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**The plimerid trilobite *Ibexaspis* and related new genera,
with species from the Early Ordovician (Floian; Tulean, Blackhillsian)
of the Great Basin, western USA**

NEO E.B. McADAMS^{1,3}, JONATHAN M. ADRAIN^{1,4} & TALIA S. KARIM²

¹*Department of Earth and Environmental Sciences, University of Iowa, 115 Trowbridge Hall, Iowa City, Iowa 52242, USA.*

E-mail: Neo.McAdams@ttu.edu; jonathan-adrain@uiowa.edu

²*University of Colorado Museum of Natural History, 265 UCB, University of Colorado, Boulder, Colorado 80309, USA.*

E-mail: talia.karim@colorado.edu

³*Present address: Department of Geosciences, Texas Tech University, P.O. Box 41053, Lubbock, Texas 79409-1053, USA*

⁴*Corresponding author*



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Abstract

Field-based revision and phylogenetic analysis demonstrate that the pliomerid trilobite taxon *Ibexaspis* Přibyl and Vaněk (in Přibyl *et al.*, 1985), previously known from a single formally named species (*I. brevis* [Young, 1973]), belongs to a complex of 14 mostly newly discovered, related species from the Early Ordovician (Floian; Tulean and Blackhillsian) of the northern Laurentian margin. The species are known from silicified samples recovered from sections in eastern Nevada, western Utah, and southeastern Idaho. The stratigraphically early *Tuleaspis* n. gen. (type species: *T. jeneki* n. sp.; Tulean; low *Protopliomerella contracta* Zone) includes its type and two species described in open nomenclature. *Tuleaspis* is sister to the remainder of the clade. *Ibexaspis* now includes three additional species: *I. coadyi* n. sp. (Blackhillsian; *Carolinites nevadensis* Zone), *I. leuppi* n. sp. (Blackhillsian; *Presbynileus ibexensis* Zone), and *I. rupauli* n. sp. (Blackhillsian; "*Pseudocybele nasuta* Zone"). *Ibexaspis* is sister to a clade of *Millardaspis* n. gen. + *Deltapliomera* n. gen. *Millardaspis* (type species *M. milsteadi* n. sp.; Tulean; *Heckethornia hyndae* Zone) also includes *M. knoxi* n. sp. (Tulean; *Panisaspis sevierensis* Zone). *Deltapliomera* (type species *D. humphriesi* n. sp.; Blackhillsian, *Carolinites nevadensis* Zone) also includes *D. inglei* n. sp. (Tulean; *Heckethornia bowiei* Zone), *D. heimbergi* (Tulean; *Panisaspis sevierensis* Zone), *D. eppersoni* n. sp. (Blackhillsian; *Bathyrina plicolabeona* Zone), and a species described in open nomenclature.

Key words: Utah, Nevada, Idaho, silicified, taxonomy, phylogenetics, trilobites

Introduction

This work is sixth in a series of papers and monographs describing pliomerid trilobites from the Early and Middle Ordovician (Floian and Dapingian) of the northern Laurentian margin, based on new field collections from Nevada, Utah, and Idaho. Previous works have been concerned with the genus *Lemureops* McAdams and Adrain, 2009, the new zonal name-bearing species *Pseudocybele paranasuta* McAdams and Adrain, 2010a, and the genera *Hintzeia* Harrington, 1957 (McAdams and Adrain, 2011a), *Panisaspis* McAdams and Adrain, 2011b, and *Protopliomerella* Harrington, 1957 (McAdams and Adrain, 2011c). Remaining works will deal with the genera

Cybelopsis Poulsen, 1927, *Pseudomera* Holliday, 1942, additional new and revised species of *Pseudocybele* Ross, 1951, and some minor, rare taxa.

Příbyl and Vaněk (in Příbyl *et al.*, 1985) established *Ibexaspis* with type species *Protopliomerops quattuor brevis* Young, 1973. Although in their discussion of the new genus they simply referred to the subspecies as a species, elsewhere (p. 119, figs 22, 23) they referred to the species as *I. brevis* (Young, 1973), so they clearly intended to elevate Young's subspecies to full species status. In their discussion of the new genus (Příbyl *et al.*, 1985, pp. 170–171) they made no mention of the classification of *Protopliomerops quattuor* Hintze, 1953. Elsewhere (Příbyl *et al.*, 1985, p. 119), however, they referred to it as *Ibexaspis* as a second species. *Protopliomerops quattuor* was revised by McAdams and Adrain (2011b, p. 17, figs 25–32) and assigned to their new genus *Paniaspis*. The likely reason for its assignment to *Ibexaspis* by Příbyl and Vaněk is that while Hintze's (1953, pl. 21, fig. 9) holotype cranidium and assigned librigena and pygidia represent *Paniaspis*, one of his assigned cranidia (1953, pl. 21, fig. 11) is much younger and in fact belongs to *Ibexaspis brevis*, while another (1953, pl. 21, fig. 10) from the same horizon (Hintze's H-20; Section H 191.7 m herein) belongs to a related new taxon, *Deltapliomera eppersoni* n. sp.

Příbyl and Vaněk interpreted *I. brevis* as a pilekiine cheirurid. Peng (1990, p. 112) rejected this assignment, concluding that *Ibexaspis* was a "protopliomeropid" (i.e., pliomerid). Apart from a genus listing by Jell and Adrain (2003, p. 387) and preliminary illustration of some of the taxa described herein in a biostratigraphy paper (Adrain *et al.*, 2009), Peng (1990), and McAdams and Adrain (2011a, p. 7; 2011b, p. 7) are the only workers to comment upon *Ibexaspis* in a systematic context since it was proposed. McAdams and Adrain (2011b) suggested that *Ibexaspis* (now the expanded group of four related genera treated herein) was the sister group of *Paniaspis* within Pliomeridae.

Hence, prior to this work, the group treated herein has been known from a single named species, *I. brevis*. In the course of our field-based revision of the Early Ordovician northern Laurentian trilobite faunas, we have recovered 13 more clearly related species, all new, ten of which are represented by enough material to formally name. It is now evident that a fairly significant clade is represented, with a considerable range of morphology. The goals of the present work are: 1) to revise *Ibexaspis brevis* on the basis of new field collections from the type horizon; 2) to describe a further 13 species on the basis of new field collections, and propose formal names for 10 of them; 3) to carry out a maximum parsimony analysis of the group, using the phylogenetically basal species of its presumptive sister clade as an outgroup; and 4) to propose three new genera for well supported and morphologically cohesive components of the resulting cladogram. In addition, we provide new details of an ongoing revision of the Floian trilobite zonation of the region and introduce a replacement name for one previously established zone.

Localities and Biostratigraphy

Adrain *et al.* (2009) introduced a new biostratigraphic scheme for most of the Tulean and Blackhillsian stages, which is largely followed herein. Full locality details (maps, lines of section, stratigraphic columns, etc.) were given in that work and are not repeated herein except as amended below. Ongoing work has led to a number of revisions, and new discoveries indicate that the succession is more complex and contains more distinct faunal assemblages than originally realized. Full documentation will be provided in forthcoming works, but we summarize the current state of knowledge in Figure 1, along with the stratigraphic occurrence of the species described herein, and provide the following notes of relevance to the present study.

Three zones have proven to contain differentiated assemblages in their lower and upper parts. Adrain *et al.* (2011b, p. 371) discussed the lower and upper *Psalikilopsis cuspidicauda* Zone, noting that the name bearer was restricted to the lower portion, but deferring any formal adjustment until more of the species diversity in either interval was formally described. Adrain *et al.* (2011a, fig. 1) and McAdams and Adrain (2011c, fig. 2) recognized this distinction along with lower and upper parts of the *Psalikilus hestoni* Zone. Herein, we introduce a distinction between differentiated lower and upper parts of the *Protopliomerella contracta* Zone (Fig. 1). The lower assemblage is represented at Ibex Section G 210.2 m, including *Tuleaspis jeneki* n. gen. n. sp. and *Tuleaspis?* n. sp. B, and the higher at G 230.1 m. Horizons at sections HC5 and HC6 in Idaho correlate with the upper assemblage.

