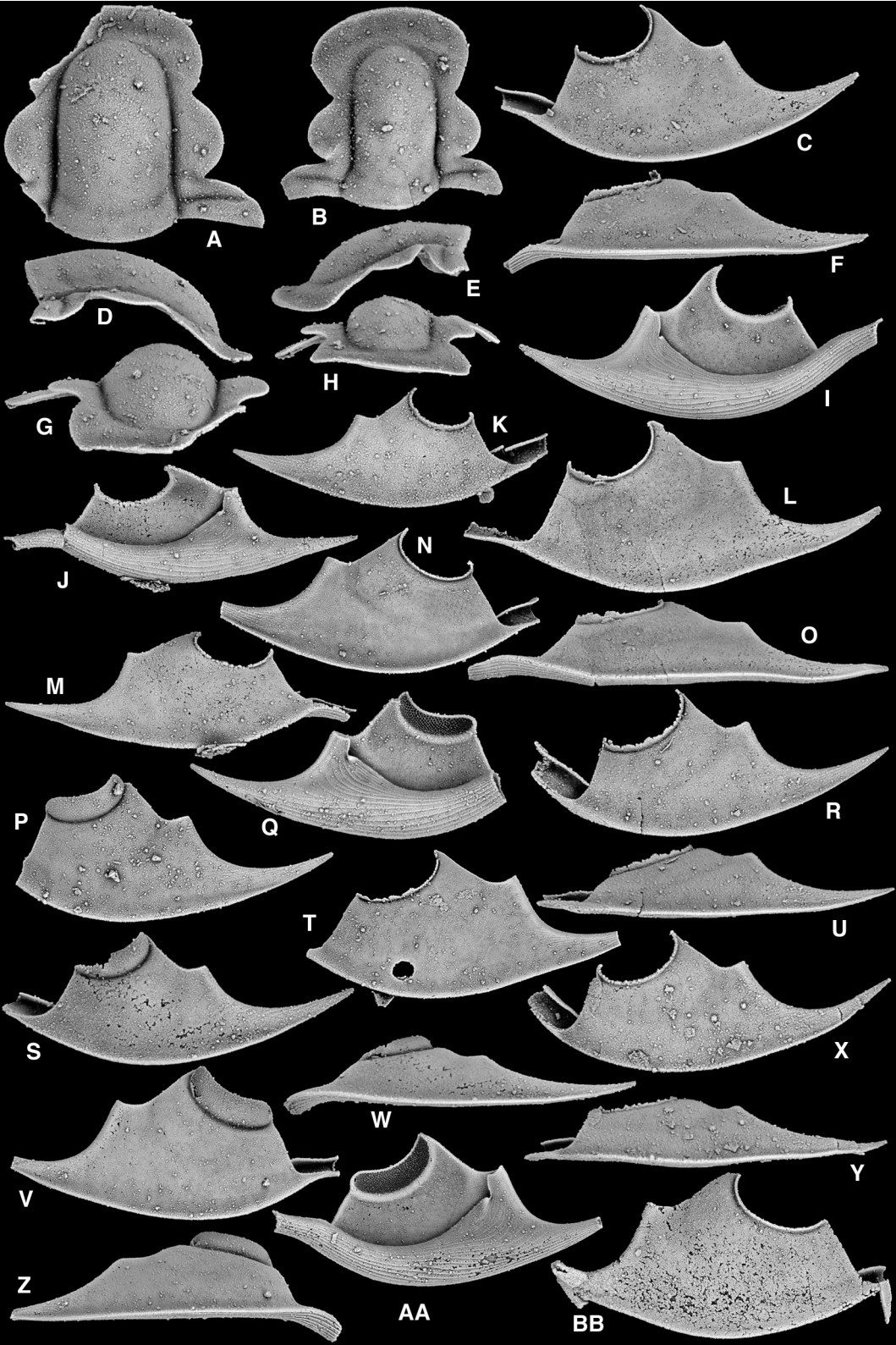
dorsally effaced occipital furrow which appears to be synapomorphic. In addition, the two younger species, *G. nielsenae* and *G. crowei*, share an unusual elongate flattened medial region of the glabella. Finally, all three species have pygidia in which the axis, including the first axial ring, is mostly dorsally effaced. *Gladiatoria gladiator*, *G. harrisi* and *G. reedi* form a second clade, synapomorphies of which include an inflated, anteriorly extended, and more strongly waisted glabella which abuts or overhangs the anterior border, with the preglabellar field absent in mature specimens, and broad librigenal fields. The species also share a relatively well expressed and medially complete occipital furrow with occipital lobes often expressed, and pygidia in which the first axial ring is prominently expressed, but these are likely symplesiomorphies as they are shared also with the two species of *Bathyuirellus* (though the status of the occipital lobes in *Bathyuirellus* is ambiguous based on the few available specimens).

***Gladiatoria gladiator* (Ross, 1951a) (Figs 2-9)**

- 1951a *Macropyge gladiator*; Ross, p. 122, pl. 30, figs 14, 22, [non pl. 27, figs 8-10 = *Aulacoparia* sp.].
 1951a *Niobe* ? sp.; Ross, p. 106, pl. 27, figs 24-26, 31.
 1951b *Macropyge gladiator* Ross; Ross, p. 585, pl. 84, figs 1-10.
 1955 *Gladiatoria gladiator* (Ross); Hupé, p. 221, fig. 190, 10a.
 1960 *Macropyge gladiator* Ross; Palmer, p. 76.
 1973 *Macropyge gladiator* Ross; Dean in Özgül *et al.*, p. 14.
 1984 *Gladiatoria gladiator* (Ross); Shergold & Sdzuy, p. 94.
 1989 *Macropyge gladiator* Ross; Dean, p. 13.
 1997 *Macropyge gladiator* Ross; Ross *et al.*, pp. 19, 44.
 1998 *Macropyge gladiator* Ross; White & Lieberman, p. 84.
 2003 *Gladiatoria gladiator* (Ross); Jell & Adrain, p. 378.
 2009 *Gladiatoria gladiator* (Ross); Adrain *et al.*, p. 559, fig. 10B, F.

Diagnosis. Preglabellar field absent in mature specimens; palpebral lobes wide, extending

Figure 3. *Gladiatoria gladiator* (Ross, 1951), from Section HC6 189.3 m, Garden City Formation (Tulean; lower *Psalikilopsis cuspidicauda* Zone), west side of Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho, USA. **A, D, G,** cranium, SUI 126572, dorsal, right lateral, and anterior views, x7.5. **B, E, H, K,** cranium, SUI 126573, dorsal, anterior, left lateral, and ventral views, x12. **C, F, I,** cranium, SUI 126574, dorsal, left lateral, and anterior views, x15. **J, M, N, Q, S,** cranium, SUI 126575, dorsal, ventral, oblique, left lateral, and anterior views, x12. **L, O, P,** cranium, SUI 126576, dorsal anterior, and right lateral views, x15. **R, U, V,** cranium, SUI 126577, anterior, dorsal, and right lateral views, x12. **T, W, X,** cranium, SUI 126578, right lateral, anterior, and dorsal views, x20.

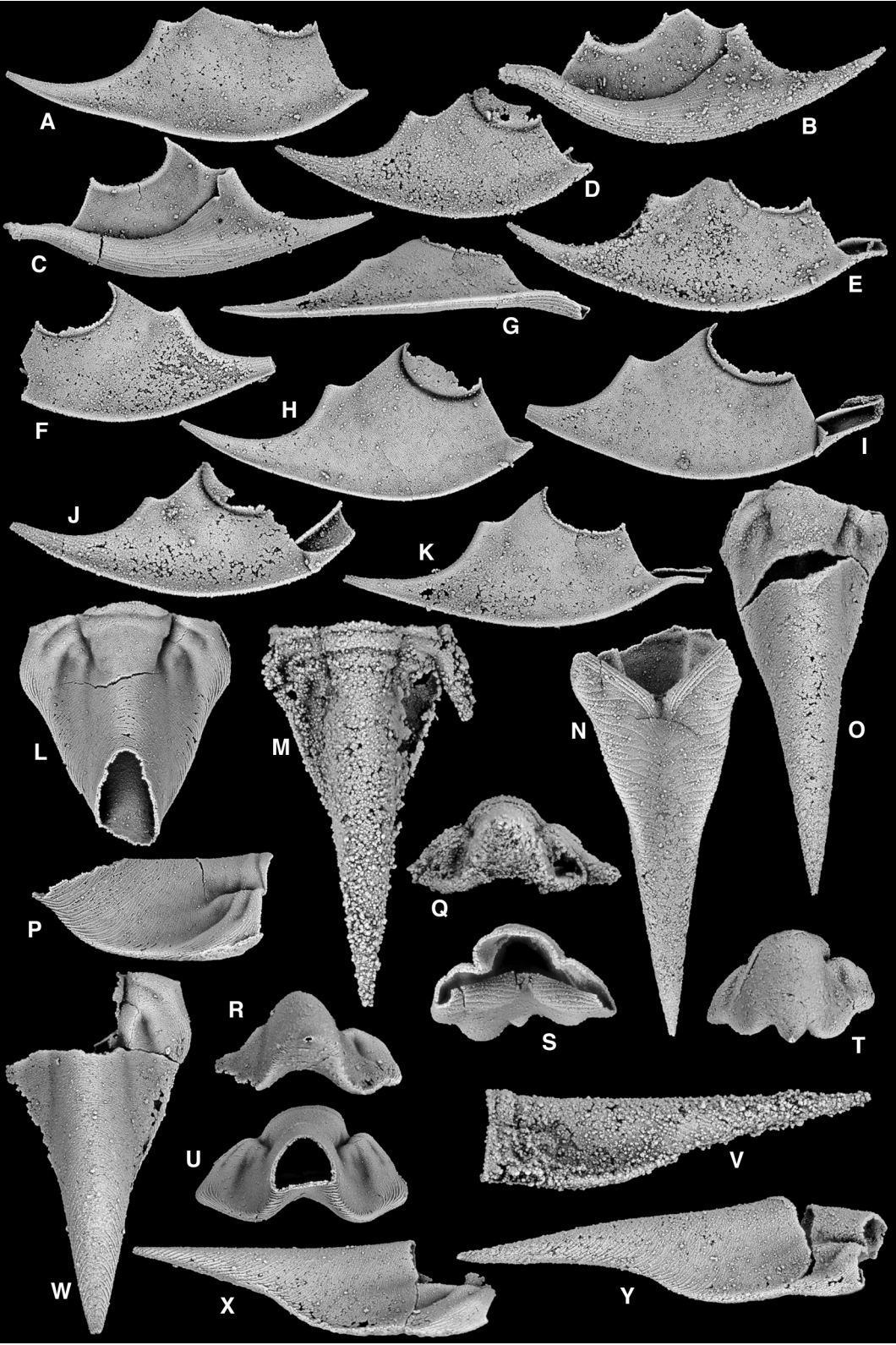


laterally well past anterior sections of facial suture; occipital furrow weak but completely expressed in most specimens; librigenal field wide; strong angle between posterior librigenal margin and abaxial edge of genal spine; pygidium broad anteriorly; pygidial margin opposite pleurae distinctly sinuous; second pygidial pleural furrow well expressed, reaching nearly to pygidial margin.

Description. Measurements were made on the largest relatively intact crania (Figs 2A, B, I, 3B, J). Cranium moderately vaulted, glabella occupying most of length, with smoothly arcuate sagittal profile; entire dorsal surface of cranium with sculpture of very fine, scrobiculate, raised lines; sculpture is so fine that it is easily lost or obscured by preservation such that surfaces appear nearly smooth; maximum width across posterior projections 125.0% (119.5-134.7) sagittal length; anterior sections of facial sutures bowed moderately laterally, parentheses shaped, width across maximum point of divergence 75.7% (71.6-81.1) sagittal cranial length; preglabellar field distinct in smaller specimens, but nearly or completely lost in larger specimens, with the anterior portion of the glabella nearly (e.g., Fig. 3B) abutting anterior border or more commonly overhanging anterior border (e.g., Figs 2A, B, I, 3A); anterior border nearly flat, with only slight dorsal convexity in sagittal and exsagittal profile, sagittal length 8.0% (6.4-10.4) that of cranium; anterior margin gently anteriorly arcuate; anterior border furrow very shallow but with distinct break in slope posteriorly to frontal areas; anterior border with a few subdued raised lines on marginal rim-like, slightly inflated region, mostly forward-facing; palpebral lobes long (exsag.), fairly wide; width across β 69.6% (65.9-74.9) cranial sagittal length; width across maximum width of palpebral lobes 96.6% (94.7-99.0) cranial sagittal length; width across ϵ 76.6% (70.8-80.5) cranial sagittal length; main body of palpebral lobe held nearly horizontally, flat; very faint swollen rim around margin; palpebral

furrow faintly impressed in some specimens, mainly posteriorly and anteriorly (e.g., Fig. 2A), entirely effaced in others; frontal area fairly broad, lacking sculpture; interocular fixigena separated from palpebral lobe by distinct break in slope, sloped toward axial furrow; anterior edge of palpebral lobe separated from axial furrow by strip of fixigena about as wide as anterior border is long, eye ridge not expressed; posterior edge of palpebral lobe set slightly farther from axial furrow than anterior edge; posterior fixigena swollen behind palpebral lobe and along axial furrow; posterior projection extended far laterally, width across projections 125.0% (119.5-134.7) cranial sagittal length; posterior border furrow running transversely to slightly anterolaterally, shallow near contact with axial furrow, deepest and short and incised in middle two thirds of course, shallowed adaxial to contact with facial suture; posterior fixigena forming wide triangular strip in front of posterior border furrow; posterior border short adaxial to fulcrum, longer abaxially; suture curved to create slightly lobate tip of projection; axial furrow quite deep and narrow, subparallel to very slightly anteriorly divergent opposite most of length of glabella, more strongly anteriorly divergent around expanded frontal lobe of glabella in most specimens; contact with preglabellar furrow marked by tiny, obliquely set ridge crossing furrow from anterior part of glabella to frontal area (seen most clearly, e.g., on Fig. 2I); preglabellar furrow very slightly narrower than axial furrow, describing smooth arc around inflated frontal lobe of glabella; axial furrows turned sharply posterolaterally opposite LO; glabella elongate, subparallel-sided to slightly waisted in front of L1, frontal part swollen and expanded in most specimens, with strong transverse dorsal convexity and moderate sagittal convexity; S1 expressed as oblique, posteromedially directed furrow impressed only near axial furrow, very weak in some specimens; S2 expressed mainly as indentation in glabella set just posterior to position of anterior edge of palpebral lobe; S3 a very subtle indentation in

Figure 4. *Gladiatoria gladiator* (Ross, 1951), from Section HC5 195.7 m, east side of Hillyard Canyon, and Section HC6 189.3 m, west side of Hillyard Canyon, Garden City Formation (Tulean; lower *Psalikilopsis cuspidicauda* Zone), Bear River Range, Franklin County, southeastern Idaho, USA. **A, D, G**, cranium, SUI 126579, dorsal, right lateral, and anterior views, x12 (HC5 195.7 m). **B, E, H**, cranium, SUI 126580, dorsal, left lateral, and anterior views, x12 (HC5 195.7 m). **C, F, I**, left librigena, SUI 126581, external, ventrolateral, and internal views, x8 (HC5 195.7 m). **J, M**, right librigena, SUI 126582, internal and external views, x8 (HC5 195.7 m). **K**, right librigena, SUI 126583, external view, x10 (HC5 195.7 m). **L, O**, left librigena, SUI 126584, external and ventrolateral views, x7.5 (HC5 195.7 m). **N**, right librigena, SUI 126585, external view, x8 (HC6 189.3 m). **P, Q**, left librigena, SUI 126586, external and internal views, x10 (HC6 189.3 m). **R, U**, left librigena, SUI 126587, external and ventrolateral views, x10 (HC5 195.7 m). **S, W**, left librigena, SUI 126588, external and ventrolateral views, x12 (HC5 195.7 m). **T**, left librigena, SUI 126589, external view, x7.5 (HC6 189.3 m). **V, Z, AA**, right librigena, SUI 126590, external, ventrolateral, and internal views, x8 (HC6 189.3 m). **X, Y**, left librigena, SUI 126591, external and ventrolateral views, x10 (HC5 195.7 m). **BB**, right librigena, SUI 126592, external view, x7.5 (HC5 195.7 m).



glabella, not clearly expressed in some specimens; L1-L3 with only slight independent inflation and definition, in some specimens barely expressed at all; SO shallow and faint but expressed across entire course in most large specimens, shallower medially in some; course posteriorly bowed across most of width, deflected sharply anteriorly near contact with axial furrow; LO with evenly arcuate posterior margin, sagittal length 11.9% (10.5-14.0) that of cranidium; length expanded near axial furrow where distinct occipital lobes are developed, weakly separated from main body of LO by faint furrow running posterolaterally from SO just behind L1, expressed only for short course near to SO; very faint median node set slightly posterior to midlength of LO expressed in some specimens (Fig. 2A, B) but obscure in most; doublure beneath LO forming articulating surface with about five faint, subparallel raised lines, anterior margin nearly transverse but describing very shallow "W" shape; doublure beneath posterior border very short adaxially, slightly lengthened abaxially near to facial suture, but only lying beneath about rear half of border at maximum length; fossula not obviously expressed.