Horizons assigned to the *Heckethornia hyndeeae* Zone have previously been documented at Ibex (Section G

238.3–258.2 m) and at Yellow Hill in eastern Nevada (Section YH 128.9–129.5 m). This zone had not been discovered in rocks of the Garden City Formation in southeastern Idaho. Collections from Section HC5 end below this level, in the high *Protopliomerella contracta* Zone. The same was thought of HC6, where the highest previously collected horizon, HC6 221.5 m, is also assigned to the high *P. contracta* Zone. Section HC6 is terminated by a fault, above which older Stairsian rocks are fault-repeated (see McAdams and Adrain, 2011c, p. 12, for discussion). Sampling during the 2011 field season, however, revealed several horizons yielding silicified fossils above 221.5 m but beneath the fault. Two of these, at 222.3 and 224.5 m, also yielded fossils of the high *P. contracta* Zone. The highest new horizon, at HC6 226.5 m, yielded very rich collections assignable to the *H. hyndae* Zone, including excellent material of *Millardaspis milsteadi* n. gen. n. sp.

In the 2009 zonation, we recognized the highest part of the Floian as a "*Pseudocybele nasuta* Zone" and the highest unstudied interval. Subsequent sampling indicated the surprising presence of multiple unique faunas turning over on a metre-level stratigraphic scale. Adrain and McAdams (2012) depicted these as a series of six unnamed assemblages which replace the "*P. nasuta* Zone" and overlying unstudied interval. These will eventually need to be recognized as separate zones, as they contain faunas as distinct as those of the zones we have recognized lower in the sequence. The idea that they are expressed over the same broad geographic range as the remainder of the zonation is supported by new data herein, in which the occurrence of *Ibexaspis rupauli* n. sp. at a single horizon in the Yellow Hill Limestone in eastern Nevada can be correlated on the basis of this and several co-occurring species with the third-from-bottom assemblage of Adrain and McAdams (2012) at Section J in western Utah. Full documentation of the biostratigraphy of this interval will be presented in a forthcoming work.

In our 2009 paper, we referred to the upper Blackhillsian horizon at Yellow Hill in eastern Nevada, containing *I. rupauli*, as "YH-2" (Adrain *et al.*, 2009, p. 548, fig. 4) in the mistaken assumption that it represented a locality described by Hintze (1953, p. 56) from a similar geographic position. It is now clear that Hintze's locality yielded a much older fauna apparently assignable to the Tulean *Protopliomerella contracta* Zone. The upper Blackhillsian fauna we recovered and reported as "YH-2" does not appear to have been previously sampled. Here we change its designation to "YH-J" (Fig. 1).

In all previous work we have depicted the strata between the *Presbynileus ibexensis* Zone and the base of the "*Pseudocybele nasuta*" assemblages as a *Pseudocybele paranasuta* Zone. This part of the section is stratigraphically complex. Subsequent sampling has revealed the presence of four completely distinct faunal intervals in these rocks, of which the *P. paranasuta* Zone is one. The remaining three will be documented in a forthcoming work, but they are depicted as unnamed zones in Figure 1.

Finally, in 2009 we recognized a *Psalikilus pikum* Zone between the *Heckethornia bowiei* Zone and the *Bathyrina plicolabeona* Zone (renamed from the *Strigigenalis plicolabeona* Zone by Adrain *et al.* [2014]). Ongoing systematic work on *Psalikilus* Ross, 1951, has demonstrated that *P. pikum* occurs only in the highest horizon assigned to this zone, and persists into the lowest horizon of the overlying *B. plicolabeona* Zone. The species of *Psalikilus* that was thought to be the zonal name bearer is actually an undescribed new species. Hence the zone requires a new name and name bearer. Work on *Psalikilus* involves a major monograph (there are at least 12 formally nameable new species, in addition to revision of the currently named taxa) and is not ready for publication. However, the pliomerid *Panisaspis sevierensis* McAdams and Adrain, 2011b, is common and occurs at all horizons assigned to the zone. Hence, we designate it the zonal name bearer, and replace the term *Psalikilus pikum* Zone with the *Panisaspis sevierensis* Zone. The concept of the zone is otherwise unaltered.

Phylogenetic Analysis

Methods. Parsimony analysis was carried out using the implicit enumeration (exact search) algorithm of TNT (Goloboff *et al.*, 2008), with branch collapsing not permitted. All characters were treated as unordered. Group support was evaluated with Bremer decay (Bremer, 1994), using PAUP* 4.0 (Swofford, 2003) and TreeRot Version 3 (Sorenson and Franzosa, 2007), and reported as absolute support. Nonparametric bootstrapping using implicit enumeration with 10,000 pseudoreplicates in TNT was also used to evaluate group support. Bootstrap frequencies are reported both as standard absolute frequencies (values greater than 50% only) and as GC (Groups supported/Contradicted) values (Goloboff *et al.*, 2003). Character optimization was explored with WinClada (Nixon, 2002).

Taxa. The outgroup taxon is *Panisaspis loganensis* McAdams and Adrain, 2011b, which is the

phylogenetically most basal (McAdams and Adrain, 2011b, fig. 4) and stratigraphically earliest species of the ingroup's likely sister clade. Monophyly of the ingroup and this putative sister group relationship are not directly tested herein. However, they have been explored in the context of a developing broader analysis of Pliomeridae (e.g., McAdams and Adrain, 2010b) in which *Ibexaspis* and *Paniaspis* have consistently been retrieved as monophyletic sister taxa. Codings for states not preserved in *P. loganensis* (e.g., genal spines and the hypostome) were made from the next most basal species, *P. quattuor* (Hintze, 1953). The ingroup comprises all named species of *Ibexaspis*, *Deltapliomera*, *Tuleaspis*, and *Millardaspis*. The species reported herein in open nomenclature are each known from either one or two specimens and, pending additional information, cannot meaningfully be coded for analysis.

Characters. Thirty-nine characters (21 cranial, four hypostomal, six librigenal, one thoracic, and seven pygidial) were coded for all members of the ingroup and the outgroup. The taxon-character matrix is shown in Table 1.

TABLE 1. Taxon-character matrix for phylogenetic analysis of *Ibexaspis* and related genera.

Taxa	Characters																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<i>Paniaspis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>T. jenek</i>	0	1	1	0	0	0	0	0	0	1	1	1	0	0	0	0	0	1	0	0
<i>D.inglei</i>	0	1	3	1	0	0	0	1	0	2	1	1	0	0	1	0	0	1	0	0
<i>D.heimbergi</i>	0	1	3	1	0	0	0	1	0	2	1	1	0	0	1	0	0	1	0	0
<i>D.eppersoni</i>	0	1	3	2	0	0	0	1	1	2	1	1	1	0	1	0	0	1	0	0
<i>D.humphriesi</i>	0	1	3	2	0	0	0	1	1	2	1	1	1	0	1	0	0	1	0	0
<i>M.milstead</i>	0	0	0	0	0	0	0	1	0	2	1	1	0	0	0	0	0	1	1	1
<i>M.knox</i>	0	0	3	1	0	0	0	1	0	2	1	1	1	0	0	0	0	1	1	0
<i>I.brevis</i>	1	0	1	0	1	1	1	2	0	1	1	2	0	1	2	1	1	1	1	1
<i>I.coadyi</i>	1	0	1	0	1	1	0	2	0	1	1	2	0	1	2	1	1	1	1	1
<i>I.leuppi</i>	1	0	2	0	1	1	1	2	0	1	1	2	0	1	2	0	1	1	1	1
<i>I.rupauli</i>	1	0	1	0	1	1	1	2	0	1	1	2	0	1	2	1	1	1	1	1

Taxa	Characters																		
	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39
<i>Paniaspis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>T. jenek</i>	0	0	0	0	1	0	0	?	0	0	0	?	0	0	0	0	0	0	0
<i>D.inglei</i>	0	0	0	0	1	?	?	?	?	?	?	?	0	0	1	0	0	1	0
<i>D.heimbergi</i>	0	0	0	0	1	1	1	0	1	1	1	0	1	0	1	0	0	1	1
<i>D.eppersoni</i>	0	0	0	0	1	1	1	0	1	1	1	0	1	0	1	0	0	1	1
<i>D.humphriesi</i>	0	0	0	0	1	1	1	0	1	1	1	0	1	0	1	0	0	1	1
<i>M.milstead</i>	0	0	0	0	1	2	2	0	1	1	1	?	0	0	1	1	2	1	0
<i>M.knox</i>	0	?	?	?	?	2	2	?	?	1	1	0	0	0	1	1	2	1	0
<i>I.brevis</i>	1	1	1	1	1	2	2	1	0	1	0	1	0	1	1	0	0	1	0
<i>I.coadyi</i>	1	1	1	1	1	2	2	1	0	1	0	1	0	1	1	0	0	1	0
<i>I.leuppi</i>	1	1	1	1	1	2	2	1	0	1	0	1	0	1	1	0	1	1	0
<i>I.rupauli</i>	1	?	?	?	?	2	2	1	0	1	0	0	0	1	1	0	1	1	0

Zones (Adrain <i>et al.</i> , 2009; McAdams & Adrain, 2010; Adrain & McAdams, 2012)	Eastern Nevada	Western Utah			Southeastern Idaho	
	Section YH Yellow Hill	Section G Southern Confusion Range	Section H Southern Confusion Range	Section J Southern Confusion Range	Section HC5 Hillyard Canyon East Side	Section HC6 Hillyard Canyon West Crest
Assemblage 6						
5						
4 "Pseudocybele nasuta"						
3	● - YH-J <i>I. rupauli</i> n. sp.			● - 28.1 ● - 28T <i>I. rupauli</i> n. sp.		
2						
Assemblage 1						
Unnamed Zone Three						
<i>Pseudocybele paranasuta</i>						
Unnamed Zone Two						
Unnamed Zone One						
<i>Presbynileus ibexensis</i>			● - 251.4 <i>I. leuppi</i> n. sp.			
<i>Carolinites nevadensis</i>			<i>I. coadyi</i> n. sp. ● - 222.1 ● - 208.2	<i>D. humphriesi</i> n. sp.		
<i>Bathyrina plicolabeona</i>		<i>I. brevis</i> (Young, 1973)	● - 191.7 ● - 187.4 ● - 186.2 ● - 185.6	<i>D. eppersoni</i> n. sp.		
<i>Panisaspis sevierensis</i>		<i>Deltapliomera</i> n. sp. A ● - 178.2 ● - 173.2 ● - 172.5T ● - 172.5 ● - 166.2	● - 163.3 <i>M. knoxi</i> n. sp.	<i>D. heimbergi</i> n. sp.		
<i>Heckethornia bowiei</i>			● - 127.1 <i>D.inglei</i> n. sp.			
<i>Heckethornia hyndeeae</i>	● - 128.9 <i>M. milsteadii</i> n. sp.					<i>M. milsteadii</i> n. sp. 226.5-●
High <i>Protopliomerella contracta</i>						
Low		<i>Tuleaspis?</i> n. sp. B ● - 210.2	<i>T. jenekii</i> n. sp.			
High <i>Psalikilus hestoni</i>						
Low						
<i>Psalikilus typicum</i>						
High <i>Psalikilopsis cuspidicauda</i>						
Low		● - 155.6 <i>Tuleaspis</i> n. sp. A				● - 203.7-204.2T <i>Tuleaspis</i> n. sp. A

FIGURE 1. Schematic diagram of stratigraphic distribution of species of *Ibexaspis*, *Deltapliomera*, *Tuleaspis*, and *Millardaspis* in Floian (Tulean–Blackhillsian) sections of the Yellow Hill Limestone in eastern Nevada (Section YH), Fillmore Formation and Wah Wah Formation in western Utah (Sections G, H, J), and the Garden City Formation in southeastern Idaho (Sections HC5, HC6). Measurements are in metres. Metreages are not to scale. The zonation is that established by Adrain *et al.* (2009), with additions and modifications by McAdams and Adrain (2010, 2011a, 2011b), Adrain and McAdams (2012), and herein (see text).

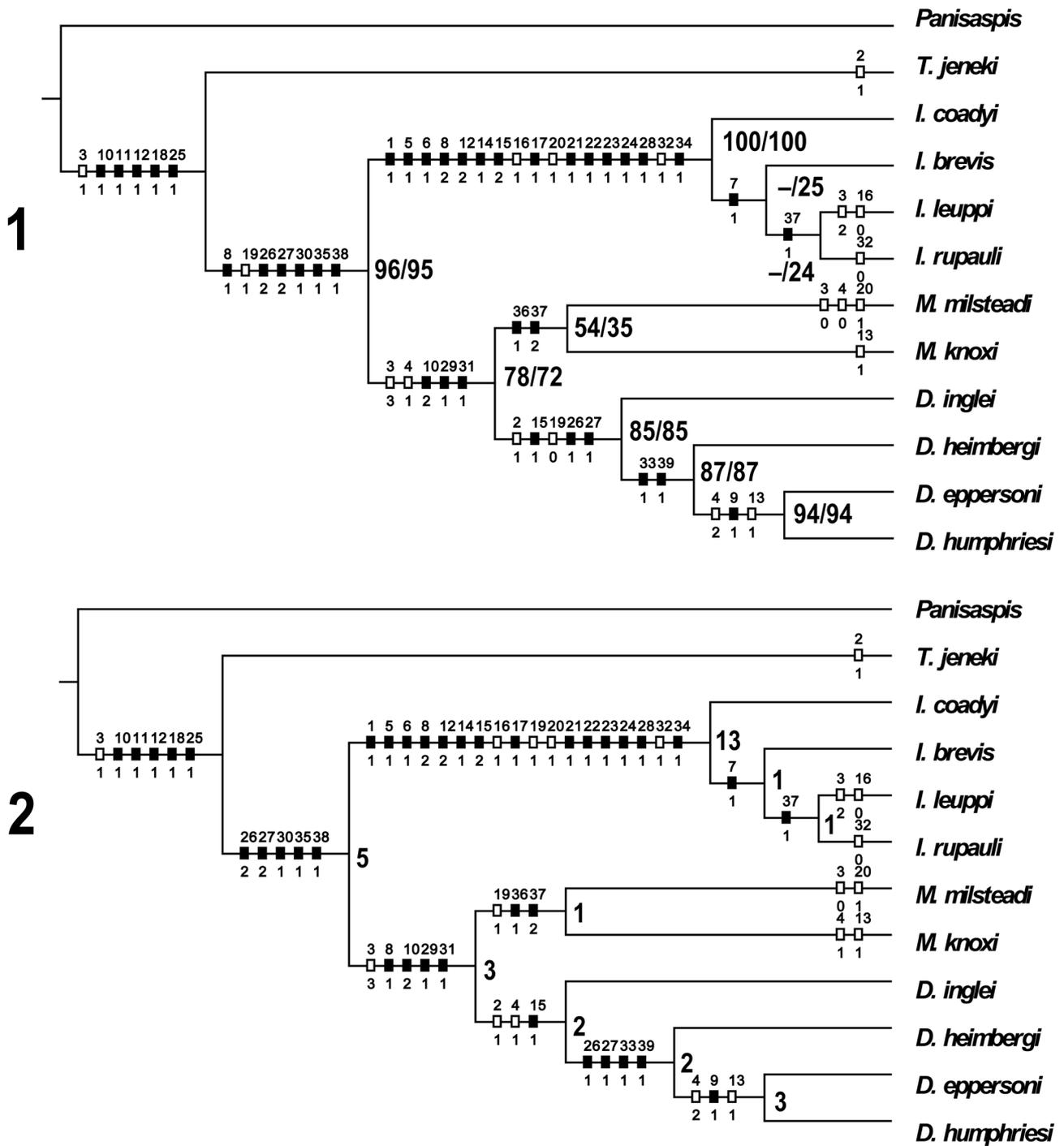


FIGURE 2. Single most parsimonious cladogram derived by implicit enumeration from the taxon-character matrix of Table 1. Length = 57, consistency index = 0.85, and retention index = 0.91. Homoplastic states are shown as open symbols. The number above each symbol is the character number and the number below is the state number. 1. Character-state transformations optimized under the accelerated transformation (ACCTRAN) criterion. Bootstrap scores are shown at each node. The first number is the absolute bootstrap frequency (only values greater than 50% are listed) and the second is the GC metric (Goloboff *et al.*, 2003). 2. Character-state transformations optimized under the delayed transformation (DELTRAN) criterion. Bremer support values are shown at each node.