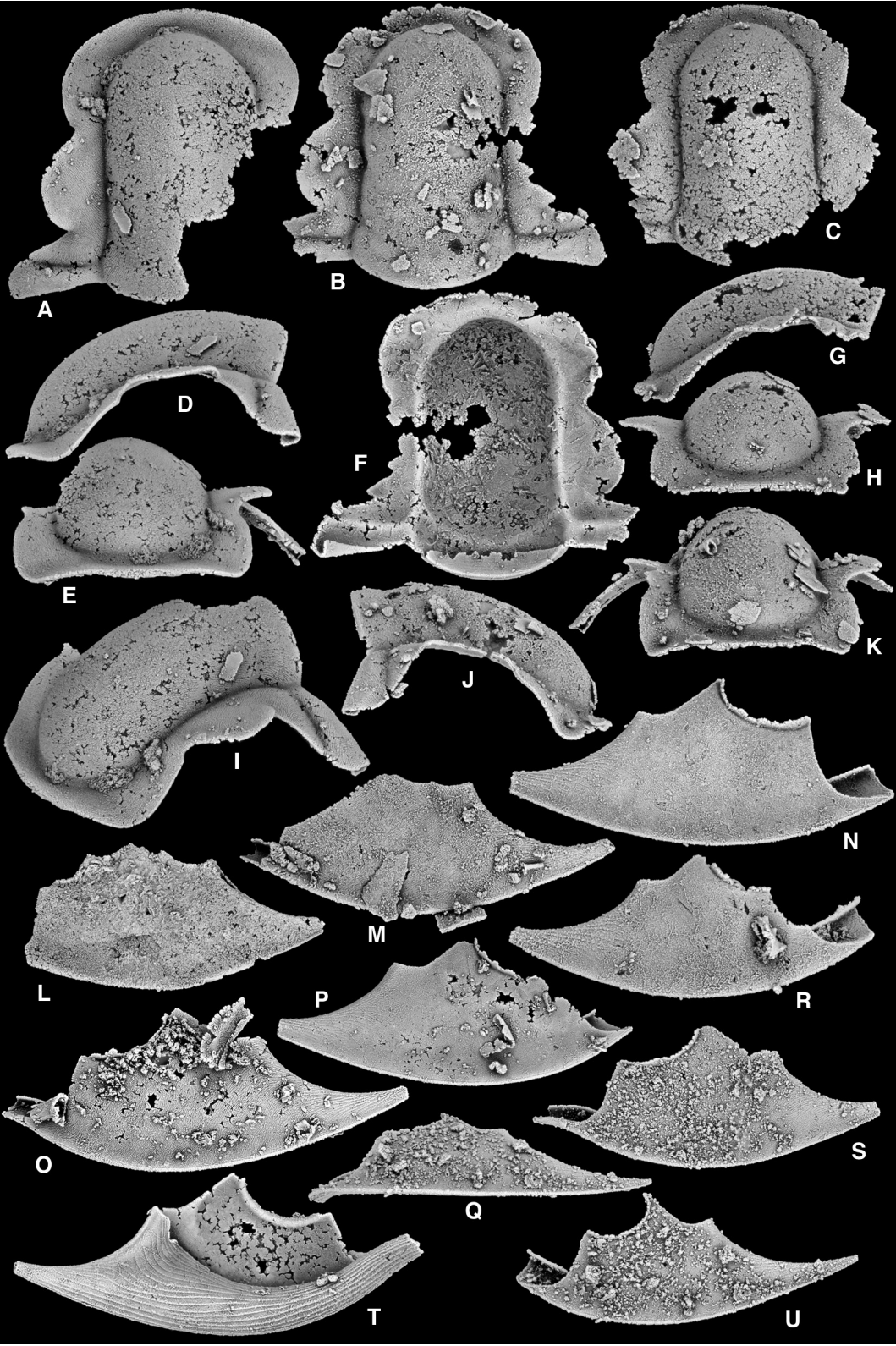
Librigena with raised line sculpture restricted to posterior part of lateral border and flat dorsal aspect of genal spine; field with very faint genal pitting in some specimens (Fig. 4L, N), completely lacking sculpture in most; eye long (exsag.) and quite narrow, separated from field by sharply incised, narrow furrow; socle barely developed as very faint, quite broad swollen area only subtly differentiated from field and not apparent in all specimens; anterior section of facial suture straight to slightly anteriorly concave, turned anteriorly across anterior projection; posterior branch of facial suture straight to distinctly sinuous, shorter than anterior section; field broad, wider posteriorly than anteriorly; lateral and posterior border furrows very shallow and faint, course clearly delineated in some specimens (e.g., Fig. 4N) but almost completely effaced and obscure in others (e.g., Fig. 4M); lateral border very broad, dorsally gently concave, with very fine scrobiculate line sculpture on rear part only, lateral margin developed into narrow slightly raised rim forming sharp lateral edge; in some specimens one or at most two raised lines running dorsally immediately beside and subparallel with margin, absent in most specimens; lateral

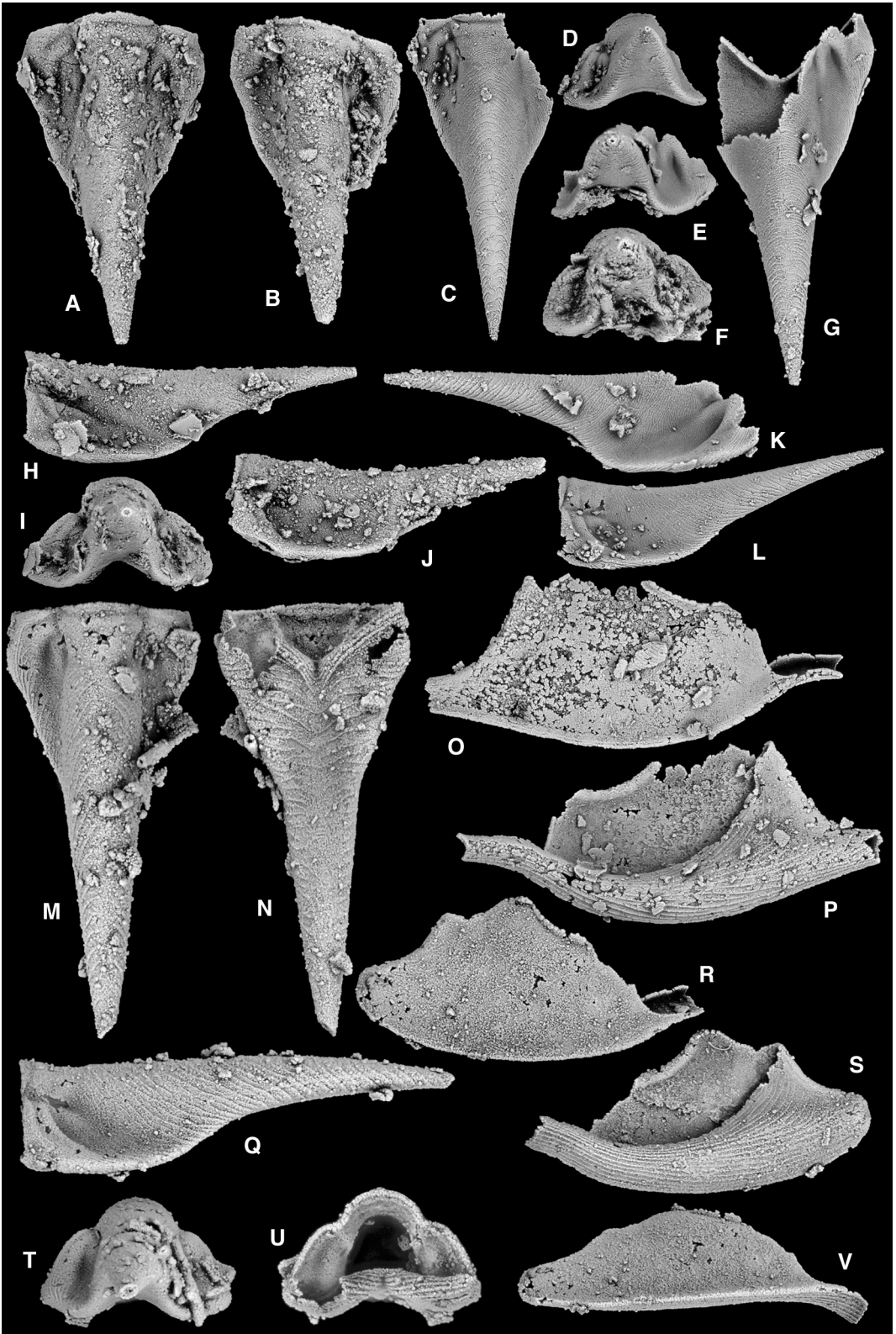
Figure 5 (opposite). *Gladiatoria gladiator* (Ross, 1951), from Section HC 5 203.7-204.2T m, east side of Hillyard Canyon, and Section HC6 189.3 m, west side of Hillyard Canyon, Garden City Formation (Tulean; lower *Psalikilopsis cuspidicauda* Zone), Bear River Range, Franklin County, southeastern Idaho, USA. **A**, right librigena, SUI 126593, external view, x8 (HC5 203.7-204.2T m). **B, E**, right librigena, SUI 126594, internal and external views, x8 (HC5 203.7-204.2T m). **C, G, K**, right librigena, SUI 126595, internal, ventrolateral, and external views, x8 (HC5 203.7-204.2T m). **D**, right librigena, SUI 126596, external view, x10 (HC5 203.7-204.2T m). **F**, left librigena, SUI 126597, external view, x8 (HC5 203.7-204.2T m). **H**, right librigena, SUI 126598, external view, x7.5 (HC5 203.7-204.2T m). **I**, right librigena, SUI 126599, external view, x7.5 (HC5 203.7-204.2T m). **J**, right librigena, SUI 126600, external view, x12 (HC5 203.7-204.2T m). **L, P, U**, pygidium, SUI 126601, dorsal, right lateral, and posterior views, x9 (HC6 189.3 m). **M, Q, V**, transitory pygidium, SUI 126602, dorsal, posterior, and left lateral views, x15 (HC5 203.7-204.2T m). **N, O, S, T, Y**, pygidium, SUI 126603, ventral, dorsal, anterior, posterior, and right lateral views, x10 (HC5 203.7-204.2T m). **R, W, X**, pygidium, SUI 126604, posterior, dorsal, and right lateral views, x9 (HC6 189.3 m).

Figure 6 (overleaf). *Gladiatoria gladiator* (Ross, 1951), from Section HC5 195.7 m and 203.7-204.2T m, east side of Hillyard Canyon, and Section HC6 189.3 m, west side of Hillyard Canyon, Garden City Formation (Tulean; lower *Psalikilopsis cuspidicauda* Zone), Bear River Range, Franklin County, southeastern Idaho, USA. **A, C, F, I, L**, pygidium, SUI 115174, dorsal, ventral, posterior, right lateral, and anterior views, x9 (HC5 195.7 m). **B, D, E, H**, pygidium, SUI 126605, posterior, dorsal, ventral, and left lateral views, x9 (HC5 195.7 m). **G, J, M**, pygidium, SUI 126606, posterior, dorsal, and right lateral views, x9 (HC5 203.7-204.2T m). **K, N, P**, pygidium, SUI 126607, dorsal, right lateral, and posterior views, x12 (HC6 189.3 m). **O, U, Y**, pygidium, SUI 126608, posterior, dorsal, and left lateral views, x8 (HC5 195.7 m). **Q, S, W**, transitory pygidium, SUI 126609, left lateral, dorsal, and posterior views, x12 (HC5 203.7-204.2T m). **R, V, Z**, pygidium, SUI 126610, dorsal, posterior, and right lateral views, x8 (HC5 195.7 m). **T, X, AA**, pygidium, SUI 126611, dorsal, posterior, and right lateral views, x9 (HC5 195.7 m).

Figure 7 (page 333). *Gladiatoria gladiator* (Ross, 1951), from Section G 155.6 m and 162T m, Fillmore Formation (Tulean; lower *Psalikilopsis cuspidicauda* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. **A, D, E, I**, cranidium, SUI 126645, dorsal, left lateral, anterior, and oblique views, x10 (G 162T m). **B, F, J, K**, cranidium, SUI 126646, dorsal, ventral, right lateral, and anterior views, x10 (G 155.6 m). **C, G, H**, cranidium, SUI 126647, dorsal, left lateral, and anterior views, x10 (G 155.6 m). **L**, left librigena, SUI 126648, external view, x7.5 (G 155.6 m). **M**, left librigena, SUI 126649, external view, x10 (G 155.6 m). **N**, right librigena, SUI 126650, external view, x12 (G 162T m). **O, T**, left librigena, SUI 126651, external and internal views, x10 (G 162T m). **P**, right librigena, SUI 126652, external view, x10 (G 162T m). **Q, U**, left librigena, SUI 126653, ventrolateral and external views, x10 (G 162T m). **R**, right librigena, SUI 126654, external view, x12 (G 162T m). **S**, left librigena, SUI 126655, external view, x7.5 (G 162T m).







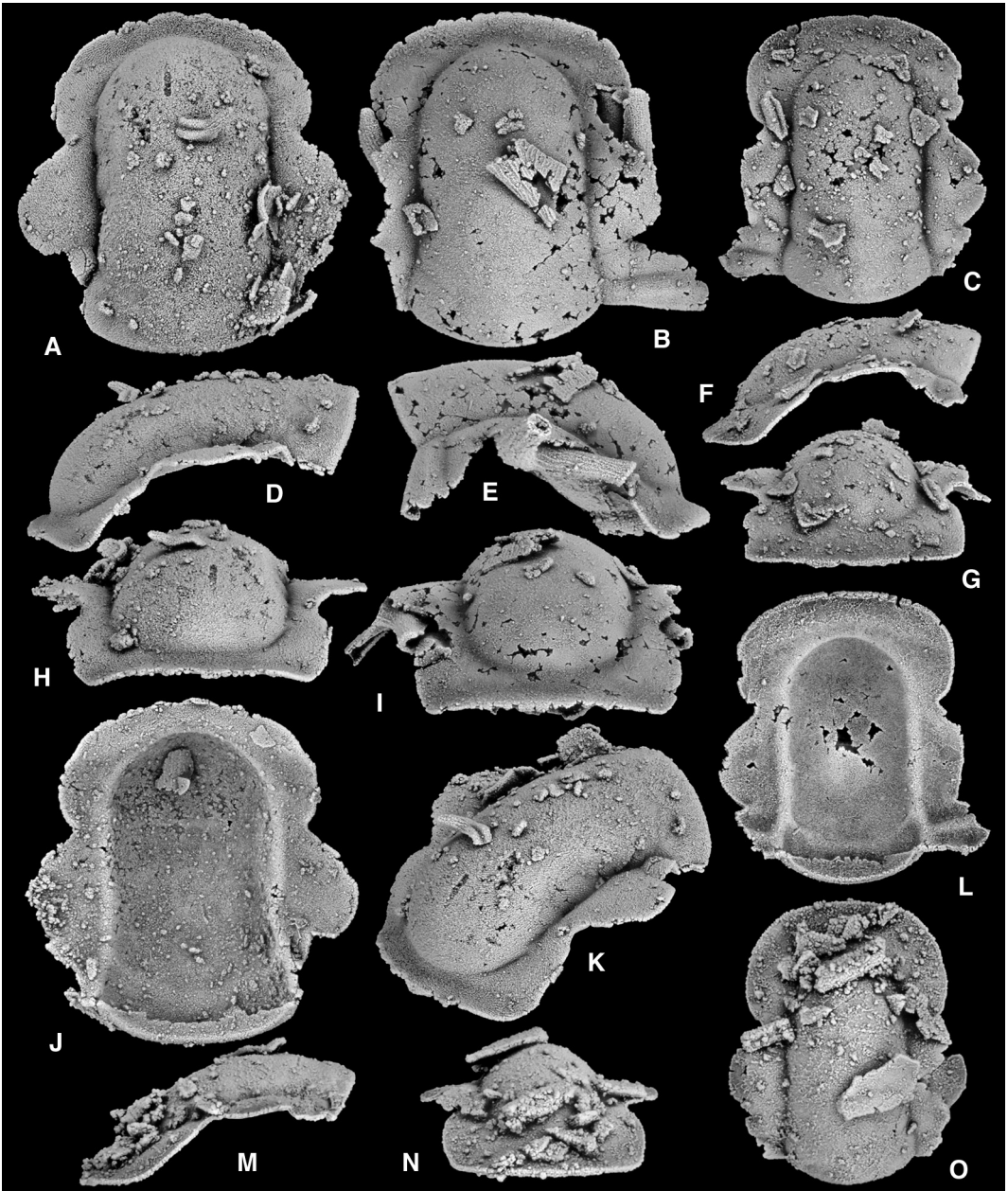


Figure 9. *Gladiatoria gladiator* (Ross, 1951), from Section D 88.9 m, Fillmore Formation (Tulean; lower *Psalikilopsis cuspidicauda* Zone), southern House Range, Ibex area, Millard County, western Utah, USA. **A, D, H, J, K,** cranidium, SUI 128775, dorsal, left lateral, anterior, ventral, and oblique views, x10. **B, E, I,** cranidium, SUI 128776, dorsal, right lateral, and anterior views, x12. **C, F, G, L,** cranidium, SUI 128777, dorsal, left lateral, anterior, and ventral views, x12. **M-O,** cranidium, SUI 128778, left lateral, anterior, and dorsal views, x15.

Figure 8 (opposite). *Gladiatoria gladiator* (Ross, 1951), from Section G 162T m, southern Confusion Range, and Section D 88.9 m, southern House Range, both Fillmore Formation (Tulean; lower *Psalikilopsis cuspidicauda* Zone), Ibex area, Millard County, western Utah, USA. **A, H, I,** pygidium, SUI 126641, dorsal, left lateral, and posterior views, x8 (G 162T m). **B, F, J,** pygidium, SUI 126642, dorsal, posterior, and left lateral views, x8 (G 162T m). **C, D, L,** pygidium, SUI 126643, dorsal, posterior, and left lateral views, x10 (G 162T m). **E, G, K,** pygidium, SUI 126644, posterior, dorsal, and right lateral views, x10 (G 162T m). **M, N, Q, T, U,** pygidium, SUI 128772, dorsal, ventral, left lateral, posterior, and anterior views, x15 (D 88.9 m). **O, P,** right librigena, SUI 128773, external and internal views, x10 (D 88.9 m). **R, S, V,** right librigena, SUI 128774, external, internal, and ventrolateral views, x12 (D 88.9 m).

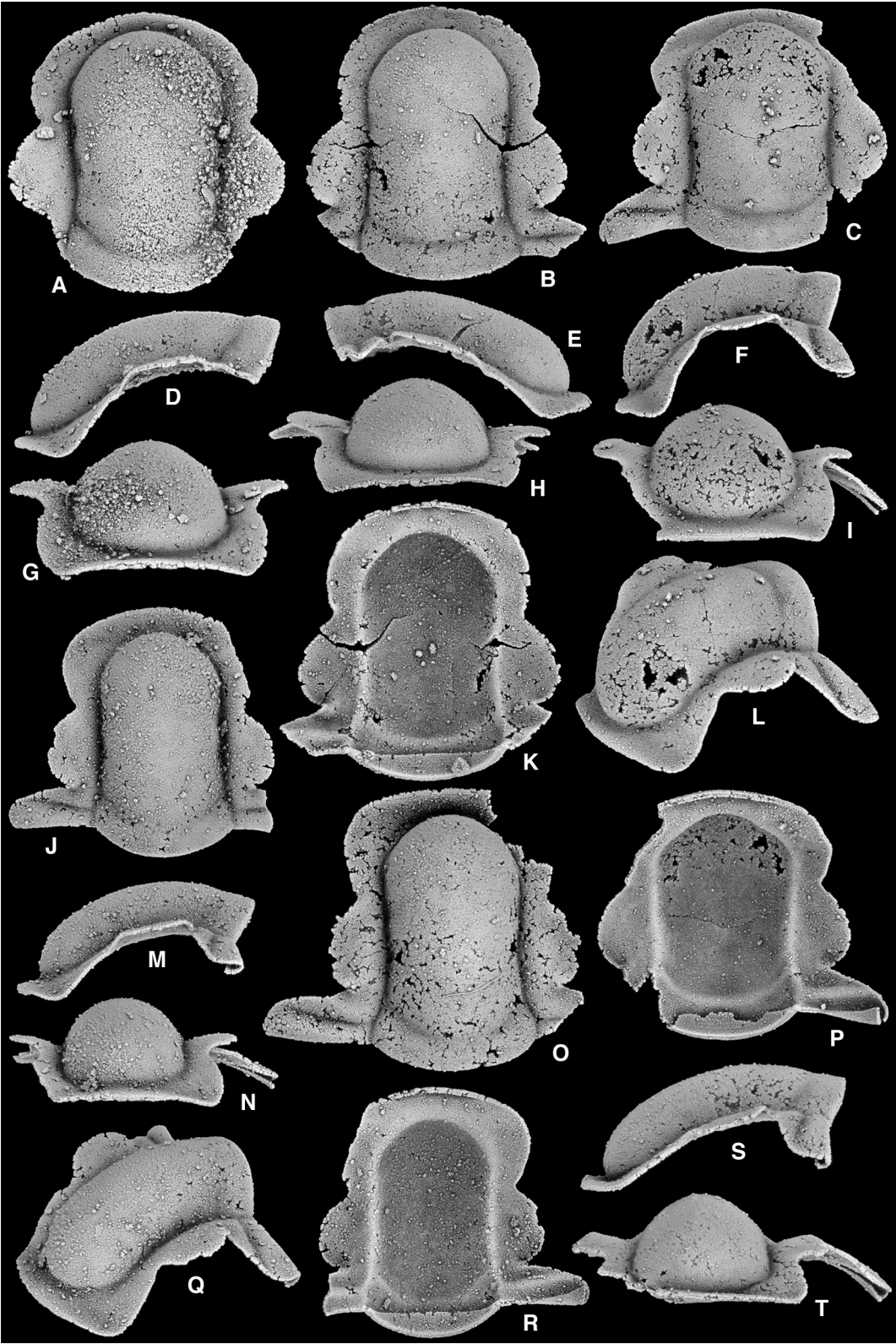
margin with fairly strong lateral curvature; posterior border also slightly expanded near posterior margin to form rim slightly wider than that on lateral border margin, and with less sharp posterior edge; posterior margin curving smoothly and evenly into adaxial margin of genal spine, no acute angle between spine and margin developed; genal spine broad at base and subtriangular, narrowing rapidly distally but with large, flat, dorsal surface, tapering into short, pointed spine; dorsal aspect of spine in most specimens with prominent raised line sculpture running more or less subparallel with lateral margins; anterior projection quite long, turned slightly anteriorly near terminus; doublure broad, with significant ventral convexity under lateral border and limited convexity under posterior border; these inflated parts are joined by a subtriangular area underlying the region in front of the genal spine base; this area is ventrally concave, and includes a prominent Panderian notch on its margin near the contact with the posterior facial suture; entire doublure is covered with prominent, well expressed raised terrace lines, larger and more widely spaced beneath lateral border, finer and more crowded on concave area, anterior projection, and genal spine, in all cases running more or less subparallel with margins.

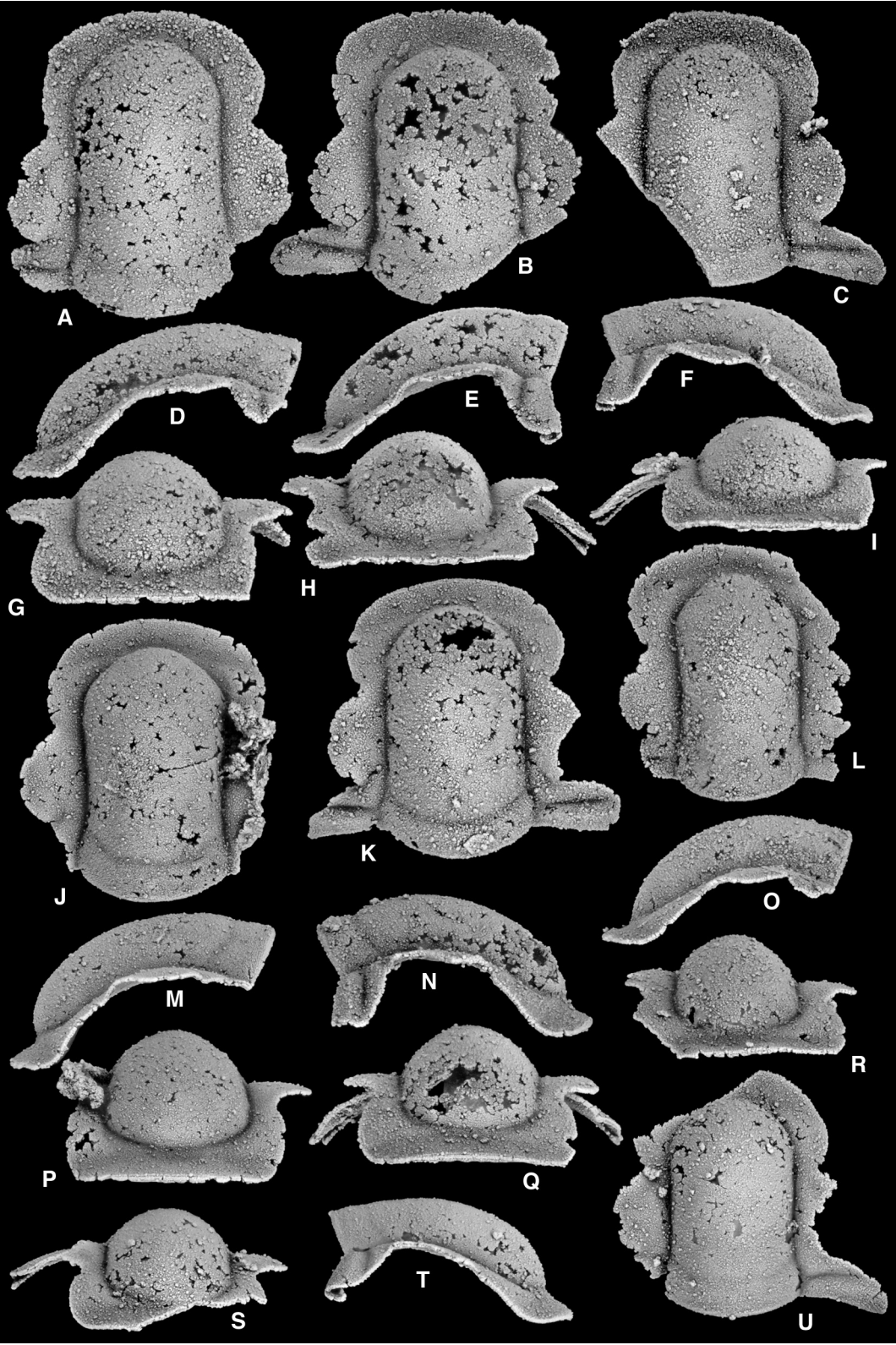
Rostral plate, hypostome and thoracic segments not identified (some thoracic segments were illustrated in articulation with pygidia by Ross [1953, pl. 30, figs 14, 22]).

Pygidial measurements are based on the specimens illustrated in Figure 6. Pygidium with maximum width across first segment 53.7% (single specimen of Fig. 6A) sagittal length; maximum width 102.3% (98.0-104.5) exsagittal length of pleurae; entire dorsal surface with sculpture of fine, raised, anastomosing lines similar to that of cephalon; in plan view pygidium is spike-shaped, with narrow pleurae and an inflated axis extended posteriorly in a long, swollen spine which tapers to a sharp point; in sagittal profile the pygidium is strongly dorsally vaulted, with the dorsal margin extending posteriorly from the articulating half ring more or less as a horizontal line, depressed slightly above waisted part of axis and raised slightly at base of swollen posterior spine; in transverse profile the pygidium has narrow but tall pleural lobes; the axis is vaulted dorsally well above the pleurae, and its dorsal margin describes a nearly even arc, flattened slightly

medially; axis with maximum anterior width 51.1% (48.5-54.5) maximum pygidial width; articulating half-ring large, bowed forward; ring furrow distinctly incised, bowed forward slightly more strongly medially than laterally, transverse in some specimens; first ring well expressed, bowed anteriorly, very faint pseudoarticulating half-ring expressed on posteromedian part, very weakly inflated, slightly longer (exsag.) abaxially, lateral margins turned obliquely along strongly posteriorly convergent axial furrows; small lateral lobe developed at anterolateral corner of first ring; first ring only very slightly dorsally swollen from main outline of pygidium in sagittal profile; second ring furrow distinctly expressed but extremely shallow, slightly better impressed abaxially; second ring with morphology and inflation similar to first, narrower, and less well defined; third ring furrow possibly very faintly expressed, difficult to discern in most specimens; only two segments are definitely expressed; there is no unambiguous evidence of a third axial ring; axis reaches narrowest point behind second ring, where width is 71.7% (67.3-76.9) maximum axial width; axial furrows narrow but incised anteriorly across first segment, wider and deeper posteriorly opposite second segment and waisted region; axial furrows strongly posteriorly convergent opposite first and second rings, deflected around swollen lateral margins of rings, gently posteriorly divergent behind waisted part of axis, shallowing posteriorly along base of swollen axial spine, in most specimens continuing as faint furrow all the way to the contact of the rear of the pleura with the median spine; anterior margin of pleura slightly posterolaterally directed to fulcrum, then turned strongly posteriorly; maximum pygidial width achieved at anterolateral corner of distal part of first pleura, lateral margin continued with sinuous course posteriorly to contact with margin of posterior spine; first pleural furrow well expressed proximally, turned posterolaterally slightly more so than anterior margin, furrow expressed across fulcrum but effaced immediately distal to fulcrum; anterior and posterior pleural bands approximately equal in length (exsag.) and inflation proximally; first interpleural furrow shallow proximally but deeper distally (in this part of its course it is the most prominent dorsal furrow expressed on the pygidium), turned posteriorly at fulcrum to run parallel with margin of spine; pleura of second segment with no pleural furrow

Figure 10. *Gladiatoria harrisi* sp. nov., from Section D 106.4 m, Fillmore Formation (Tulean; upper *Psalikilopsis cuspidicauda* Zone), southern House Range, Ibex area, Millard County, western Utah, USA. **A, D, G**, cranium, SUI 126612, dorsal, left lateral, and anterior views, x10. **B, E, H, K**, cranium, **holotype**, SUI 126613, dorsal, right lateral, anterior, and ventral views, x10. **C, F, I, L, P**, cranium, SUI 126614, dorsal, left lateral, anterior, oblique, and ventral views, x10. **J, M, N, Q, R**, cranium, SUI 126615, dorsal, left lateral, anterior, oblique, and ventral views, x10. **O, S, T**, cranium, SUI 126616, dorsal, left lateral, and anterior views, x12.





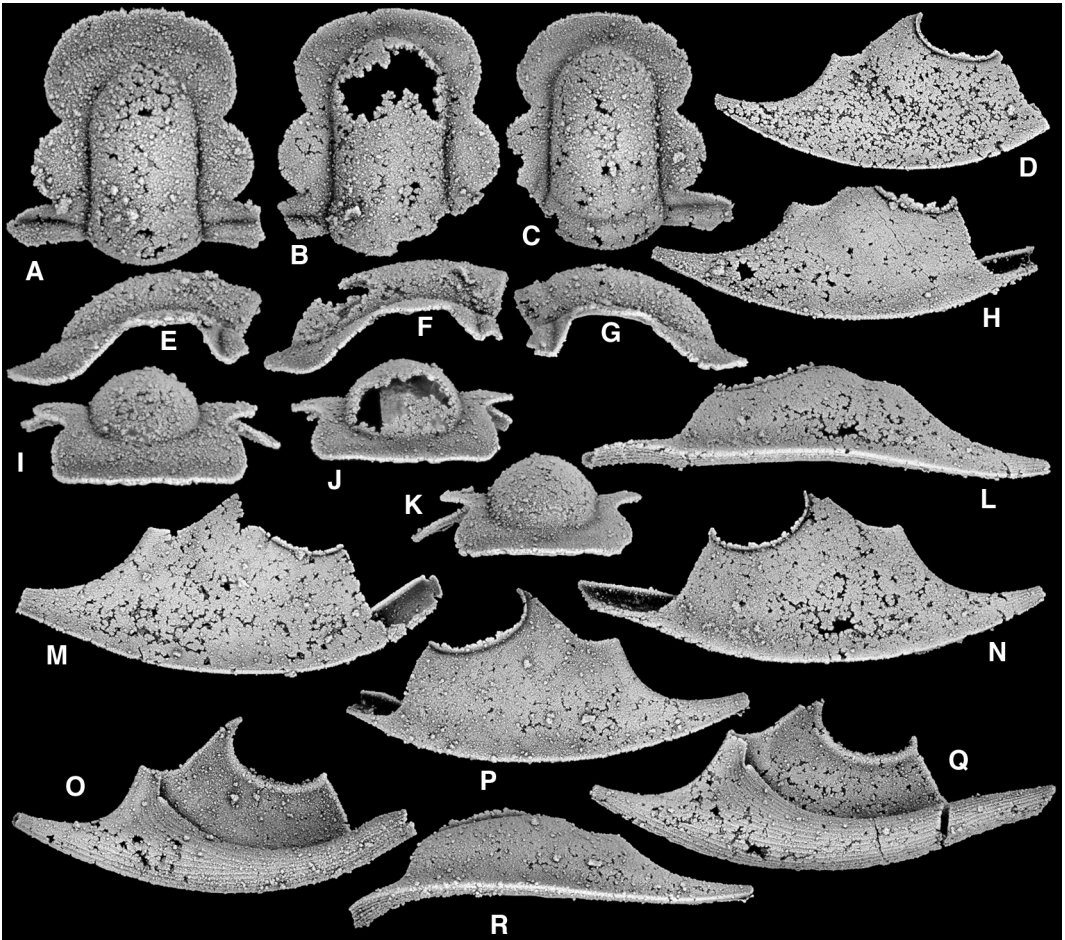


Figure 12 (above). *Gladiatoria harrisi* sp. nov., from Section D 106.4 m, Fillmore Formation (Tulean; upper *Psalikilopsis cuspidicauda* Zone), southern House Range, Ibex area, Millard County, western Utah, USA. **A, E, I,** cranidium, SUI 126633, dorsal, left lateral, and anterior views, x15. **B, F, J,** cranidium, SUI 126634, dorsal, left lateral, and anterior views, x12. **C, G, K,** cranidium, SUI 126635, dorsal, right lateral, and anterior views, x12. **D,** right librigena, SUI 126636, external view, x7.5. **H,** right librigena, SUI 126637, external view, x10. **L, N, Q,** left librigena, SUI 126638, ventrolateral, external, and internal views, x10. **M,** right librigena, SUI 126639, external view, x10. **O, P, R,** left librigena, SUI 126640, internal, external, and ventrolateral views, x10.

developed, bands not differentiated, represented as independently inflated region (more so proximally), somewhat wider distally, bounded by first interpleural furrow and axial furrow; doubleure forming a broad, nearly horizontal shelf under entire pygidium except for small anterior triangle comprising narrow proximal pleural regions of first two segments and anterior part of axis; shelf is bounded anteriorly by prominent rim along anterior margin, interrupted medially by fairly wide median furrow; rim with sculpture

of closely spaced raised lines running parallel with margin; median part of shelf with shallow medial depression, in some specimens a distinct posteriorly extended furrow (Fig. 6E); shelf with sculpture of raised lines, larger, more widely spaced, and only slightly posteromedially aligned on lateral parts, smaller, more closely spaced, and bowed posteromedially in a U-shape along medial aspect.

Ontogeny. The smallest recovered cranidia (Figs

Figure 11 (opposite). *Gladiatoria harrisi* sp. nov., from Section D 106.4 m, Fillmore Formation (Tulean; upper *Psalikilopsis cuspidicauda* Zone), southern House Range, Ibex area, Millard County, western Utah, USA. All magnifications are x15. **A, D, G,** cranidium, SUI 126617, dorsal, left lateral, and anterior views. **B, E, H,** cranidium, SUI 126618, dorsal, left lateral, and anterior views. **C, F, I,** cranidium, SUI 126619, dorsal, right lateral, and anterior views. **J, M, P,** cranidium, SUI 126620, dorsal, left lateral, and anterior views. **K, N, Q,** cranidium, SUI 126621, dorsal, right lateral, and anterior views. **L, O, R,** cranidium, SUI 126622, dorsal, left lateral, and anterior views. **S-U,** cranidium, SUI 126623, anterior, right lateral, and dorsal views.



3X, 4A, B) display morphology much more like that of *Bathyuirellus* and the *Gladiatoria crowei* clade. They have a distinct preglabellar field, a much better impressed anterior border furrow, and a more prominent anterior border. The glabella is not anteriorly swollen, and the axial furrows are subparallel. The cranidium changes little through ontogeny in its posterior morphology, but the anterior part of the glabella becomes progressively swollen, the preglabellar field is lost, the anterior border furrow is progressively effaced, and the anteromedian part of the glabella moves forward to overhang the anterior border. Transitory pygidia and small holaspide pygidia demonstrate few fundamental morphological changes through ontogeny, except that the pleural regions become markedly broader with increasing overall pygidial size.

Material. Assigned specimens SUI 115173, 115174, 126566-126611, from Section HC5 195.7 m and 203.7-204.2T m, east side of Hillyard Canyon, and Section HC6 189.3, west side of Hillyard Canyon, all Garden City Formation (Tulean; lower *Psalikilopsis cuspidicauda* Zone), Bear River Range, Franklin County, southeastern Idaho, USA; assigned specimens SUI 126641-126655 from Section G 155.6 m, 162T m, southern Confusion Range, and SUI 128772-128778, from Section D 88.9 m, southern House Range, all Fillmore Formation (Tulean; lower *Psalikilopsis cuspidicauda* Zone), Ibex area, Millard County, western Utah, USA.

Remarks. Although *Gladiatoria gladiator* occurs together with *G. nielsenae* at horizons in both the Garden City Formation and the Fillmore Formation, there is little potential for confusion given that each belongs to a distinct clade (see genus discussion above), and other members of either clade occur at horizons by themselves, without any congeners with which they might be confused. In addition, *G. gladiator* occurs by itself, with no evidence of *G. nielsenae*, at horizon D 88.9 m, and at horizons where they do co-occur, *G. gladiator* is much more common. Hence we are confident in the association of sclerites.