Cranidium

1. Shape of course of anterior border furrow in anterior view: 0, transversely straight; 1, M-shaped.
2. Maximum glabellar width versus width across posterior projections (excluding genal spines): 0, 31.5–35.2%; 1, 37.0–42.9%.
Species of *Deltapliomera* have a wider glabella relative to maximum cranial width (across posterior projections), which is quantified using natural gaps in the distribution.
3. Sagittal glabellar height in anterior view versus width across posterior projections (excluding genal spines): 0, 18.6–21.4%; 1, 22.3–25.8%; 2, 26.8–28.2%; 3, 29.9–35.0%.
The glabella is more inflated in *Deltapliomera* than in all other members of the *Ibexaspis* group, while members of *Ibexaspis* have a glabella that is more inflated than more basal members of the group, but not to the extent of members of *Deltapliomera*. This is quantified using natural gaps in the distribution.
4. Anterior inflation of glabella: 0, not inflated; 1, inflated, encroaching on rear of anterior border in sagittal profile; 2, strongly inflated, overhanging median anterior border in dorsal view.
5. Faint median notch or furrow in LF: 0, absent; 1, present.
6. S4 clearly, if slightly, expressed: 0, absent; 1, present.
7. Morphology of glabellar furrows: 0, conventional linear furrows; 1, reduced to lateral notches.
8. Morphology of L1: 0, large and inflated; 1, moderate; 2, small, describing oblique ellipsoid in dorsal view.
9. Punctate paired tubercles on glabella: 0, absent; 1, present.
10. Presence of corona-like cluster of tubercles on lateral occipital lobes, lateral glabellar lobes, adaxial end of posterior border, and adaxial edge of fixigena: 0, absent; 1, present, retained in large holaspids; 2, present earlier in ontogeny, greatly reduced or effaced in large holaspids.
11. Transversely aligned row of small tubercles near or at posterior margin of LO: 0, absent; 1, present.
12. Anteroposterior position of transverse tubercle row near rear of LO: 0, absent; 1, definitely anterior of posterior margin; 2, aligned immediately along posterior margin.
13. Transverse row of tubercles near rear of LO effaced medially in large holaspids: 0, absent; 1, present.
14. Expression of median occipital tubercle: 0, weakly expressed, in many specimens effaced; 1, strong.
15. Anterior course of axial furrows: 0, anteriorly convergent from near front of L1; 1, strongly anteriorly divergent; 2, subparallel to very slightly anteriorly divergent at L3.
16. Width of axial furrows: 0, relatively broad; 1, very narrow.
17. Expression of eye ridge: 0, not expressed; 1, clearly expressed.
18. Palpebro-ocular ridge: 0, strongly expressed to anterior border; 1, with distinct break on frontal area in front of palpebral lobe.
19. Width and sculpture of palpebral lobe: 0, narrow and dorsally effaced; 1, broad, with dense dorsal tuberculate sculpture.
20. Width of fixigena opposite anterior portion of palpebral lobe: 0, very narrow; 1, moderately wide.
21. Length of genal spine: 0, short, in some species lost in large specimens; 1, long.

Hypostome

22. Shape of middle body: 0, broad relative to sagittal length; 1, narrow relative to sagittal length.
23. Length of posterior lobe of middle body: 0, long; 1, very short.
24. Ventral sculpture: 0, fine, dense tubercles, effaced in some species; 1, robust tubercles.
25. Presence of paired border spines: 0, present; 1, absent.

Librigena

26. Size and shape of librigenal field: 0, large, subtriangular; 1, reduced, more trapezoidal; 2, strongly reduced, anterior section of facial suture very short.
27. Length of posterior branch of facial suture along lateral border: 0, moderately long; 1, very short; 2, elongate.
28. Caecal pitting on librigenal field: 0, strong and extensive, clearly visible externally; 1, weak or absent, not expressed or obscured by tubercles externally.
29. Librigenal field with swollen rim adjacent to lateral border furrow: 0, absent; 1, present.
30. Width of lateral border furrow along course: 0, of similar width anteriorly and posteriorly; 1, clearly wider anteriorly than posteriorly.
31. Average width of lateral border furrow: 0, narrow; 1, very broad.

Thorax

32. Presence of preannulus on thoracic segments: 0, absent; 1, present.

Pygidium

33. Effacement of tuberculate sculpture on first axial ring: 0, tuberculate structure strong medially; 1, tuberculate structure effaced at least medially.

34. Presence of distinct median nodes on axial rings of large specimens; 0, absent; 1, present.

35. Space between proximal regions of first and second pleural ribs; 0, very little space, ribs nearly abutting; 1, long gap between ribs.

36. Cross-sectional shape of pleural ribs: 0, rounded or elliptical; 1, laterally compressed, blade-like.

37. Direction of pleural ribs: 0, directed slightly posteroventrally from base; 1, directed mainly posteriorly from base; 2, directed strongly ventrally from base.

38. Posterior divergence of pygidial pleural ribs: 0, barely posterior splayed, subparallel; 1, strongly splayed, posteriorly divergent.

39. Shape of distal tips of pleural spines: 0, simple, bluntly pointed; 1, expanded, club-shaped.

Results

Analysis yielded a single most parsimonious tree, depicted with character optimizations and support values in Figure 2. The clade comprises four morphologically distinctive and well supported subclades which are recognized as separate genera. Stratigraphic congruence is excellent. At species level, only *I. coadyi* and *I. brevis* have first appearance data slightly out of predicted stratigraphic order; other species of both *Ibexaspis* and *Deltapliomera* are sampled in the order of FAD predicted by the cladogram. *Ibexaspis* is particularly well supported, with 100% bootstrap metrics and a Bremer support score of 13. *Deltapliomera* has 85% bootstrap support and a Bremer score of two, while *Millardaspis* has 54% absolute bootstrap support and a Bremer score of one. A clade of *Deltapliomera* + *Millardaspis* has 78% absolute bootstrap support and a Bremer score of three, and a sister group relationship between this clade and *Ibexaspis* has 96% absolute bootstrap support and a Bremer score of five.

Systematics

Repository. Type and figured specimens are housed in the Paleontology Repository, Department of Earth and Environmental Sciences, University of Iowa, Iowa City, Iowa, USA, with specimen number prefix SUI.

Family Pliomeridae Raymond, 1913

Ibexaspis Přibyl and Vaněk in Přibyl *et al.*, 1985

Type species. *Protopliomerops quattuor brevis* Young, 1973, from the Fillmore Formation (Floian; Blackhillsian; *Bathyrina plicolabeona* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

Other species. *Ibexaspis coadyi* **n. sp.**, Fillmore Formation (Blackhillsian; *Carolinites nevadensis* Zone), western Utah; *I. leuppi* **n. sp.**, Fillmore Formation (Blackhillsian; *Presbynileus ibexensis* Zone), western Utah; *I. rupauli* **n. sp.**, Wah Wah Formation (Blackhillsian; "*Pseudocybele nasuta* Zone"), western Utah, and Yellow Hill Limestone, eastern Nevada.