Ross (1951a) based *Gladiatoria gladiator* on two specimens, each consisting of a pygidium

with attached thoracic segments. He also assigned a cranidium (Ross 1951a, pl. 27, figs 8-10) which in his text (Ross 1951a, p. 122) he termed an "asaphid-type cranidium tentatively assigned". This cranidium clearly belongs to the asaphid *Aulacoparia*, as noted by Dean (1989, pp. 13, 38). Ross subsequently (1951b) documented an ontogenetic series of transitory and holaspide pygidia. To date this has been all of the described material of the genus. Ross (1951a, p. 106, pl. 27, figs 24-26, 31) did in fact have the correct cephalic material (two illustrated cranidia and a librigena) at his disposal, but misinterpreted it as asaphid, assigned with question to *Niobe* Angelin, 1851. The association of parts made herein is based on morphological correspondence, shared frequency of occurrence, reference to the morphology of the closely related *Bathyuirellus*, and the repeated co-occurrence of similar sets of matched sclerites representing multiple species at multiple distinct horizons.

Gladiatoria gladiator and the small clade to which it belongs were distinguished from the *G. phoenixi*-*G. nielsenae*-*G. crowei* clade in the genus discussion above. It is distinguished from the more closely related *G. harrisi* and *G. reedi* via differential diagnoses and remarks on each of those species below.

***Gladiatoria harrisi* sp. nov. (Figs 10-13, 14A-N)**

Diagnosis. Generally similar to *G. gladiator*, but with the following consistent differences: cranidium with anterior margin of anterior border markedly anteriorly arcuate; anterior border poorly expressed, anterior border furrow weak or entirely effaced; anterior part of glabella more strongly inflated, axial furrows clearly deflected laterally around bulbous anterior glabella; glabella with slightly stronger waisting opposite palpebral lobes; librigena with narrower field in largest specimens of similar size; pygidium with relatively broader pleurae, with the axial furrow deeply impressed only slightly past rear of second segment, and clearly distinct from a separate second interpleural furrow which runs posteriorly to the margin; swollen posterior spine in large specimens directed fairly strongly posterodorsally versus nearly directly posteriorly.

Figure 13. *Gladiatoria harrisi* sp. nov., from Section D 106.4 m, Fillmore Formation (Tulean; upper *Psalikilopsis cuspidicauda* Zone), southern House Range, Ibex area, Millard County, western Utah, USA. **A, H, N**, pygidium, SUI 126624, dorsal, posterior, and right lateral views, x10. **B, L, Q**, pygidium, SUI 126625, posterior, dorsal, and right lateral views, x10. **C, V, W, T, BB**, pygidium, SUI 126626, anterior, dorsal, ventral, left lateral, and posterior views, x10. **D, I, O**, pygidium, SUI 126627, dorsal, posterior, and left lateral views, x10. **E, F, K, S**, pygidium, SUI 126628, posterior, dorsal, ventral, and right lateral views, x10. **G, J, R**, pygidium, SUI 126629, dorsal, posterior, and right lateral views, x10. **M, P, U**, pygidium, SUI 126630, dorsal, posterior, and right lateral views, x10. **X-Z**, pygidium, SUI 126631, posterior, dorsal, and left lateral views, x12. **AA, CC, DD**, pygidium, SUI 126632, dorsal, posterior, and right lateral views, x12.



Description. The cranidium, librigena, and pygidium are very similar to those of *G. gladiator*, and all differences are listed in the differential diagnosis above. However the hypostome of *G. gladiator* was not recovered, whereas that of *G. harrisi* has been identified based on good material. A full description of the hypostome, which is the best known for the genus, is therefore presented.

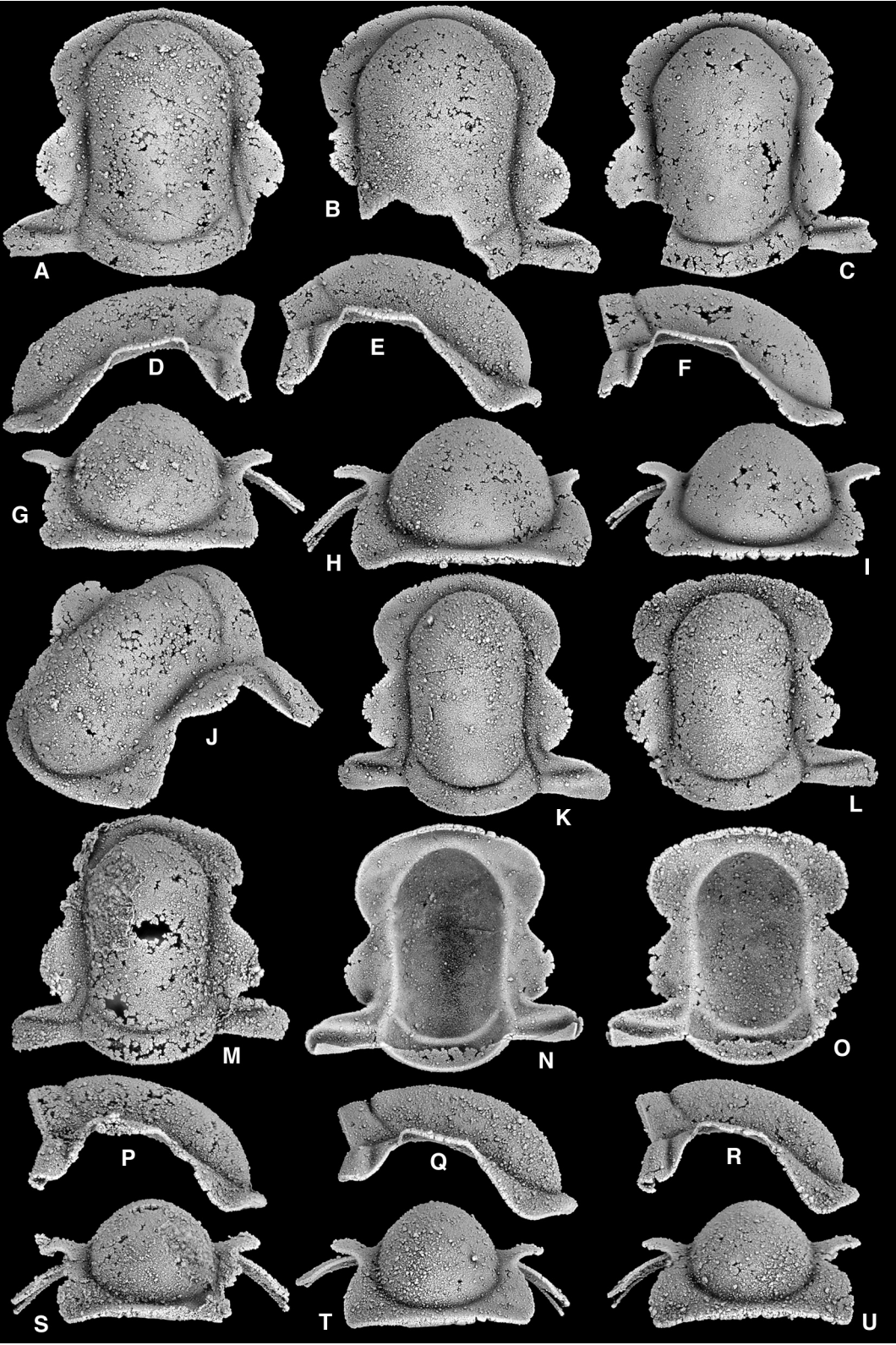
Hypostome with maximum width (excluding anterior wings) across middle body, 83.0% (81.6-84.4) sagittal length; entire ventral surface with raised line sculpture, anastomosing on middle body, aligned subparallel with margins on borders and anterior wings; sculpture on middle body with lines broken up into closely spaced, aligned, partially merged small tubercles; anterior margin turned up to form anterior-facing wall, with sculpture of subparallel raised lines sweeping around from anterior wings; anterior area grades into middle body across sharp break in slope but with no border or ridge, lines grading from contiguous to tuberculate across break in slope; anterior wings long and large, extended dorsolaterally, strap-like; lateral border arising from anterior region as ascendent ridge; lateral border furrow initiated opposite midlength of base of anterior wing; lateral and posterior border with tall wall-like lateral and posterior aspect,

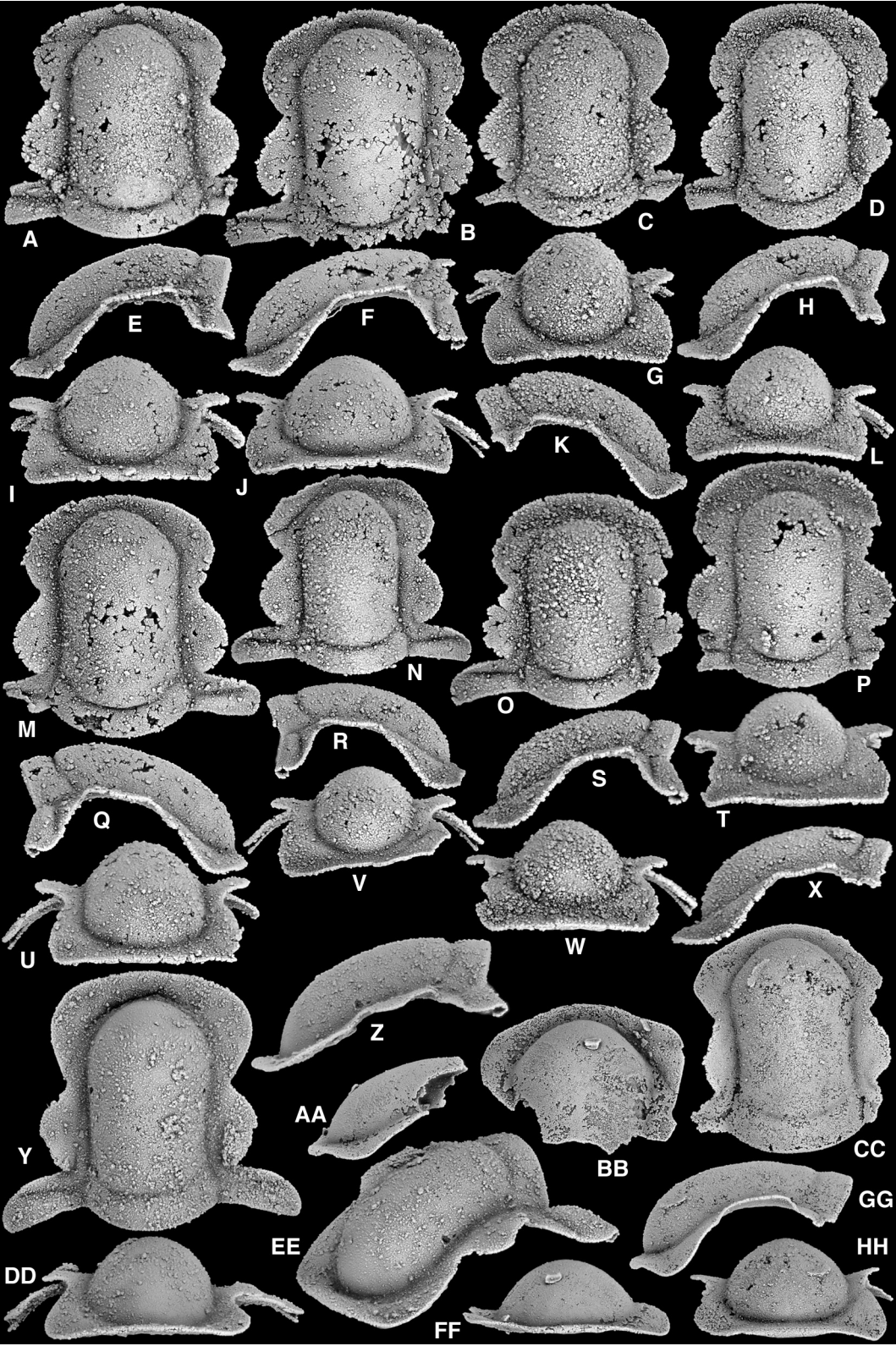
strongly expressed ventrally, forming thick, rim-like ridge enclosing middle body; lateral and posterior border furrows deep and trench-like; distinction between lateral and posterior border and border furrows unclear, as each describes an overall ovate course with no firm transition points, however there is a distinct subparallel region anteriorly behind anterior wings to just past rear of maculae; at rear of this subparallel part, the border and furrow turns posteromedially; the posterior arc of the border and furrow is not even, but reaches a more strongly curved median point; middle furrow set at about half distance posteriorly on middle body, expressed only adaxially as oblique, slot-like furrow, separated from lateral border furrow by strip of inflated middle body; small swollen maculae set immediately behind middle furrow on either side; middle body with gentle ventral inflation, pinched slightly at middle furrow; doublure forming moderately broad shelf posteriorly behind anterior wings; section between anterior wing and posterior wing exsagittally aligned and ventrally concave in middle part; posterior wing small and subquadrate, about one third the size of anterior wing, running slightly dorsomedially; posterior part of doublure behind posterior wing narrowed posteromedially; entire doublure with

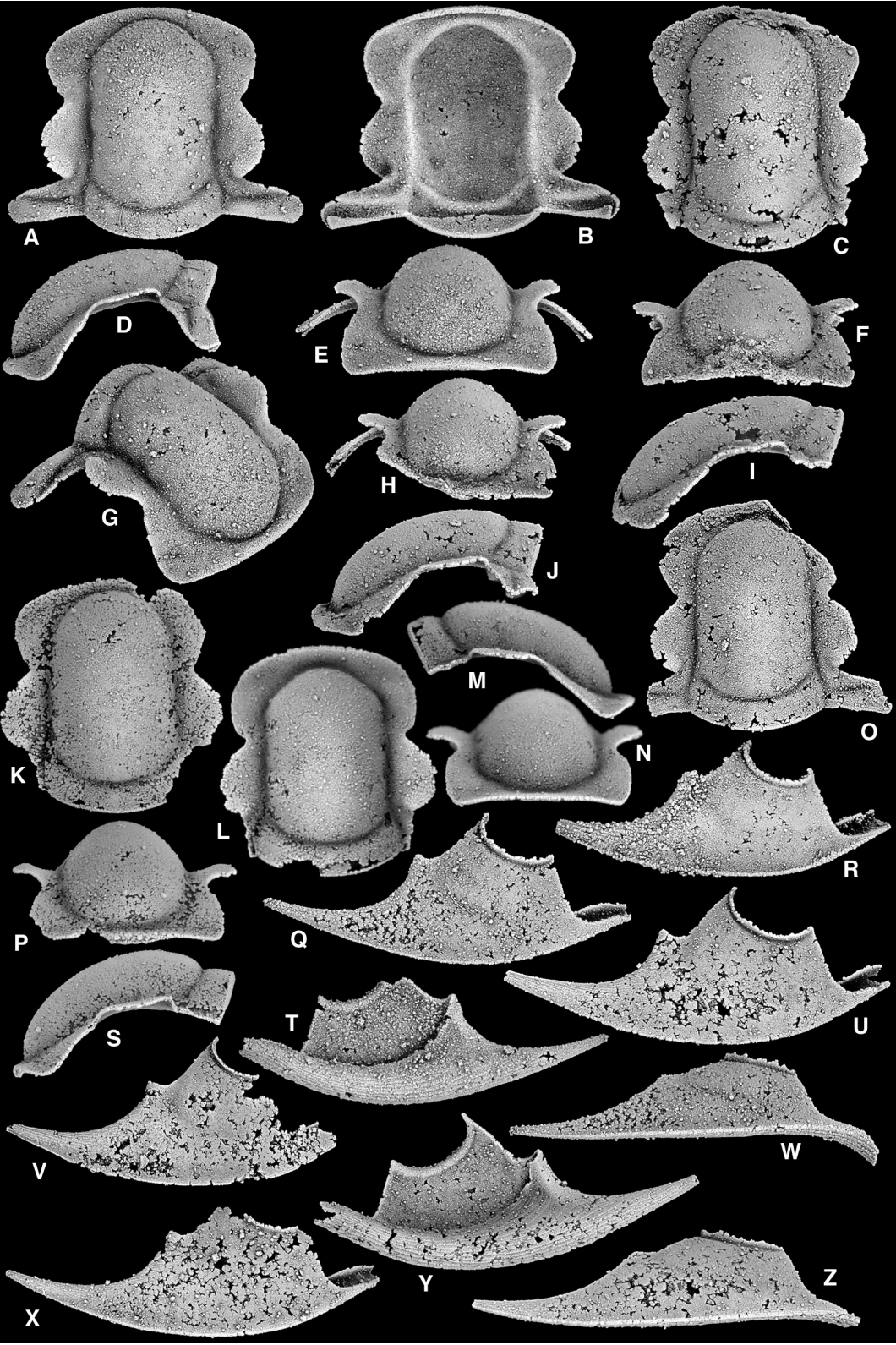
Figure 14 (opposite). A-N, *Gladiatoria harrisi* sp. nov., from Section D 106.4 m, Fillmore Formation (Tulean; upper *Psalikilopsis cuspidicauda* Zone), southern House Range, Ibex area, Millard County, western Utah, USA. A, E, F, G, hypostome, SUI 126787, ventral, dorsal, posterior, and right lateral views, x15. B-D, I, hypostome, SUI 126788, right lateral, posterior, ventral, and dorsal views, x15. H, M, N, hypostome, SUI 126789, right lateral, posterior, and ventral views, x20. J-L, hypostome, SUI 126790, ventral, posterior, and left lateral views, x20. O, V-X, *Gladiatoria reedi* sp. nov., from Section G 181.8 m, Fillmore Formation (Tulean; lower *Psalikilus hestoni* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA, hypostome, SUI 126791, ventral, dorsal, left lateral, and posterior views, x20. P-U, Y, *Gladiatoria crowei*, from Section G 210.2 m, Fillmore Formation (Tulean; *Protophiomerella contracta* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. P-R, hypostome, SUI 126792, ventral, posterior, and right lateral views, x15. S-U, Y, hypostome, SUI 126793, ventral, dorsal, right lateral, and posterior views, x20.

Figure 15 (overleaf). *Gladiatoria reedi* sp. nov., from Section G 181.8 m, Fillmore Formation (Tulean; lower *Psalikilus hestoni* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. A, D, G, J, cranidium, SUI 126656, dorsal, left lateral, anterior, and oblique views, x10. B, E, H, cranidium, SUI 126657, dorsal, right lateral, and anterior views, x10. C, F, I, cranidium, SUI 126658, dorsal, right lateral, and anterior views, x10. K, N, Q, T, cranidium, SUI 126659, dorsal, ventral, right lateral, and anterior views, x10. L, O, R, U, cranidium, SUI 126660, dorsal, ventral, right lateral, and anterior views, x12. M, P, S, cranidium, SUI 126661, dorsal, right lateral, and anterior views, x12.