Diagnosis. Anterior border furrow M-shaped in anterior view; sagittal glabellar height in anterior view 22.3–25.8% width across posterior projections (excluding genal spines); median furrow in LF present; S4 expressed; glabellar furrows usually reduced to lateral notches; L1 small, describing oblique ellipsoid in dorsal view; presence of corona-like cluster of tubercles on lateral occipital lobes, lateral glabellar lobes, adaxial end of posterior border, and adaxial edge of fixigena in large holaspids; transverse tubercle row near rear of LO aligned immediately along posterior margin; strongly expressed median occipital tubercle; anterior course of axial furrows subparallel to very

slightly anteriorly divergent at L3; axial furrows usually very narrow; eye ridge clearly expressed; fixigena opposite anterior portion of palpebral lobe moderately wide; long genal spine; middle body of hypostome narrow relative to sagittal length; posterior lobe of middle body very short; ventral sculpture of robust tubercles on hypostome; caecal pitting on librigenal field weak or absent; preannulus usually present on thoracic segments; distinct median nodes present on axial rings of large pygidial specimens.

Discussion. When they proposed the genus, Přibyl and Vaněk (in Přibyl *et al.*, 1985, p. 170) spelled it "*Ybexaspis*". This is certainly a misspelling, as everywhere else in their paper the name was either spelled *Ibexaspis* or abbreviated "*I.*" and the derivation of the name was given as the Ibex area in Utah. All subsequent workers (Peng, 1990; Jell and Adrain, 2003; Adrain *et al.*, 2009; McAdams and Adrain, 2011a, 2011b) have used the *Ibexaspis* spelling.

Přibyl and Vaněk in Přibyl *et al.* (1985, p. 170–171) diagnosed *Ibexaspis* with the following characteristics: "Glabella spherical, widening anteriorly, with 3 pairs of very short glabellar furrows (1S–3S) and minute glabellar lobes. 3S and 2S run almost transversely; 1S is inclined diagonally backwards to the occipital ring. 1L incompletely separated. Eyes large, situated opposite 3S and 2S. Fixigenae vaulted with short genal spines. Number of thoracic segments unknown. Pygidium with 3–4 rings and terminal piece on the axis, and 4 pairs of pleural spines, which are arranged radially, gradually decrease towards the sag. axis of the pygidium".

This diagnosis now consists mainly of symplesiomorphic characters, either shared among the *Ibexaspis* group or more widely with other pliomerid genera. The glabella is not "spherical" and widens only slightly anteriorly, and the strong glabellar inflation is shared by other members of the *Ibexaspis* group. The glabellar furrows are similar in course to those of species of *Deltapliomera*, *Tuleaspis*, and *Millardaspis*, as well as *Paniaspis*, but they are indeed "shorter" (narrower). It is unclear which pygidial specimens with three axial rings that Přibyl and Vaněk examined; all members of *Ibexaspis* possess four rings, which is shared with other members of the *Ibexaspis* group, and also *Paniaspis*. The radial arrangement of the spines is common in the *Ibexaspis* group, and similar to that seen in species of *Paniaspis*, except that the latter taxon has a characteristically longer third pygidial spine. Large palpebral lobes are common in many pliomerid taxa. Those of *Ibexaspis* are located further anteriorly than in other members of the *Ibexaspis* group, although not so far forward as in *Protopliomerella* Harrington, 1957, and *Pseudocybele* Ross, 1951.

Přibyl and Vaněk (in Přibyl *et al.*, 1985) assigned *Protopliomerops quattuor* Hintze, 1953, to *Ibexaspis*, but McAdams and Adrain (2011b) assigned this species to their new *Paniaspis*. Přibyl and Vaněk (in Přibyl *et al.*, 1985, p. 119) did not consider any of the pygidia assigned to *Paniaspis quattuor* to belong to that species, but did not give any indication of what they considered their identity to be. McAdams and Adrain (2011b, p. 21) demonstrated that both of Hintze's pygidia, as well as the pygidium that Demeter (1973, pl. 3, fig. 6) assigned to *Protopliomerops quattuor*, do in fact belong to the species, although a number of other sclerites assigned by Hintze (1953) and Demeter (1973) to *P. quattuor* do not. A full synonymy of *Paniaspis quattuor* and discussion of both Hintze's and Demeter's sclerite associations was given by McAdams and Adrain (2011b).

Přibyl and Vaněk (in Přibyl *et al.*, 1985) briefly compared *Ibexaspis* to *Pilekia* Barton, 1915; *Parapilekia* Kobayashi, 1934; and *Protopliomerops* Kobayashi, 1934. The first two are cheirurid taxa with no close relationship to the pliomerid *Ibexaspis*. *Protopliomerops* is a "wastebasket" pliomerid taxon with a very poorly understood type species (see discussion in McAdams and Adrain [2011b, p. 7]). It currently contains a mix of cheirurid and pliomerid species, none of which are closely related to *Ibexaspis*. Přibyl and Vaněk (in Přibyl *et al.*, 1985, p. 116) also discussed *Ibexaspis* as part of an "evolutionary lineage" from *Eocheirurus* Rozova, 1960, to *Parapilekia*, to *Ibexaspis*. They also suggested (1985, p. 126) that *Ibexaspis* was the "ancestor" or sister taxon of *Pseudosphaerexochus* Schmidt, 1881. Again, the other genera, as cheirurids, are not germane to the phylogenetic relationships of *Ibexaspis*. Ongoing work on a broader phylogeny of Pliomeridae (e.g., McAdams and Adrain, 2010b) indicates that the broad *Ibexaspis* group described herein is monophyletic and sister to *Paniaspis*.

***Ibexaspis brevis* (Young, 1973)**

Plates 1–6

- 1953 *Protopliomerops quattuor* Hintze, p. 209, pl. 21, fig. 11 [only; pl. 21, figs 9, 12–14 = *Paniaspis quattuor* (Hintze, 1953); pl. 21, fig. 10 = *Deltapliomera eppersoni* n. sp.].
- 1973 *Protopliomerops quattuor brevis* Young, p. 106, pl. 3, figs 1, 5–7, 9, 10.

- 1973 *Kanoshia* (?) *depressus* Young (*partim*), p. 102, pl. 3, figs 25–27 [only; pl. 3, figs 21–24 = *Cybelopsis depressa* (Young)].
- 1985 *Ibexaspis brevis* (Young, 1973); Přibyl *et al.*, p. 119, text-figs 22, 23.
- 1990 *Ibexaspis brevis* (Young); Peng, p. 112.
- 1997 *Protopliomerops*? *quattuor brevis* Young; Ross *et al.*, pp. 20, 44.
- 2003 *Ibexaspis brevis* (Young, 1973); Jell and Adrain, p. 387.
- 2009 *Ibexaspis brevis* (Young, 1973); Adrain *et al.*, p. 570, fig. 17L, M.
- 2011b *Ibexaspis brevis* (Young, 1973); McAdams and Adrain, pp. 4, 17, 21.

Material. Assigned specimens SUI 115330, 115331, 129762–129804, from Section H 186.2–191.7 m, Fillmore Formation (Blackhillsian; *Bathyrina plicolabeona* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

Diagnosis. Glabellar sculpture very fine and dense; glabellar lobes weakly expressed, glabellar furrows S2 and S3 narrow; librigenal field narrow; pygidial axial ring median nodes pronounced.