Figure 16 (page 345). A-X, *Gladiatoria reedi* sp. nov., from Section G 181.8 m, Fillmore Formation (Tulean; lower *Psalikilus hestoni* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, and Section HC6 202T m and 203.0 m, Garden City Formation (Tulean; *Psalikilus typicum* Zone), west side of Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho, USA. A, E, I, cranidium, SUI 126662, dorsal, left lateral, and anterior views, x12 (G 181.8 m). B, F, J, cranidium, SUI 126663, dorsal, left lateral, and anterior views, x12 (G 181.8 m). C, G, K, cranidium, SUI 126664, dorsal, anterior, and right lateral views, x12 (G 181.8 m). D, H, L, cranidium, SUI 126665, dorsal, left lateral, and anterior views, x12 (G 181.8 m). M, Q, U, cranidium, SUI 126666, dorsal, right lateral, and anterior views, x12 (G 181.8 m). N, R, V, cranidium, SUI 126667, dorsal, right lateral, and anterior views, x12 (G 181.8 m). O, S, W, cranidium, SUI 126668, dorsal, left lateral, and anterior views, x15 (G 181.8 m). P, T, X, cranidium, SUI 126669, dorsal, anterior, and left lateral views, x17 (G 181.8 m). Y, Z, DD, EE, cranidium, SUI 126670, dorsal, left lateral, anterior, and oblique views, x12 (HC6 202T m). AA, BB, FF, cranidium, SUI 126671, left lateral, dorsal, and anterior views, x8 (HC6 203.0 m). CC, GG, HH, cranidium, SUI 126672, dorsal, left lateral, and anterior views, x8 (HC6 203.0 m).







sculpture of several fine raised lines similar to that on lateral aspects of borders.

Material. Holotype, cranidium, SUI 126613 (Fig. 10B, E, H), and assigned specimens SUI 126612, 126614-126640, 126787-126790, from Section D 106.4 m, Fillmore Formation (Tulean; upper *Psalikilopsis cuspidicauda* Zone), southern House Range, Ibex area, Millard County, western Utah.

Etymology. After Richard Harris.

Remarks. As is the case with the co-occurring bathyurid *Psalikilopsis* Ross, 1953 (Adrain *et al.*, 2011), species of *Gladiatoria* from the lower and upper parts of the *Psalikilopsis cuspidicauda* Zone are very similar to one another, yet pervasively differentiated, with clear contrasts on all comparable sclerites. Large cranidia of *G. harrisi* are much more similar to those of *G. reedi* than to those of *G. gladiator*. In particular, they share the effacement of the anterior border furrow, anteriorly arcuate anterior border margin with little distinct angle between the margin and the anterior facial suture, and the anterior bulbous expansion of the glabella. Smaller cranidia of *G. harrisi* (e.g., Fig. 11A, C, J-L) more closely

resemble the largest cranidia of *G. gladiator*, and demonstrate that the effacement of the anterior border furrow and anterior expansion of the glabella are late ontogenetic transitions in the younger species.

***Gladiatoria reedi* sp. nov.** (Figs 14O, V-X, 15-18)

2009 *Gladiatoria* sp. 1; Adrain *et al.*, p. 561.

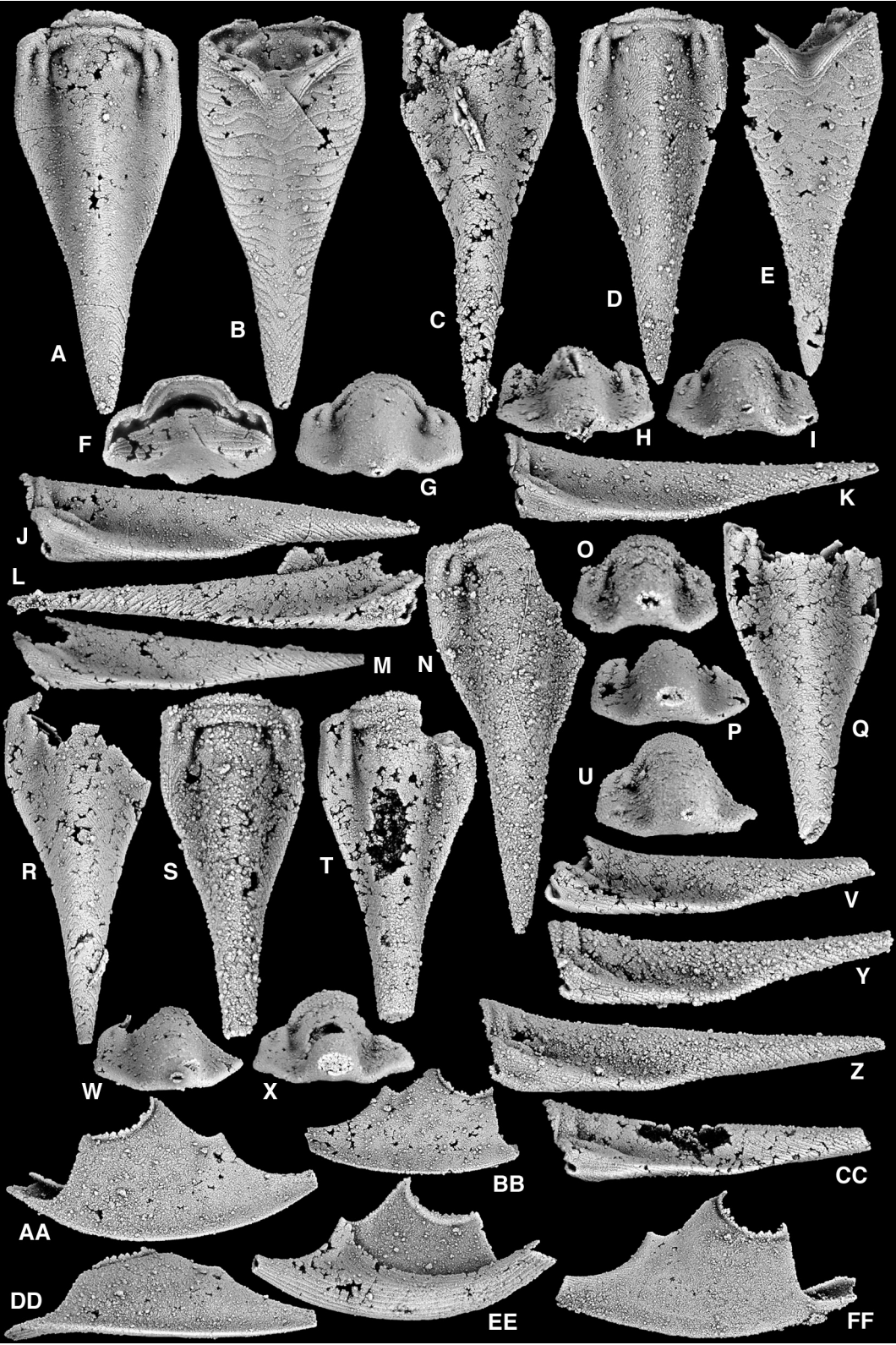
Diagnosis. Glabella overhanging much of anterior border medially; occipital furrow prominent and incised in most specimens; palpebral furrow prominent posteriorly; posterior branch of facial suture on librigena nearly aligned with posterior margin; pygidium narrow, second axial ring poorly expressed and second segment barely expressed at all on pleurae; first pygidial pleural furrow turned distally to run posteriorly.

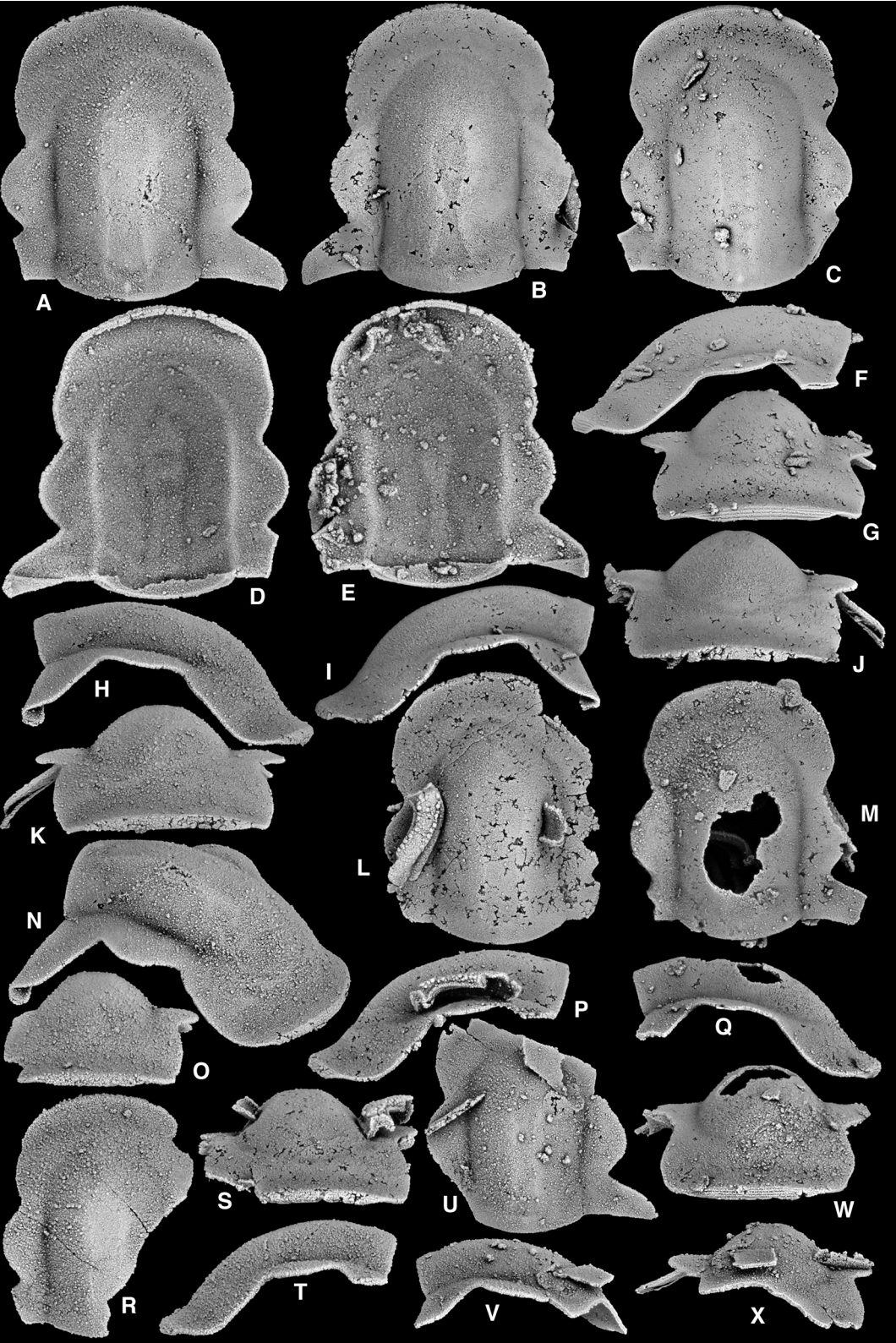
Material. Holotype, pygidium, SUI 126683 (Fig. 18A, B, F, G, J), from Section G 181.8, and assigned specimens SUI 126656-126680, 126684-126693, 126791, from Section G 181.8 m and 187.4 m, Fillmore Formation (Tulean; *Psalikilus hestoni* Zone), Ibex area, Millard County, western Utah, USA; assigned specimens

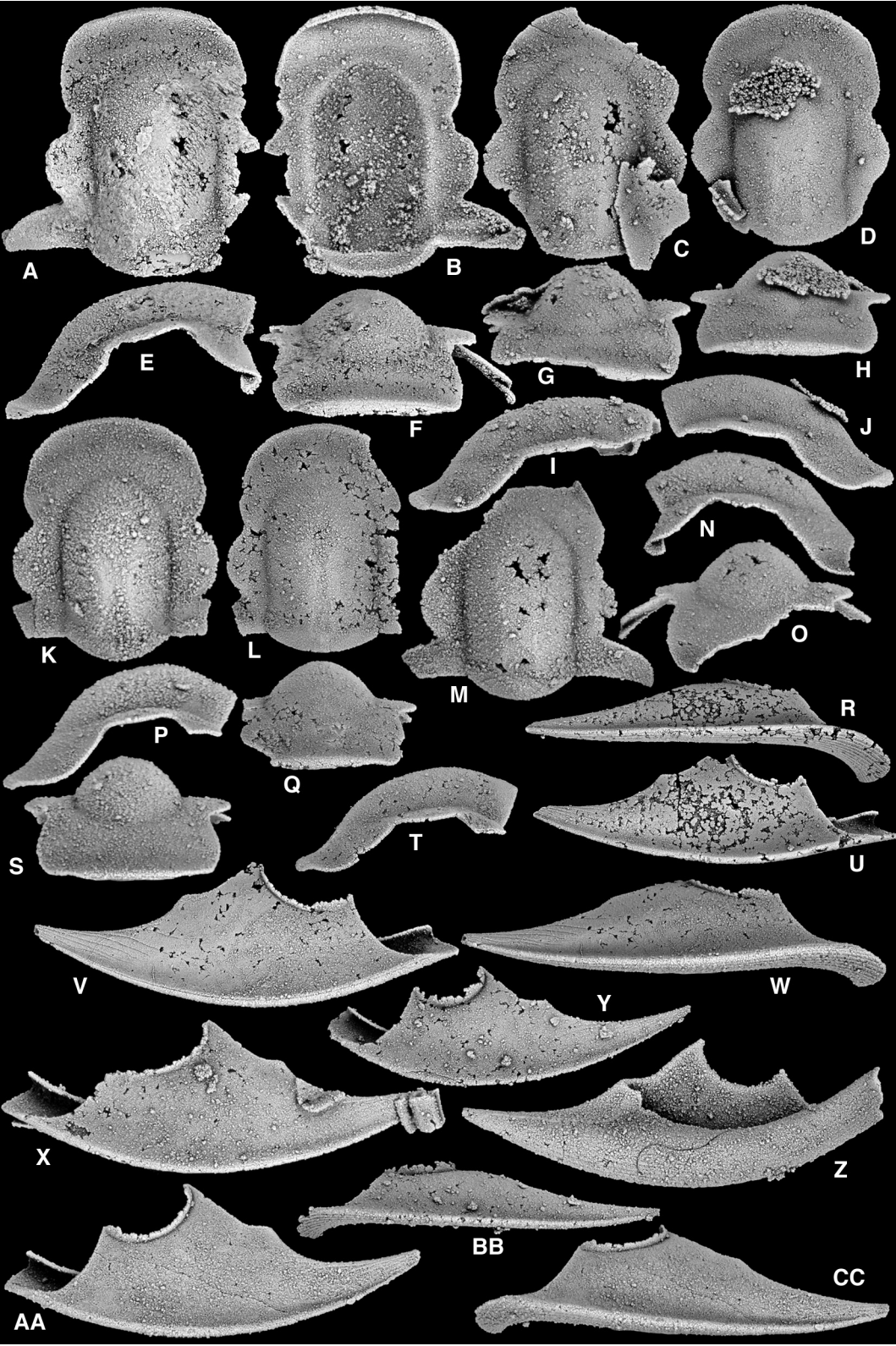
Figure 17 (opposite). *Gladiatoria reedi* sp. nov., from Section G 181.8 m and 187.4 m, Fillmore Formation (Tulean; *Psalikilus hestoni* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, and Section HC6 205.5 m, Garden City Formation (Tulean; lower *Psalikilus hestoni* Zone), west side of Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho, USA. **A, B, D, E, G**, cranidium, SUI 126673, dorsal, ventral, left lateral, anterior, and oblique views, x10 (G 187.4 m). **C, F, I**, cranidium, SUI 126674, dorsal, anterior, and left lateral views, x12 (G 187.4 m). **H, J, O**, cranidium, SUI 126675, anterior, left lateral, and dorsal views, x12 (G 187.4 m). **Q, T, W**, right librigena, SUI 126676, external, internal, and ventrolateral views, x10 (G 181.8 m). **R**, right librigena, SUI 126677, external view, x12 (G 181.8 m). **U, Y, Z**, right librigena, SUI 126678, external, internal, and ventrolateral views, x10 (G 181.8 m). **V**, right librigena, SUI 126679, external view, x9 (G 181.8 m). **X**, right librigena, SUI 126680, external view, x9 (G 181.8 m). **K, P, S**, cranidium, SUI 126681, dorsal, anterior, and left lateral views, x12 (HC6 205.5 m). **L-N**, cranidium, SUI 126682, dorsal, right lateral, and anterior views, x12 (HC6 205.5 m).

Figure 18 (overleaf). *Gladiatoria reedi* sp. nov., from Section G 181.8 m and 187.4 m, Fillmore Formation (Tulean; *Psalikilus hestoni* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. **A, B, F, G, J**, pygidium, **holotype**, SUI 126683, dorsal, ventral, anterior, posterior, and left lateral views, x12 (G 181.8 m). **C, H, L**, pygidium, SUI 126684, dorsal, posterior, and right lateral views, x12 (G 181.8 m). **D, E, I, K**, pygidium, SUI 126685, dorsal, ventral, posterior, and left lateral views, x12 (G 181.8 m). **M, R, W**, pygidium, SUI 126686, left lateral, dorsal, and posterior views, x12 (G 181.8 m). **N, U, Z**, pygidium, SUI 126687, dorsal, posterior, and left lateral views, x12. **O, S, Y**, pygidium, SUI 126688, posterior, dorsal, and left lateral views, x15. **P, Q, V**, pygidium, SUI 126689, posterior, dorsal, and left lateral views, x12 (G 181.8 m). **T, X, CC**, pygidium, SUI 126690, dorsal, posterior, and left lateral views, x10 (G 187.4 m). **AA, DD, EE**, left librigena, SUI 126691, external, ventrolateral, and internal views, x10 (G 187.4 m). **BB**, right librigena, SUI 126692, external view, x10 (G 187.4 m). **FF**, right librigena, SUI 126693, external view, x9 (G 187.4 m).

Figure 19 (page 349). *Gladiatoria crowei* sp. nov., from Section G 210.2 m, Fillmore Formation (Tulean; *Protopliomerella contracta* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, and Section HC6 221.5 m, Garden City Formation (Tulean; *Protopliomerella contracta* Zone), west side of Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho, USA. **A, D, H, K, N**, cranidium, SUI 126694, dorsal, ventral, right lateral, anterior, and oblique views, x10 (G 210.2 m). **B, E, I, J**, cranidium, SUI 115244, dorsal, ventral, left lateral, and anterior views, x10 (G 210.2 m). **L, P, S**, cranidium, SUI 126695, dorsal, left lateral, and anterior views, x10 (G 210.2 m). **M, Q, W**, cranidium, SUI 126696, dorsal, right lateral, and anterior views, x10 (G 210.2 m). **O, R, T**, cranidium, SUI 126697, anterior, dorsal, and left lateral views, x10 (G 210.2 m). **U, V, X**, cranidium, SUI 126698, dorsal, right lateral, and anterior views, x8 (G 210.2 m). **C, F, G**, cranidium, SUI 126699, dorsal, left lateral, and anterior views, x10 (HC6 221.5 m).