Description. Cranidial measurements were made on sufficiently complete large specimens of Plates 1–4. Measurements were doubled from the sagittal midline if necessary, e.g., for a specimen with a damaged fixigena. Cranidium roughly semicircular in outline, with sagittal length 109.5% (102.2–117.3%) width across γ , 75.5% (71.6–79.6%) width across δ , 77.9% (73.3–82.7%) width across ϵ , and 53.2% (50.2–56.0%) maximum width across genal angles, very highly vaulted (sag., tr.) and medially domed, with dense tuberculate sculpture; anterior border short, 7.4% (5.4–8.7%) cranidial sagittal length, relatively broad, moderately anteriorly bowed, well inflated, densely tuberculate, broadly M-shaped in anterior view, with lateral thirds dorsally arched and median third gently ventrally projecting, doublure expressed as anterior face, rim-like ventrally; anterior border furrow very short (dorsal view), deep, distinct, median section broadly anteriorly bowed, lateral sections transverse to gently anterolaterally directed, slightly overhung by glabella medially; glabella strongly vaulted (sag., tr.), oblong with maximum width across L3 81.0% (77.7–84.4%) glabellar length (sag.), slightly tapered posteriorly, tapered and rounded anteriorly, with very dense, finely tuberculate sculpture; glabellar lobes independently inflated, well defined and separated by lateral furrows; L1 short and very narrow, subtriangular, nearly isolated by S1, with slightly coarser tubercles than other lobes, L2 and L3 roughly equal in size, each longer and wider than L1, laterally rounded, with coarser tubercles on lateral edges, LF very large, long and wide, anteriorly rounded with small median anterior furrow, also with small accessory S4 furrow located far exsagittally almost at anterolateral corner on smaller specimens (seen best on Pl. 2, figs 2, 11, 14); lateral glabellar furrows all deep, fairly short and with little median extension, S1 strongly posteromedially directed across inner margin of L1, deepest at midlength, then increasingly shallow posteriorly, separated from SO by only a few tubercles, S2 and S3 roughly transverse, deep at junctions with axial furrows, then abruptly shallowed and shortened to point on glabella; SO moderately short and deep, exsagittal portions behind L1 deeper, slightly longer, and slightly posteriorly directed into apodemal pits, furrow mainly smooth, but median section with few granules in some specimens (Pl. 3, figs 1, 9); LO moderately long (sag., exsag.), length 15.0% (13.3–17.4%) cranidial sagittal length, posterior width 29.9% (27.1–32.1%) maximum cranidial width, exsagittal sections shorter and gently anteriorly directed, ring dorsally inflated with inflation higher posteriorly, and with dense sculpture of fine tubercles and small median node; doublure semilunate, laterally pinched off, effaced, long, reaches posterior of SO medially; axial furrows moderately wide and deep, roughly parallel to slightly anteriorly divergent along glabella, confluent with all but palpebro-ocular furrows and wider at these junctions; palpebro-ocular ridges mainly expressed as palpebral lobes, with poorly delineated ridge extending sagittally to junction of glabella and anterior border (seen well on Pl. 2, fig. 3), lobe fairly narrow, semi-elliptical to half-teardrop shaped, narrow anteriorly and expanded posteriorly to maximum width across from L3, strongly anteriorly downturned (sagittal profile), exsagittal edge slightly raised above horizontal (anterior view), densely tuberculate; palpebro-ocular furrows sigmoidal, but poorly expressed anteriorly on most specimens, narrow, deep, incised along lobe part of palpebro-ocular ridge, then short and shallow along ridge part, short and shallower posterior of lobe along very narrow post-ocular ridge; interocular fixigenae about half total fixigenal width and length, triangular, roughly transverse dorsally, with anterior portions strongly sloped down to anterior border; posterior fixigenae about twice as wide as long, with length slightly ventrolaterally tapered, strongly ventrolaterally sloped, both areas of fixigena with dense tuberculate sculpture somewhat coarser than that of glabella; posterior border furrow short, deep, transverse to gently anterolaterally curved adaxially, and with stronger anterolateral curve at genal angle; posterior border short adaxially, gradually

expanded ventrolaterally to maximum at genal angle and then sharply tapered at cut of posterior branch of facial suture, well inflated, with very dense tuberculate sculpture similar to that of glabella, and with small, short genal spine tapered to blunt point (Pl. 2, fig. 5); doublure turned outward abaxially to fulcrum as articulating furrow, expressed ventrally and lengthened from fulcrum to maximum at genal angle, then cut by posterior facial suture, smooth.

Rostral plate unknown.

Hypostome fairly narrow and elongate, with width across shoulders 77.5% sagittal length (and approximately equal to width across anterior wings), strongly ventrally vaulted (sag., tr.); anterior border extremely short, overhung by anterior margin of middle body medially, expanded laterally; anterior wings small, strongly upturned, subtriangular, a little longer than wide, with small, deep wing process pit; border and wings granulose; anterior border furrow likewise very short and overhung medially, deep, shallowed exsagittally toward base of wings; middle body composed of large, ovoid, posteriorly tapered anterior lobe with dense sculpture of small tubercles and short, U- or V-shaped posterior lobe with similar sculpture and effaced posteromedian margin; middle body furrow short and narrow, shallow, not well impressed except anterolaterally toward junction with lateral border furrow, mainly marked by effacement of sculpture (Pl. 2, fig. 22), very strongly posteriorly bowed in course; lateral border furrows narrow, shallow anteriorly, deep posteriorly toward posterior border furrow; lateral border very narrow anteriorly, expanded to shoulders, then narrowed again, densely covered in very small tubercles, moderately ventrally downturned; posterior border furrow short, moderately shallow medially, deep exsagittally; posterior border a little longer than width of lateral border at shoulders, with similar sculpture and slightly more downturned; doublure poorly preserved, probably reaches border furrows (see posteromedian section of Pl. 2, fig. 23), shows moderately long and shallow lateral notch and small posterior wing.

Librigena wedge-shaped, narrow and elongate, with width under midpoint of eye 39.1% (38.0–40.1%) length along lateral border; ocular surface not preserved, raised above field by smooth platform enlarged into roughly semicircular patch on field at anterior end; anterior branch of facial suture long, with section along field shorter than section along anterior projection of border, sections meet at angle of about 115° at lateral border furrow, suture very steeply sloped along field, nearly flat along projection; posterior branch of facial suture long, fairly steeply sloped along field, flat along posterior projection, cut exposes triangle of doublure at tip of projection; librigenal field subtrapezoidal, with width under midpoint of eye 30.7% (29.6–31.7%) length along lateral border furrow, longer posteriorly, very gently laterally convex, with sculpture of small pits concentrated posteriorly, overlain by dense mix of granules and tiny and small tubercles; lateral border furrow moderately narrow and deep, deeper and narrower posteriorly, shallowed anterior of midpoint of eye; lateral border wide, slightly tapered posteriorly, strongly inflated, a little lower posteriorly, with very dense sculpture of small tubercles, smaller and more dense exsagittally; doublure broad along field, reaches lateral margin of lateral border furrow, tapered to point above posterior projection, rotated out anteroventrally along long anterior projection, smooth except for fine ridge running along outer margin.

Total number of thoracic segments unknown; thoracic segments short and broad, with width of axis 30.7% (30.3–31.1%) width across tips of pleural spines; segment strongly vaulted, with axis strongly dorsally arched and pleurae strongly downturned abaxially from fulcrum; articulating half ring semilunate to almost semicircular, long medially and laterally tapered, situated just higher than axial ring in sagittal profile, smooth except for transverse line of very fine tubercles across posterior margin; articulating furrow long, moderately deep, with anterolateral corners deepest, shallowly U-shaped, with broad, transverse midsection, line of approximately seven small tubercles situated medially and a few more smaller tubercles anteriorly (Pl. 5, fig. 20); axial ring short, about as wide as inner pleurae, mildly inflated, shallowly U-shaped like furrow, with slightly anteriorly bowed posterior margin, and with dense sculpture of small tubercles and a few tiny tubercles, exsagittal tubercles along lateral rims of ring taller and more spinose, with distinct pair of tubercles at anterolateral and posterolateral corners of ring; doublure long and broad, pinched out laterally, with anteriorly bowed anterior margin, smooth but for several fine transverse ridges at posterior margin; axial furrows moderately narrow and shallow, overhung by spinose tubercles on axial ring and posterior pleural band (anterior, posterior views), slightly anteriorly convergent in course; anterior pleural band gently inflated, very short, appears narrower than posterior band due to base of pleural spine, but is same width, effaced, and with very short articulating furrow just behind anterior margin; pleural furrow short and moderately deep, shallower at junction with axial furrows and deeper toward exsagittal end; posterior pleural band about twice the length of anterior band (same length as axial ring), well inflated, with dense sculpture of small

tubercles with tiny tubercles intercalated transversely along mid-length, and with very short articulating furrow just anterior to posterior margin; pleural spine produced from posterior band and of same length, very wide, strongly downturned, with tips very slightly turned out laterally, robustly inflated, especially at base, tapered and laterally compressed toward bluntly pointed tip, with sculpture similar to posterior band on outer face, smaller, more widely spaced tubercles on posterior face, and very tiny, densely spaced tubercles on anterior face and toward tip; doublure just a rim curved in medially from tips of pleural bands, very slightly wider posteriorly.