SUI 126681, 126682, from Section HC6 205.5 m, Garden City Formation (Tulean; lower *Psalikilus hestoni* Zone), west side of Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho, USA.

Etymology. After Oliver Reed.

Remarks. Given the close similarity of *Gladiatoria reedi* to *G. harrisi* (particularly in cranidial morphology), extended written description is redundant. Cephalic similarities of *G. reedi* to *G. harrisi* were listed above, centered around the shared anterior bulbous expansion of the glabella and effacement of the anterior border furrow. Cranidia differ in that those of *G. reedi* have more prominently anteriorly divergent anterior facial sutures, and they commonly have a fairly well impressed palpebral furrow expressed at the rear of the palpebral lobe (e.g., Fig. 15A, C, K), whereas this furrow is typically entirely effaced in *G. harrisi*. In pygidial morphology, the species are dramatically different. *Gladiatoria harrisi* has a pygidium much more similar to that of *G. gladiator*, whereas that of *G. reedi* is very narrow, with the pleural region of the second segment

completely reduced so that the posteriorly turned distal portion of the first segment abuts the axis. The axis is also not prominently waisted, with the axial furrows subparallel where expressed anteriorly, versus prominently posteriorly convergent.

***Gladiatoria crowei* sp. nov.** (Figs 14P-U, Y, 19-23)

2009 *Gladiatoria* sp. nov. 3; Adrain *et al.*, p. 563, fig. 13Q, U.

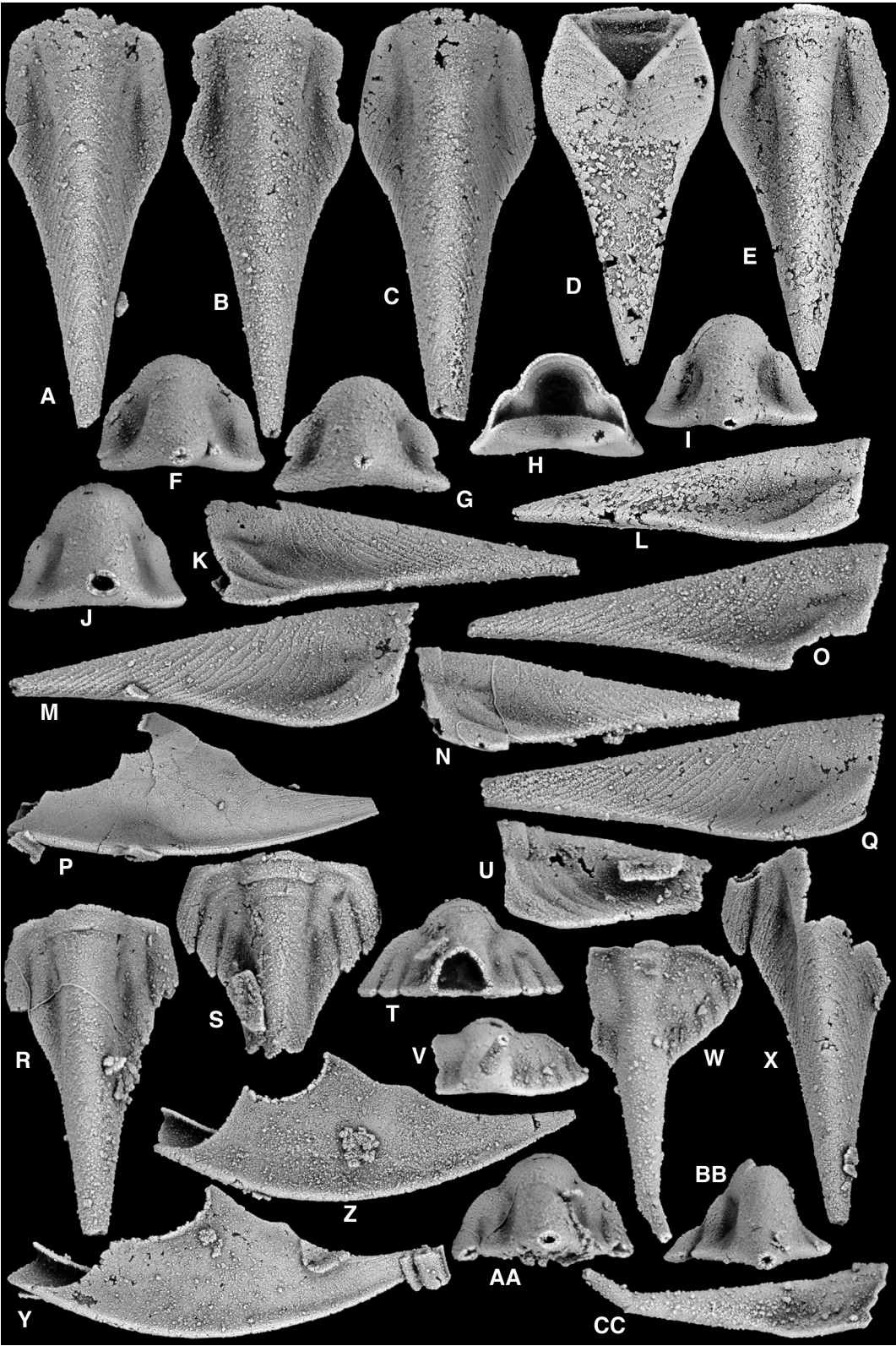
Diagnosis. Anterior sections of facial suture less laterally bowed than in any other species; preglabellar furrow weakly expressed, nearly effaced in large specimens; median part of glabella with elongate dorsally flattened region bounded by faintly swollen ridges, wider anteriorly and posteriorly, waisted in middle part; cranidial posterior border furrow almost completely effaced; pygidial axial furrows reduced to short anterior portion, more posteriorly convergent than axis in general; only first interpleural furrow definitely expressed on pleurae; ridge bounding pygidial doublure anteriorly weaker than in any

Figure 20 (opposite). *Gladiatoria crowei* sp. nov., from Section G 210.2 m, Fillmore Formation (Tulean; *Protopliomerella contracta* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. **A, B, E, F**, cranidium, SUI 126700, dorsal, ventral, and anterior views, x10. **C, G, I**, cranidium, SUI 126701, dorsal, anterior, and left lateral views, x10. **D, H, J**, cranidium, SUI 126702, dorsal, anterior, and right lateral views, x10. **K, P, S**, cranidium, SUI 126703, dorsal, left lateral, and anterior views, x17. **L, Q, T**, cranidium, SUI 126704, dorsal, anterior, and left lateral views, x10. **M, N, O**, cranidium, SUI 126705, dorsal, right lateral, and anterior views, x15. **R, U**, right librigena, SUI 126706, ventrolateral and external views, x7.5. **V, W**, right librigena, SUI 126707, external and ventrolateral views, x10. **X**, left librigena, SUI 126708, external view, x10. **Y, BB**, left librigena, SUI 126709, external and ventrolateral views, x10. **Z, AA, CC**, left librigena, SUI 126710, internal, external, and ventrolateral views, x10.

Figure 21 (overleaf). *Gladiatoria crowei* sp. nov., from Section G 210.2 m, Fillmore Formation (Tulean; *Protopliomerella contracta* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. **A, J, L**, pygidium, SUI 126711, dorsal, left lateral, and posterior views, x12. **B, F, G**, pygidium, SUI 126712, dorsal, left lateral, and posterior views, x12. **C, D, H, O**, pygidium, **holotype**, SUI 126713, ventral, dorsal, posterior, and left lateral views, x12. **E, I, K**, pygidium, SUI 126714, dorsal, posterior, and left lateral views, x10. **M, N, P**, pygidium, SUI 126715, posterior, dorsal, and right lateral views, x15. **Q-S, V, AA**, pygidium, SUI 115245, dorsal, posterior, ventral, anterior, and left lateral views, x12. **T**, left librigena, SUI 126716, external view, x10. **U, X, Z**, left librigena, SUI 126717, external, internal, and ventrolateral views, x10. **W**, right librigena, SUI 126718, external view, x10. **Y**, left librigena, SUI 126719, external view, x10. **BB**, right librigena, SUI 126720, external view, x10. **CC**, left librigena, SUI 126721, external view, x10.

Figure 22 (page 353). *Gladiatoria crowei* sp. nov., from Section G 210.2 m, Fillmore Formation (Tulean; *Protopliomerella contracta* Zone), Section G 187.4 m Fillmore Formation (Tulean; upper *Psalikilus hestoni* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, and Section HC6 221.5 m, Garden City Formation (Tulean; *Protopliomerella contracta* Zone), west side of Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho, USA. **A, F, M**, pygidium, SUI 126722, dorsal, posterior, and right lateral views, x15 (G 210.2 m). **B, G, O**, pygidium, SUI 126723, dorsal, posterior, and right lateral views, x15 (G 210.2 m). **C, J, Q**, pygidium, SUI 126724, dorsal, posterior, and right lateral views, x15 (G 210.2 m). **K, X, BB**, transitory pygidium, SUI 126725, left lateral, dorsal, and posterior views, x15 (G 210.2 m). **N, R, AA**, transitory pygidium, SUI 126726, left lateral, dorsal, and posterior views, x15 (G 210.2 m). **P**, left librigena, SUI 126727, external view, x10. **S-U**, transitory pygidium, SUI 126728, dorsal, posterior, and left lateral views, x15 (G 210.2 m). **V**, left librigena, SUI 126729, external view, x10 (G 210.2 m). **Z**, left librigena, SUI 126730, external view, x10 (G 210.2 m). **D, E, H, I, L**, pygidium, SUI 126731, ventral, dorsal, anterior, posterior, and right lateral views, x10 (G 187.4 m). **V, W, CC**, transitory pygidium, SUI 126732, posterior, dorsal, and right lateral views, x20 (HC6 221.5 m).







other species; medial gap in ridge reduced to small slit.

Description. Cranidial measurements were made on the three largest and most intact specimens (Fig. 19A-C). Entire exoskeleton generally lacking dorsal surface sculpture. Cranidium elongate and low; maximum width across posterior projections (calculated by doubling distance from center of median node distally in specimens of Fig. 19A, B) 105.5% (102.6-108.4) sagittal length; maximum point of divergence of anterior facial sutures achieved in posterior position, opposite glabellar frontal lobe, 73.3% (72.7-74.3) sagittal length; distance across β 66.1% (63.6-67.4) sagittal length; distance across midlength of palpebral lobes 83.1% (81.0-84.9) sagittal length; distance across rear terminus of palpebral lobes 70.0% (68.5-71.4) sagittal length; anterior margin of anterior border nearly evenly anteriorly arcuate, only slightly more flexed medially; anterior rim of anterior border slightly inflated, with several very fine, closely spaced raised lines on anteriormost dorsal aspect and three or four more prominent lines on forward-facing aspect; facial sutures cut border laterally at shallow, oblique angle; posterior part of anterior border long, featureless, sloped slightly downward and forward from border furrow; sagittal length of anterior border 12.4% (11.8-12.8) that of cranidium; anterior border furrow long and very shallow, expressed as a subtle, trough-like depression with anterior arc slightly shallower than that of anterior margin of border; anterior facial sutures curved strongly around anterior border, deflected adaxially opposite anterior border furrow, deflected strongly abaxially posterior to border furrow to reach maximum point of divergence about two thirds of course posteriorly toward palpebral lobe, strongly posteriorly convergent in front of lobe; distinct, short preglabellar field present, slightly shorter than anterior border sagittally; frontal areas slightly inflated and quite broad; palpebral lobes narrow, with exsagittal length 29.9% (29.2-30.4) cranidial sagittal length, not perfectly parabolic in outline but with anterior margin slightly longer than posterior margin, relative to point of maximum width; faint eye ridge running from anterior part of palpebral lobe at strongly oblique

angle toward frontal glabellar lobe (best expressed dorsally on Fig. 19B, especially right side, and ventrally on both sides on Fig. 19D); interocular fixigena scarcely differentiated from surface of palpebral lobe, even lacking distinct change in slope, nearly horizontal; posterior projection short (exsag.), posterior fixigena sloped posteriorly to base of projection; posterior border and posterior border furrow very weakly expressed, in some specimens almost entirely effaced; tip of posterior projection narrowed, not lobate, and directed slightly posteriorly; glabella with maximum width developed opposite midlength of palpebral lobe, 65.7% (65.3-66.3) sagittal length (excluding LO); width across rear of LO 48.6% (48.2-49.3) cranidial sagittal length; glabellar sagittal length (excluding LO) 73.1% (72.1-74.1) that of cranidium; axial furrows deepest in middle part of course, from just behind rear of palpebral lobes to just behind anterior edge of lobes, shallower posteriorly opposite LO and anteriorly near adaxial terminus of eye ridge; axial furrows anteriorly convergent across and in front of LO to narrow waist opposite rear edge of palpebral lobe, bowed laterally around widest part of glabella, convergent opposite second, less narrow, waist opposite about two thirds distance forward on palpebral lobe, subparallel to slightly laterally deflected around anterior part of glabella, turned sharply into preglabellar furrow at terminus of eye ridge, eye ridge very faintly interrupting furrow; preglabellar furrow only slightly shallower than anterior part of axial furrow laterally, progressively shallower medially, but still clearly defined sagittally; axial and preglabellar furrows very narrow; posterior margin of LO evenly posteriorly arcuate, LO not inflated separately from main part of glabella in sagittal profile, with sagittal length 9.9% (9.4-10.2) that of cranidium; SO nearly effaced dorsally, course clearly visible ventrally, bowed posteriorly abaxially, more nearly transverse in median third of course; distinct though subdued median node positioned slightly anteriorly to half length of LO; glabella elongate and low, glabellar furrows completely effaced, lobes not distinctly inflated and obscure; most prominent feature on glabella is an unusual flattened median region extending from anterior edge of LO across

Figure 23. *Gladiatoria crowei* sp. nov., from Section D 155.9 m, Fillmore Formation (Tulean; *Protopliomerella contracta* Zone), southern House Range, Ibex area, Millard County, western Utah, USA. **A, B, D, F, G**, cranidium, SUI 128968, dorsal, anterior, ventral, left lateral, and oblique views, x8. **C**, right librigena, SUI 128969, external view, x10. **E, H, K**, right librigena, SUI 128970, internal, external, and ventrolateral views, x7.5. **I, F, L**, right librigena, SUI 128971, internal, external, and ventrolateral views, x8. **M, P, V**, pygidium, SUI 128972, right lateral, posterior, and dorsal views, x10. **N**, left librigena, SUI 128973, external view, x8. **O, S, T, U, Z**, pygidium, SUI 128974, anterior, dorsal, ventral, posterior, and left lateral views, x10. **Q, X, BB**, transitory pygidium, SUI 128975, left lateral, dorsal, and posterior views, x10. **R, U, W, AA**, transitory pygidium, SUI 128976, left lateral, dorsal, ventral, and posterior views, x10.

SO and anteriorly to opposite anterior edge of palpebral lobes; this region varies in shape from subrectangular (Fig. 19C) to weakly (Fig. 19A) to strongly (Fig. 19B) waisted and figure-8 shaped; while appearing flat dorsally, in ventral view there is a depressed band around the edges of the region (expressed ventrally as a positive feature) surrounding a narrow median slightly raised ridge (expressed ventrally as a shallow sagittal furrow); doublure beneath LO with distinct posterior rim with narrow furrow beneath it, flattened ellipsoid articulating surface apparently smooth, lacking raised lines; narrow subtriangular strip of doublure underlies posterolateral region of posterior projection; fossulae not discernible ventrally.

Librigena elongate and generally narrow; visual surface not fully preserved on any specimen but eye relatively long, separated from field by inflated, narrow socle and very narrow, incised furrow; posterior branch of facial suture short, straight, with only one change in course across posterior border; anterior section of facial suture describing nearly evenly bowed arc; field narrow and long, very slightly dorsally convex beneath eye, slightly dorsally concave in other regions, lacking sculpture; lateral and posterior border furrows completely effaced, inner edge of doublure not marked dorsally in any fashion; lateral border broad, but most of width not clearly differentiated from field; secondary furrow very shallow, clearly expressed only posteriorly as shallow trough running along lateral margin; lateral margin of lateral border developed into distinct sharp rim with a few closely spaced raised lines running subparallel with and immediately adaxial to margin; lateral margin sharp and flattened, blade-like; anterior projection large; genal spine very broad at base, with subtle dorsal inflation, tapered gradually posteriorly to sharp distal point; marginal rim continued along abaxial edge of genal spine to distal point; adaxial edge of genal spine flattened but not developed into rim; dorsal aspect of genal spine with several prominent raised lines originating on rear of field and running distally toward tip (best preserved on Fig. 20V); doublure broad and ventrally inflated, with dense sculpture of closely spaced raised lines running subparallel to adaxial and lateral margins; doublure beneath genal spine base ventrally

concave; prominent Panderian notch developed in front of genal spine base, just below contact with posterior facial suture.

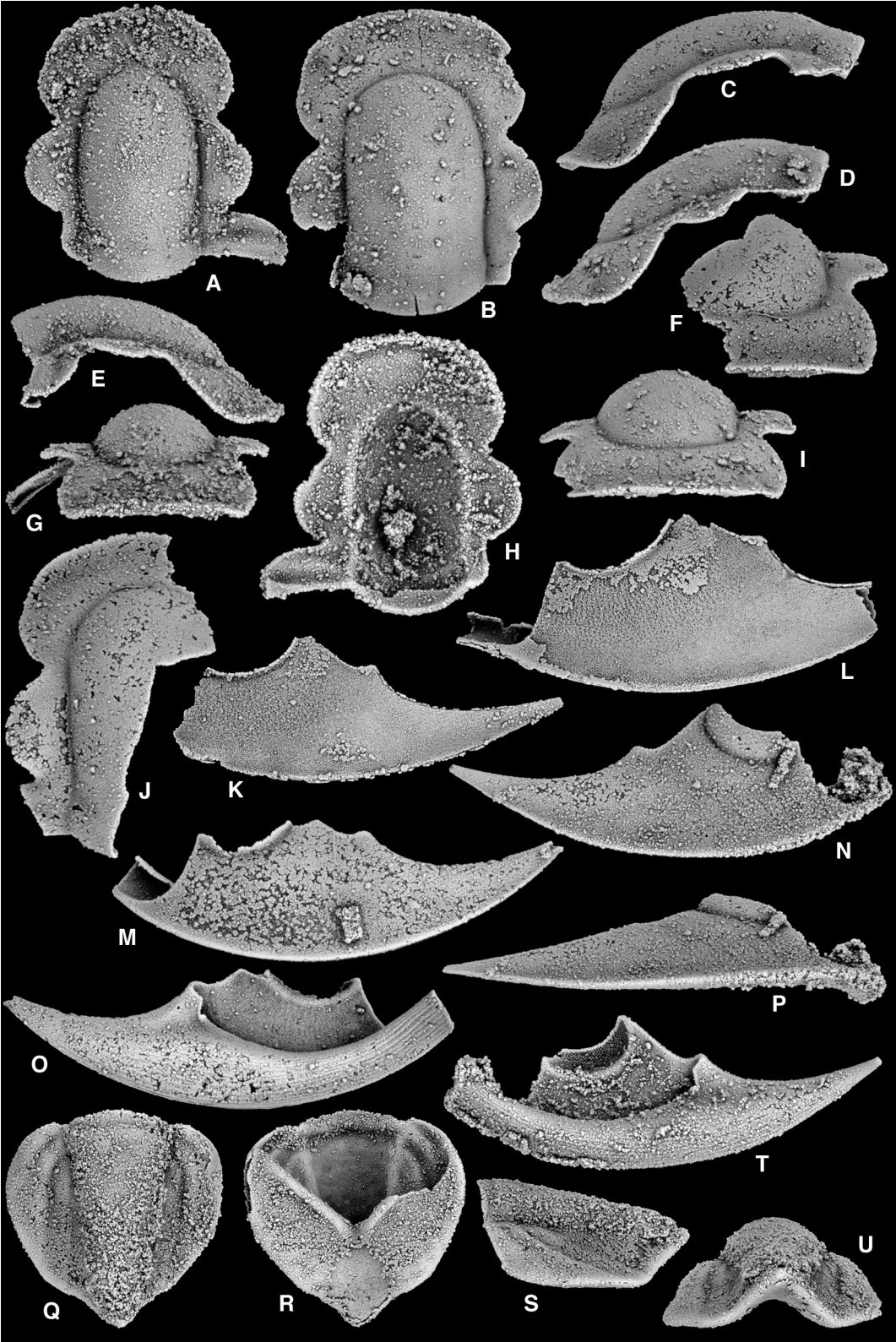
Rostral plate not identified, but well preserved anterior projections on librigena indicate a fairly broad, subtrapezoidal plate.

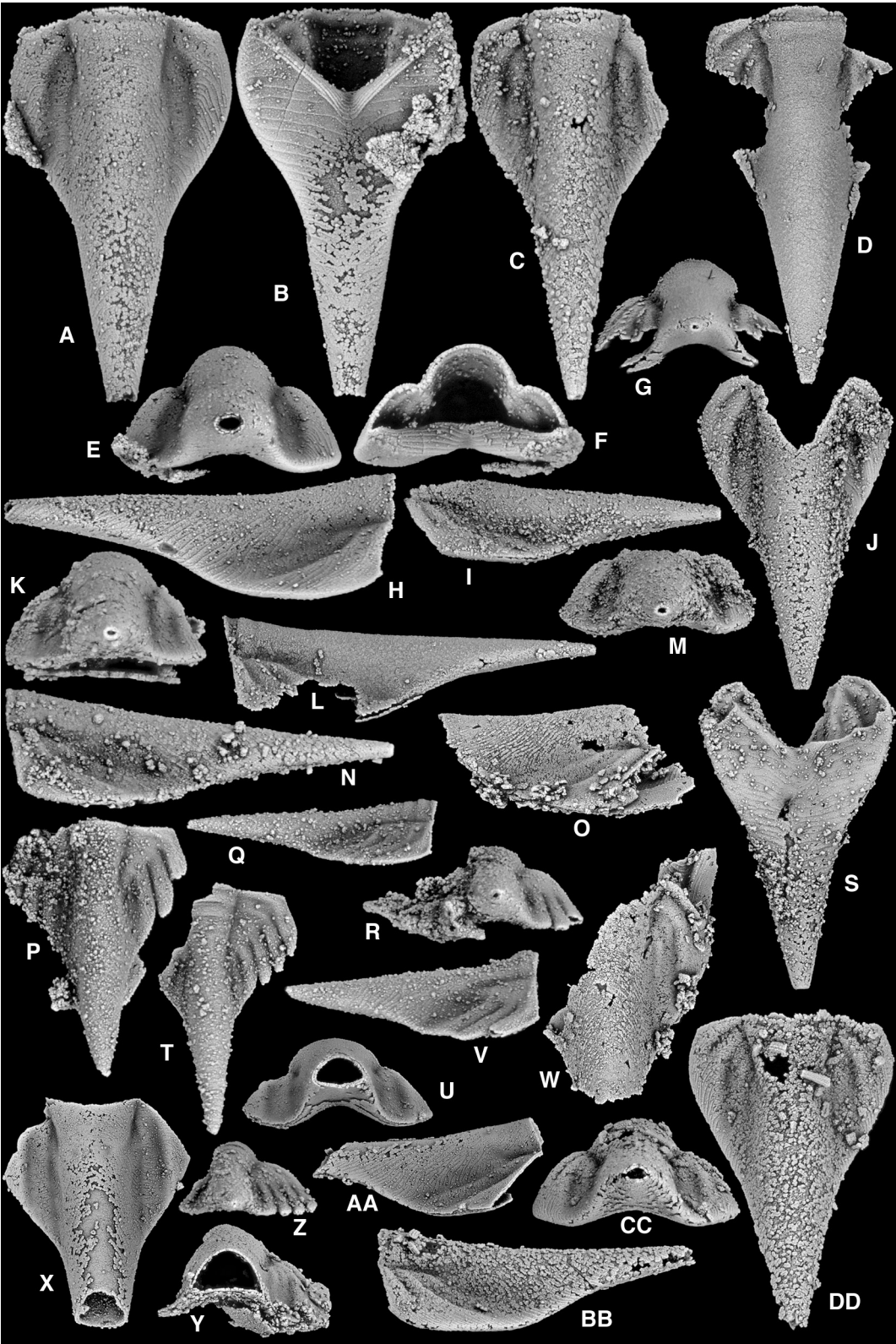
Hypostome with anterior wings not preserved on available specimens (Fig. 14P, S); anterior face and lateral faces beneath anterior wings developed into tall wall-like rim with coarse raised line sculpture; anterior part of middle body extended anteriorly to blunt, transverse anterior margin (with wall-like rim running dorsally), anterior lobe of middle body surrounded and bound by subovate raised lines, with median sculpture of loosely organized, scrobiculate lines; lateral border developed near posterior base of anterior wing, narrow, slightly wider anteriorly, running without clear distinction into posterior border, with closely spaced raised line sculpture set somewhat obliquely to course of border and margin; lateral border furrow narrow and quite deep; posterior border furrow distinctly widened/lengthened adaxially/posteromedially; middle furrow only expressed abaxially as relatively shallow, obliquely inclined depression not fully in contact with lateral border furrow laterally; slightly swollen, but poorly expressed maculae set just behind middle furrow; posterior lobe of middle body crescentic in shape, with slightly finer, poorly organized raised line sculpture similar to that on median part of anterior lobe; posterior wings short, set dorsally from border by laterally concave strip of doublure, raised lines from lateral rim running onto base of wing.

Thorax not identified, but form of posterior thoracic segments is revealed by several transitory pygidia (Figs 22R, S, W, X, 23U, W).

Pygidial measurements were made on two large, mostly nearly intact specimens from the type horizon (Fig. 21D, Q). Pygidium long, narrow, and dagger-like, maximum width across distal parts of first segment 38.9% (37.9-39.9) sagittal length; almost all pygidial structures dorsally effaced, only pleurae of first segment partially expressed; all dorsal surfaces of pygidium with prominent raised line sculpture, arranged broadly in inverted chevrons across axis and continuing uninterrupted onto pleurae all the way to margin, lines regular and organised

Figure 24. All specimens are from Section HC5 186.5 m, Garden City Formation (Tulean; *Hintzeia celsaora* Zone), east side of Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho, USA. **A-P, T, *Gladiatoria phoenixi* sp. nov.** **A, E, G, H,** cranium, SUI 126733, dorsal, right lateral, anterior, and ventral views, x15. **B, D, I,** cranium, SUI 115170, dorsal, left lateral, and anterior views, x15. **C, F, J,** cranium, SUI 126734, dorsal, left lateral, and anterior views, x15. **K,** left librigena, SUI 126735, external view, x10. **L,** left librigena, SUI 126736, external view, x10. **M, O,** left librigena, SUI 126737, external and internal views, x15. **N, P, T,** right librigena, SUI 126738, external, ventrolateral, and internal views, x12. **Q, R, S, U, *Gladiatoria* sp.,** pygidium, SUI 126739, dorsal, ventral, left lateral, and posterior views, x7.5.





on axis and posteriorly on posterior spine, but becoming slightly irregular and occasionally confluent on pleurae; pleurae narrow, consisting mainly of merged anterior and posterior bands of first segment; first pleural furrow completely effaced; first segment pleura is turned almost completely posteriorly; first interpleural furrow expressed as shallow, nearly exsagittally aligned furrow not extending anteriorly to contact axial furrow and not extending posteriorly to margin; the first interpleural furrow is separated from the axis by a narrow strip of gently inflated pleura which is likely a part of the second segment but which is difficult to interpret in detail; the pygidial margin features an anterolateral corner which is the fulcrum, with width here 31.9% (31.7-32.0) sagittal length and 82.0% (80.3-83.6) maximum width, a lateral margin which is actually the anterior edge of the first pygidial segment, which runs somewhat posterolaterally to a maximum width opposite the rear of the first interpleural furrow, then is turned posteromedially to grade posteriorly into the lateral margin of the inflated posterior spine; axis with anterior width 64.3% (63.9-64.7) anterior width of pygidium, first axial ring discernible with faint first ring furrow in some specimens (e.g., Fig. 21E), completely effaced in most; axis narrowed posterior to first ring to waisted point with width 70.5% (66.4-76.4) anterior axial width, broadened posterior to waist into inflated posterior spine; axial furrow defined anteriorly to opposite about half distance of first interpleural furrow, then effaced posteriorly; pygidium with strong dorsal vaulting in transverse profile, portions of pleurae distal to fulcrum held almost vertically; large spine slightly deflected dorsally in sagittal profile in some specimens (Fig. 21J), not markedly deviating from slope of axis in some (Fig. 21F), turned slightly down from slope of axis in several (Fig. 21K, O, P); doublure forming flat shelf beneath almost entire pygidium, apart from small triangle near front of axis, with sculpture of strong raised lines with chevron pattern centered on midline; anterior edge of doublure formed into subtle raised ridge, with posteriorly directed small slit

medially.

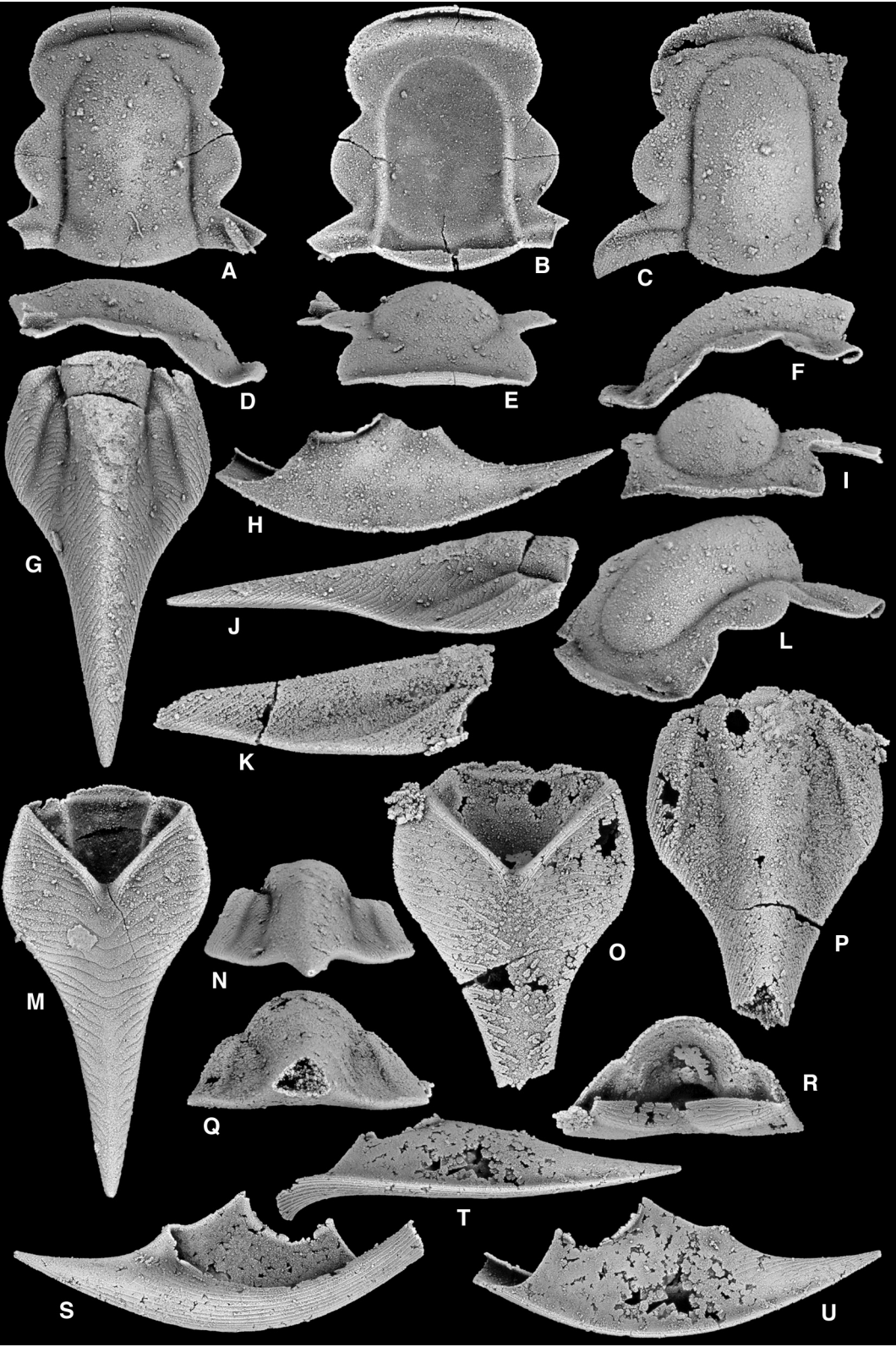
Ontogeny. Probable late meraspid to holaspid ontogenetic changes in *G. crowei* are less marked than in some other species. The main cranidial changes involve a general elongation of the cranidium and of the glabella, shortening of the preglabellar field, some expansion of the frontal area, and differential shallowing of the axial furrow. There is almost no noticeable change in proportions of the librigenae across the documented size range. Similarly, the morphology of the holaspid pygidium was established in overall proportions by at least the second-last meraspid degree (Fig. 22S) and shows no substantial change with substantially increased size.

Material. Holotype, pygidium, SUI 126713 (Fig. 21C, D, H, O), and assigned specimens SUI 126694-126698, 126700-126712, 126714-126730, 126792, 126793, from Section G 210.2 m, Fillmore Formation (Tulean; *Protopliomerella contracta* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA; assigned specimen SUI 126731, from Section G 187.4 m, Fillmore Formation (Tulean; upper *Psalikilus hestoni* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA; assigned specimens SUI 128968-128976, from Section D 155.9 m, Fillmore Formation (Tulean; *Protopliomerella contracta* Zone), southern House Range, Ibex area, Millard County, western Utah, USA; assigned specimens SUI 126699, 126732, from Section HC6 221.5 m, Garden City Formation (Tulean; *Protopliomerella contracta* Zone), west side of Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho, USA.

Etymology. After Russell Crowe.

Remarks. *Gladiatoria crowei* is compared with *G. phoenixi* and *G. nielsenae* in their differential diagnoses below. Differences between these three species collectively and other members of

Figure 25. *Gladiatoria phoenixi* sp. nov., from Section HC5 186.5 m, Garden City Formation (Tulean; *Hintzeia celsaora* Zone), east side of Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho, and Section G 118.6 m, Fillmore Formation (Tulean; *Hintzeia celsaora* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. **A, B, E, F, H,** pygidium, **holotype**, SUI 115169, dorsal, ventral, posterior, anterior, and right lateral views, x15 (HC5 186.5 m). **C, K, N,** pygidium, SUI 126740, dorsal, posterior, and left lateral views, x15 (HC5 186.5 m). **D, G, L,** pygidium, SUI 126741, dorsal, posterior, and left lateral views, x10 (HC5 186.5 m). **I, J, M, S,** pygidium, SUI 126742, left lateral, dorsal, posterior, and ventral views, x10 (HC5 186.5 m). **P, R, V,** transitory pygidium, SUI 126743, dorsal, posterior, and right lateral views, x15 (HC5 186.5 m). **Q, T, Z,** transitory pygidium, SUI 126744, right lateral, dorsal, and posterior views, x15 (HC5 186.5 m). **U, X, AA,** pygidium, SUI 126745, posterior, dorsal, and right lateral views, x6 (HC5 186.5 m). **O, W, Y,** pygidium, SUI 126746, right lateral, dorsal, and posterior views, x6 (G 118.6 m). **BB-DD,** pygidium, SUI 126747, left lateral, posterior, and dorsal views, x10 (G 118.6 m).



the genus were discussed above under the genus.

***Gladiatoria phoenixi* sp. nov.** (Figs 24A-P, T, 25)

2009 *Gladiatoria* sp. nov. 1; Adrain *et al.*, p. 557, fig. 9BB, CC.

Diagnosis. Axial and preglabellar furrows deep and well defined throughout course; preglabellar field long; librigenal lateral border furrow faintly expressed dorsally, but more so than in any other species; librigenal doublure narrower anteriorly and broader posteriorly; pygidium with pleural region relatively broad and subtriangular; first pleural furrow distinctly expressed, deepest proximally.

Description. *Gladiatoria phoenixi* is similar enough to *G. crowei* that extended written description is redundant. Instead, all perceived differences are listed here. Anterior sections of facial suture more laterally bowed; preglabellar field slightly longer; axial and particularly preglabellar furrows much deeper and better expressed; preglabellar furrow less parabolic and more transverse medially; palpebral lobes relatively larger and wider; median part of glabella smooth and unmarked, lacking elongate flattened region. Librigenae very similar, but

lateral marginal rim and associated furrow not as prominent; librigenal doublure markedly narrowed anteriorly, versus much more nearly the same width (cf. Fig. 24O, T, with Fig. 20Z). Pygidium markedly different, with much broader pleurae; distal part of first segment not as long, so that widest part of pygidium is set farther anteriorly; first pleural segment clearly expressed proximally, versus nearly totally effaced; pleura of second segment broader and better expressed; first axial ring faint but definitely expressed versus nearly completely effaced; anterior doublural rim much larger, medial furrow in rim large versus small and slit-like.