Pygidium of four segments and terminal piece, roughly semicircular in outline, with sagittal length from articulating furrow 47.1% (43.6–49.1%) width across anterior pleural band of first segment, widest across tips of first pair of spines, very strongly vaulted (sag., tr.) in axis and due to pleural spines, with dense sculpture of small tubercles all over dorsal surface; articulating half ring crescentic, moderately short medially, laterally tapered, slightly narrower than first axial ring, with transverse line of very fine tubercles on posterior margin; articulating furrow long, slightly laterally tapered and deep, with scattered fine tubercles on median section of some specimens (Pl. 5, fig 4, Pl. 6, figs 10, 16); axis long, approximately equal in length to main body of pygidium, broad and highly vaulted anteriorly, strongly tapered and decreasingly convex posteriorly, with width across first ring 33.8% (31.6–36.2%) width across anterior band of first segment, and width across fourth ring 57.3% (50.0–64.8%) width across first ring; axial rings well defined and independently inflated, median part of anterior rings anteriorly bowed, posterior rings with straight margins, posterior rings increasingly shorter and narrower than anterior rings, all with sculpture of small tubercles with intercalated tiny tubercles, and with denser cluster of sculpture on sagittal axis at mid-length or toward posterior of ring (distinct larger tubercle/median node present in this cluster on smaller specimens, e.g., Pl. 6, fig. 8); inter-ring furrows moderately long to long, anterior furrows longer, moderately deep (deeper toward posterior of each furrow and on smaller specimens), with tiny tubercles in transverse line at midlength of furrows in many specimens (e.g., Pl. 5, fig. 4, Pl. 6, figs 3, 8, 16); terminal piece triangular, short, narrow, and strongly posteriorly tapered, about half as inflated as fourth axial ring anteriorly, and deflated posteriorly to merge into upper surface of pygidial border (on most specimens, but see Pl. 5, fig. 12), absent or poorly expressed on a few specimens (Pl. 6, figs 1, 18); axial furrows moderately narrow and deep, less well impressed over fourth pleurae, strongly anteriorly divergent, confluent with fourth interpleural furrows and median furrow behind terminal piece posteriorly; anterior pleural band present only on first segment, similar to thoracic anterior bands, very short, slightly longer exsagittally, moderately inflated, with articulating furrow just posterior to anterior margin; pleural furrow deep, short, slightly longer laterally, transverse sagittally, gently posterolaterally directed exsagittally; posterior pleural bands long (sag., exsag.), expanded exsagittally into bases of spines, strongly inflated, posterolaterally directed, increasingly so posteriorly so that fourth pleurae are parallel to each other, with dense sculpture of small tubercles; spines similar to thoracic spines, long and strongly downturned, well inflated, tapered and laterally compressed ventrally to blunt point, with sculpture becoming finer and denser toward tips, and effaced on ventral/inner side of spines (ventral, anterior views); interpleural furrows long (posterior furrows shorter, median interpleural furrow behind terminal piece fairly wide in most specimens), moderately deep, deeper sagittally, increasingly posteromedially directed; pygidial border visible dorsally as swollen area at base of pleural spines crossed by interpleural furrows, but mainly expressed ventrally as moderately inflated swollen rim sagittal from base of spines, with granulose sculpture; doublure strongly upturned, subvertical, and visible only in anterior view (Pl. 5, figs 14, 17, Pl. 6, fig. 9), fairly long, longest medially, anterolaterally tapered, smooth.

Ontogeny. Cranidial ontogenetic changes are well represented in *I. brevis* (cf. cranidia of Pls 1, 2; Pl. 4, fig. 24). The cranidium becomes broader and slightly shorter overall, as well as more strongly vaulted (tr., especially sag.), and the tuberculate sculpture becomes more densely distributed and slightly finer in texture; the transverse branches of the anterior border furrow separating the border from the palpebro-ocular ridges lengthen and deepen considerably, while the median part of the furrow develops into the characteristic M-shaped curve (anterior view); the glabella inflates and becomes more peaked dorsomedially (anterior view), while overall it becomes shorter and considerably wider; the glabellar furrows and SO lengthen and shallow somewhat; the axial furrows broaden and shallow; the interocular fixigena lengthens and narrows slightly, while the posterior fixigenae shorten; the palpebro-ocular ridge widens and becomes more distinctly lobate; the large tubercles on the posterior rim of LO and the posterior border shrink; the tubercles at the posterior end of the postocular ridge and just anterior from the genal spine become more effaced; and the genal spine becomes much shorter and blunter.

The two known librigenae (Pl. 2, fig. 25 and Pl. 5, fig. 29) are similar in size (exsagittal length 3.52 mm and

2.95 mm respectively), but it appears that the librigenal field broadens slightly and the adaxial region lengthens, changing from a more triangular to a more trapezoidal shape overall. The hypostome of *I. brevis* is represented by two specimens of almost identical size; its ontogeny is therefore unknown.

The two thoracic segments (Pl. 5, figs 20, 25) are very similar morphologically and appear to be from the same part of the thorax, which makes ontogenetic comparison feasible. However, they are rather close in size (width across anterior pleural band 3.75 and 4.12 mm, respectively). The most noticeable change is that the spinose tubercles at the lateral and posterolateral edges of the axial ring become less prominent, and the tuberculate sculpture overall becomes finer.

Pygidia (cf. Pl. 5, figs 1, 4 with Pl. 6, fig. 24) become slightly shorter relative to width; the tuberculate sculpture becomes slightly finer overall, and the occipital nodes in particular start to blend in more with the background sculpture; the axis elongates and narrows; articulating half ring, inter-ring, and interpleural furrows lengthen and shallow; axial furrows widen and shallow; and the pleural spines lengthen (oblique), spread further apart, and become more tapered toward the tips.

Discussion. Compared to *Ibexaspis coadyi*, *I. brevis* possesses a narrower, more strongly vaulted cranium with slightly finer glabellar sculpture and coarser fixigenal sculpture; longer, less overhung anterior border; narrower glabella with much smaller lateral lobes and narrower lateral furrows defining them, except L1, which is longer and more posteromedially directed in *I. brevis*, and a less distinct median furrow on the frontal lobe; slightly wider and deeper axial furrows; smaller palpebral lobes; wider interocular fixigenae, particularly anteriorly; less distinct eye ridge; less distinct median LO tubercle; narrower postocular fixigenae; and shorter genal spines. The hypostomes are very similar, but that of *I. brevis* is slightly narrower and more elongate; more strongly posteriorly tapered; with a more inflated middle body; much more clearly defined (very effaced) middle body furrow; coarser sculpture overall, but especially on the middle body; narrower lateral border, particularly at the shoulders; and slightly shorter posterior border. The librigenae differ mainly in that those of *I. brevis* are narrower overall, with a distinctly narrower field and relatively wider lateral border; the effaced patch at the anterolateral corner of the eye is smaller; the lateral border furrow is wider and shallower, particularly anteriorly; and the lateral border is slightly more strongly inflated. Thoracic segments are very similar, but those of *I. brevis* possess more robust sculpture overall; have longer, more spinose tubercles at the posterolateral corners of the axial ring; and the tubercles in the articulating furrow are also larger and arranged in a more linear fashion. Pygidia of *I. brevis* (cf. Pl. 6, fig. 16, Pl. 10, fig. 1) are narrower overall; with a relatively wider, more strongly tapered and more strongly inflated axis; more strongly independently inflated axial rings; wider axial furrows and longer furrows between pleural ribs; slightly shorter, more strongly inflated pleural ribs with longer spines; the sculpture is finer and more densely spaced, but the axial ring nodes are more pronounced; and the doublure is longer, particularly medially.