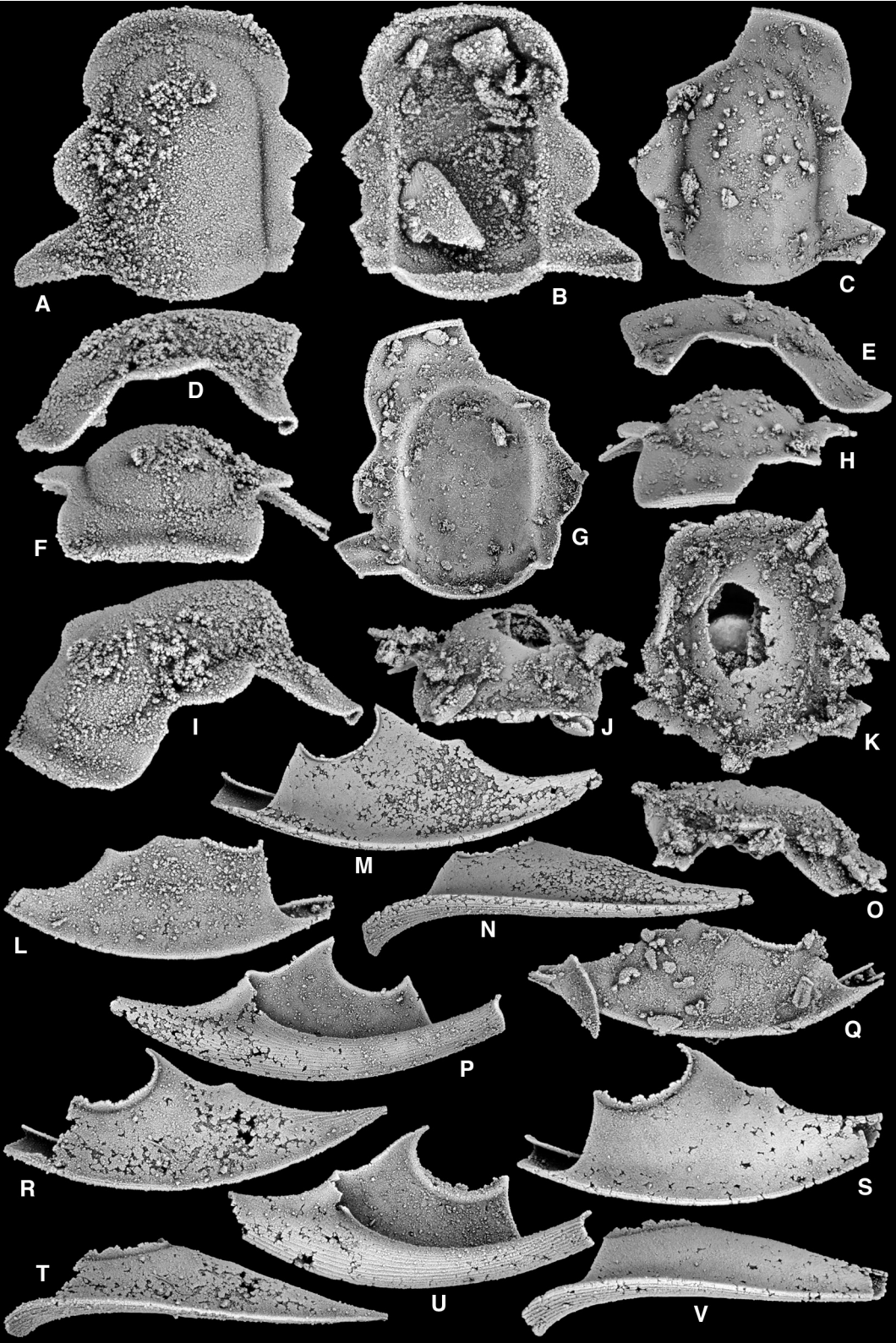
Material. Holotype, pygidium, SUI 115169 (Fig. 25A, B, E, F, H), and assigned specimens SUI 115170, 126733-126738, 126740-126745, from section HC5 186.5 m, Garden City Formation (Tulean, *Hintzeia celsaora* Zone), west side of Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho, USA; assigned specimens SUI 126746, 126747, from Section G 118.6 m, Fillmore Formation (Tulean, *Hintzeia celsaora* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

Etymology. After Joaquin Phoenix.

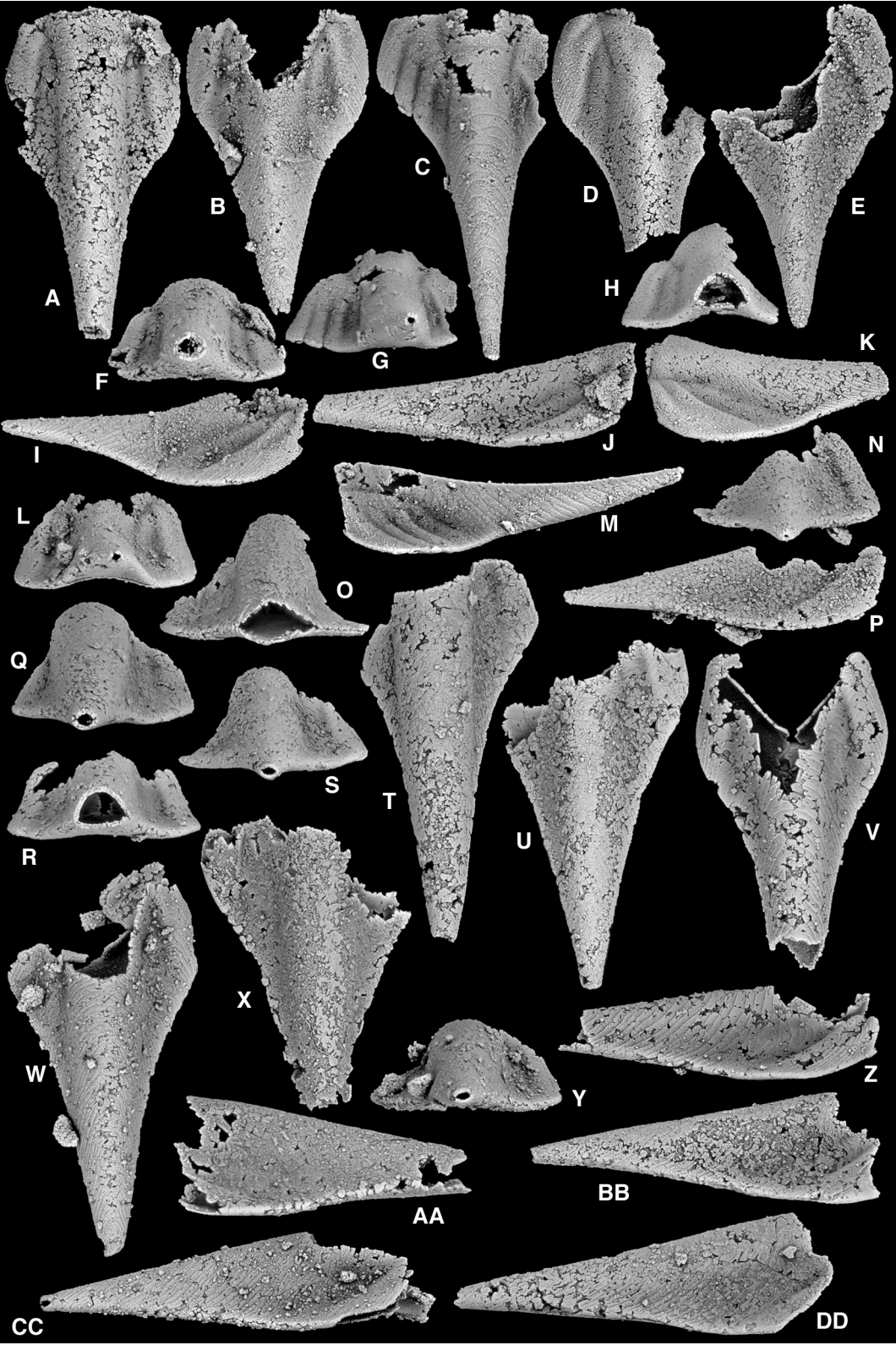
Figure 26 (opposite). *Gladiatoria nielsenae* sp. nov., from Section HC5 195.7 m and 203.7-204.2T m, Garden City Formation (Tulean; lower *Psalikilopsis cuspidicauda* Zone), east side of Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho, and Section G 174.0 m, Fillmore Formation (Tulean; *Psalikilus typicum* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. **A, B, D, E**, cranium, SUI 115200, dorsal, ventral, right lateral, and anterior views, x12 (HC5 195.7 m). **C, F, I, L**, cranium, SUI 126748, dorsal, left lateral, anterior, and oblique views, x15 (HC5 195.7 m). **G, J, M, N**, pygidium, SUI 126749, dorsal, right lateral, ventral, and posterior views, x12 (HC5 195.7 m). **H**, left librigena, SUI 126750, external view, x15 (HC5 195.7 m). **K, O-R**, pygidium, SUI 126751, right lateral, ventral, dorsal, posterior, and anterior views, x10 (HC5 203.7-204.2T m). **S-U**, librigena, SUI 126752, internal, ventrolateral, and external views, x10 (G 174.0 m).

Figure 27 (overleaf). *Gladiatoria nielsenae* sp. nov., from Section G 148.2 m, 155.6 m and 162T m (all Tulean; lower *Psalikilopsis cuspidicauda* Zone), Section G 174.0 m (Tulean; *Psalikilus typicum* Zone), all southern Confusion Range, and Section D 106.4 m (Tulean; upper *Psalikilopsis cuspidicauda* Zone), southern House Range, all Fillmore Formation, Ibex area, Millard County, western Utah, USA. **A, B, D, F, I**, cranium, SUI 126753, dorsal, ventral, left lateral, anterior, and oblique views, x12 (G 148.2 m). **C, E, H**, cranium, SUI 126754, dorsal, right lateral, and anterior views, x12 (G 162T m). **Q**, right librigena, SUI 126755, external view, x10 (G 155.6 m). **S, U, V**, left librigena, SUI 126756, external, internal, and ventrolateral views, x12 (G 148.2 m). **J, K, O**, cranium, SUI 126757, anterior, dorsal, and right lateral views, x10 (G 174.0). **L**, right librigena, SUI 126758, external view, x10 (G 174.0). **M, N, P**, left librigena, SUI 126759, external, ventrolateral, and internal views, x6 (G 174.0). **R, T**, left librigena, SUI 126760, external and ventrolateral views, x12 (D 106.4 m).

Figure 28 (page 363). *Gladiatoria nielsenae* sp. nov., from Section G 148.2 m and 162T m (Tulean; lower *Psalikilopsis cuspidicauda* Zone) and Section G 174.0 (Tulean; *Psalikilus typicum* Zone), all Fillmore Formation, southern Confusion Range, Ibex area, Millard County, western Utah, USA. **A**, right librigena, SUI 126761, external view, x12 (G 174.0). **B**, left librigena, SUI 126762, external view, x12 (G 174.0). **C-E, I**, pygidium, SUI 126763, dorsal, posterior, ventral, and left lateral views, x10 (G 174.0). **M, S, W, Y, BB**, pygidium, SUI 126764, left lateral, dorsal, posterior, ventral, and anterior views, x12 (G 174.0). **Z, AA, DD**, transitory pygidium, SUI 126765, posterior, dorsal, and left lateral views, x12 (G 174.0). **F, O, V**, transitory pygidium, SUI 126766, dorsal, right lateral, and posterior views, x12 (G 162T m). **G, H, J, L, P**, pygidium, **holotype**, SUI 115201, dorsal, ventral, right lateral, anterior, and posterior views, x10 (G 162T m). **K, Q, R**, transitory pygidium, SUI 126767, dorsal, right lateral, and posterior views, x15 (G 162T m). **N, T, U, X, CC**, pygidium, SUI 126768, left lateral, ventral, dorsal, anterior, and posterior views, x10 (G 148.2 m).







Remarks. *Gladiatoria phoenixi* is the oldest known species and, as discussed above, together with *G. nielsenae* the most similar to the two known species of *Bathyurellus*. It is distinguished from *G. nielsenae* in its more anteriorly rounded anterior border, shallower anterior border furrow, and longer preglabellar field. The pygidium is quite similar to that of *G. nielsenae*, but differs in that the distal part of the first segment is shorter, and particularly in that the first interpleural furrow is turned at the fulcrum and runs almost exactly posteriorly distally, compared with running in an almost completely straight posterolateral direction from the axial furrow to the margin.

***Gladiatoria nielsenae* sp. nov.** (Figs 26-29)

2009 *Gladiatoria* sp. nov. 2; Adrain *et al.*, p. 559, 561, fig. 10CC, JJ, fig. 11G.

Diagnosis. Anterior border furrow transverse and deepest known in the genus; median part of the glabella with subtly developed flattened region, not obvious in all specimens; pygidium with distal part of first pleura long and first interpleural furrow almost completely straight, deflected only very slightly across fulcrum, and set obliquely to run posterolaterally from the axial furrow to the margin, in most specimens effaced just before reaching the margin.

Description. As with *G. phoenixi* above, *G. nielsenae* is sufficiently similar to *G. crowei* that extended written description is redundant and all differences are noted in the following comparison. Anterior border shorter and anterior margin more transverse; anterior border furrow much deeper and more transverse; preglabellar furrow much deeper medially; anterior sections of facial sutures more laterally bowed; palpebral lobes longer and wider; LO relatively wider versus glabella, axial furrows turned more obliquely opposite LO; medial part of glabella with only very subtly developed (most clearly on Fig. 27C, but also on Fig. 26A, B) flattened portion versus prominently expressed; occipital node obscure versus obvious. Librigena narrower behind eye,

with less prominent lateral rim and associated furrow; genal spine more sharply tapering. Pygidia narrower; distal portion of first pleura shorter, more obliquely versus more posteriorly aligned; first pleural furrow impressed though shallow proximally versus completely effaced; first interpleural furrow deeper, impressed much better proximally, and more obliquely aligned; second pleura broader and larger; first axial ring faint versus nearly completely obscure; anterior doublural rim smaller than in *G. phoenixi*, but still larger than in *G. crowei*; median furrow slit-like as in *G. crowei*, but slightly larger.

Material. Holotype, pygidium, SUI 115201 (Fig. 28G, H, J, L, P), and assigned specimens SUI 126753-126756, 126766-126773, from Section G 155.6 m, 162T m (Tulean; lower *Psalikilopsis cuspidicauda* Zone); assigned specimens SUI 126752-126757-126759, 126761-126765, 126774-126778, from Section G 174.0 m (Tulean; *Psalikilus typicum* Zone), all southern Confusion Range; assigned specimen SUI 126760 from Section D 106.4 m (Tulean; upper *Psalikilopsis cuspidicauda* Zone), southern House Range, all Fillmore Formation, Ibex area, Millard County, western Utah, USA; assigned specimens SUI 115200, 126748-126751, from Section HC5 195.7 m and 203.7-204.2T m, Garden City Formation (Tulean; lower *Psalikilopsis cuspidicauda* Zone), east side of Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho, USA.

Etymology. After Connie Nielsen.

Remarks. Two specimens from Section G 148.2 are assigned to *Gladiatoria nielsenae* for the time being, but may represent a distinct species. A cranium (Fig. 27A, B, D, F, I) seems to have less laterally bowed anterior facial sutures and a shorter (sag.) preglabellar field. A pygidium (Fig. 28, N, T, U, X, CC) has a shorter first distal pleura, and more sharply posteromedially converging lateral margins posterior to the widest point. In other respects they are very similar to sclerites assigned with confidence to *G. nielsenae*. More material would be required to assess whether the

Figure 29. *Gladiatoria nielsenae* sp. nov., from Section G 148.2 m and 155.6 m (Tulean; lower *Psalikilopsis cuspidicauda* Zone), and Section G 174.0 (Tulean; *Psalikilus typicum* Zone), all Fillmore Formation, southern Confusion Range, Ibex area, Millard County, western Utah, USA. **A, F, J**, pygidium, SUI 126769, dorsal, posterior, and right lateral views, x10 (G 155.6 m). **B, I, L**, pygidium, SUI 126770, dorsal, right lateral, and posterior views, x10 (G 155.6 m). **C, G, M**, transitory pygidium, SUI 126771, dorsal, posterior, and left lateral views, x15 (G 155.6 m). **D, H, K**, pygidium, SUI 126772, dorsal, posterior, and left lateral views, x10 (G 148.2 m). **E, N, P**, pygidium, SUI 126773, dorsal, posterior, and right lateral views, x10 (G 155.6 m). **O, X, AA**, pygidium, SUI 126774, posterior, dorsal, and left lateral views, x8 (G 174.0). **Q, T, DD**, pygidium, SUI 126775, posterior, dorsal, and right lateral views, x10 (G 174.0). **R, V, Z**, pygidium, SUI 126776, posterior, dorsal, and right lateral views, x10 (G 174.0). **S, U, BB**, pygidium, SUI 126777, posterior, dorsal, and right lateral views, x10 (G 174.0). **W, Y, CC**, pygidium, SUI 126778, dorsal, posterior, and right lateral views, x8 (G 174.0).

taxon at this horizon is consistently differentiated. The criteria for assigning sclerites to the co-occurring species *G. nielsenae* and *G. gladiator* were discussed under remarks on the latter above.

Gladiatoria sp. 1 (Fig. 24Q-S, U))

Material. Assigned specimen SUI 126739, from Section HC5 186.5 m, Garden City Formation (Tulean; *Hintzeia celsaora* Zone), east side of Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho, USA.

Remarks. A single large pygidium occurs at the type horizon of *G. phoenixi* but obviously differs from pygidia of that species and all other members of the genus in the lack of a large posteriorly extended pygidial spine. In its place is a very small, bluntly terminated triangular spine which extends only a short distance posteriorly. Ventrally, this spine is underlain by a ventrally concave region of doublure. Apart from these differences, the remaining morphology of the specimen is very like that of *G. phoenixi*, with similar expression of the first pleural furrow and the first ring furrow, and similar general proportions of the pleura and axis. It is possible that it represents a pathological or teratological specimen of *G. phoenixi*. However the pygidium is symmetrical and shows no sign of damage or repair. Alternatively, the specimen could represent a second, closely related, species occurring at HC5 186.5 m. This would be confirmed if a larger sample was obtained and yielded additional specimens with this morphology (as well as, presumably, different cranidial and librigenal morphs to associate with it). Given its lack of obvious irregularity and radical morphological difference we consider it more likely that a separate species is represented and report the prospective taxon in open nomenclature.

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