Ibexaspis brevis is compared with *I. rupauli* and *I. leuppi* in the discussions of those species.

Specimens of *Ibexaspis brevis* from H 186.2 m and 191.7 m may display some minor variation between the horizons. The specimens from H 191.7 m have finer tuberculate sculpture, particularly on the hypostome and the glabella. The pygidia from H 191.7 m also seem to have a less prominent or less well expressed terminal piece, but the sample size overall is rather small (four pygidia from H 186.2 m; seven from H 191.7 m). Only a single librigena is known from each horizon, but it appears that the specimen from H 191.7 m has a narrower, longer field with a less steeply sloped posterior branch of the facial suture. Intraspecific variation could thus also account for some or all of the differences noted above in the discussion of librigenal ontogenetic change.

The terminal piece of one specimen (Pl. 5, fig. 12) is unusually elongate and strongly inflated compared to those of other pygidia, and in fact is extended posteriorly as a short posteromedian spine. This is the only known pygidium from H 185.6 m, the lowest horizon in the *Bathyrina plicolabeona* Zone. Its significance is hence difficult to determine, but it could represent a different species.

***Ibexaspis coadyi* n. sp.**

Plates 7–10

2009 *Ibexaspis* sp. nov. 9; Adrain *et al.*, p. 573, fig. 18L, M.

Material. Holotype, pygidium, SUI 129830 (Pl. 10, figs 1, 4, 7, 8, 11), and assigned specimens SUI 115362,

129805–129829, 129831–129836, from Section H 222.1 m, Fillmore Formation (Blackhillsian; *Carolinites nevadensis* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

Etymology. After Aaron Coady.

Diagnosis. Cranidial axial furrows very narrow; thoracic segments with large, dense patch (not transverse line) of tiny tubercles on median portion of articulating furrows; pygidial pleural ribs and spines relatively large; interpleural furrows narrow, nearly completely blocking view of underlying pleurae.

Description. This species is similar enough to *Ibexaspis leuppi* that it is described via differential discussion. Cranidia of *I. coadyi* differ from those of *I. leuppi* in being wider overall, particularly axially and across the posterior fixigenae; the glabellar sculpture is slightly coarser and the other cranidial sculpture is finer, so that the textural contrast between areas is less apparent; the anterior border is a little shorter and broader and less strongly medially depressed; the anterior border furrow is shorter, particularly exsagittally, slightly shallower, and less strongly M-shaped, with narrower transverse exsagittal sections, and is more overhung by the anterior of the glabella; the interocular fixigenae are narrower anteriorly and wider posteriorly, so that the palpebral lobes are positioned further anterolaterally; the palpebral lobes are also slightly narrower and more elongate; the glabella is broader overall and more strongly sagittally vaulted; the glabellar furrows are shorter and extend a little further medially; likewise the lateral glabellar lobes are slightly wider and less independently inflated; the axial furrows are narrower, particularly across the posterior border, and are shallower except across the posterior border; tubercles from the posterior of the glabella and anterior edge of LO overhang into SO and there are granules or tiny tubercles in SO on most specimens; LO is broader, the median node is larger and more prominent, and the tubercles on the posterior edge are longer; the posterior border is longer at the genal angle and its tubercles are coarser and more spinose posteriorly; genal spine is longer.

Hypostomes of *I. coadyi* are more strongly posteriorly tapered; the anterior border is more overhung by the middle body; the middle body is narrower and more posteriorly tapered, and its sculpture similar, but tubercles less clearly distinct; the posterior lobe of the middle body is slightly longer; the lateral border furrows are shallower anteriorly; the lateral border is narrower; the posterior border furrow is much shorter medially and deeper; and the posterior border is longer medially.

Librigenae differ in that those of *I. coadyi* are wider and shorter overall; the posterior branch of the facial suture is more steeply sloped; the ocular surface is slightly smaller; the librigenal field is wider and slightly shorter, with denser tuberculate sculpture and fewer pits and granules, and the smooth patch is smaller; the lateral border furrow is slightly narrower; the lateral border is a little wider, with a slightly longer posterior projection and slightly shorter anterior projection, and with coarser sculpture.

Thoracic segments differ mainly in that those of *I. coadyi* possess more densely packed, finer, slightly smaller sculpture in general, with less apparent granulose underlying sculpture; the articulating furrow has a large patch of tiny tubercles medially; and the axial furrows are slightly narrower and deeper.

Pygidia of *I. coadyi* are a little shorter overall; the axis is narrower, particularly anteriorly, and less vaulted; likewise the axial rings are narrower, and their sculpture is less spinose (cf. Pl. 10, fig. 1; Pl. 15, fig. 1); the terminal piece is smaller; the axial furrows are wider and shallower; the pleurae are wider; the pleural spines are a little shorter (oblique), thicker, and more strongly downturned; the pygidial border is not granulose; and small pygidia have less distinct axial nodes due to the generally coarser sculpture.

Ontogeny. Cranidia (cf. Pl. 7, fig. 1, Pl. 8, fig. 15) become broader overall, more strongly sagittally vaulted, and slightly less strongly transversely vaulted; the tuberculate sculpture becomes finer and more densely spaced (particularly noticeable on the fixigenae), with more tiny intercalating tubercles appearing on the glabella, and the spinose tubercles near the furrows become slightly shorter (cf. Pl. 7, fig. 1, Pl. 8, fig. 23); cranidial furrows all become shallower and slightly longer or wider; the anterior border elongates slightly; the palpebro-ocular ridges become differentiated into ridge and lobe, and the lobes widen; the glabella widens and becomes less strongly convex (tr.) but more strongly convex (sag.); the posterior fixigenae become longer and wider; the posterior border and LO develop a posterior fringe of elongate tubercles; and the genal spines shorten relative to overall cranidial size.

The hypostome (cf. Pl. 9, figs 15, 18) elongates and narrows overall; the lengthening occurs particularly in the anterior part of the hypostome (mainly the anterior lobe of the middle body), also resulting in elongation of the lateral notch; the tubercles become slightly larger, more closely spaced, and more effaced; the anterior wings become longer and more posteriorly directed; the lateral border furrows narrow and deepen; the posterior border

furrow shortens and deepens; the middle body furrow deepens laterally; the lateral border widens slightly, but the shoulders (widest point) shift posteriorly due to elongation of the hypostome overall; and the posterior border lengthens.

The librigenae are close in size, prohibiting observation of much ontogenetic change. However, the smallest specimen (Pl. 9, fig. 2) has a relatively longer and narrower field, with a more gently sloped posterior branch of the facial suture. The thoracic segments are too similarly sized to observe any ontogenetic change.

Pygidia (cf. Pl. 10, figs 1, 25) become broader overall; the tuberculate sculpture becomes coarser and more densely spaced in general, while the prominent pair of tubercles near the axis on the pleurae of the first two segments and the median nodes on the axial rings become effaced and blend in with the rest of the sculpture; the articulating furrow lengthens and tiny tubercles develop medially on the preannulus of the first pygidial segment; the inter-ring furrows and the furrows between pleural bands lengthen and shallow; the axial furrows widen and shallow anteriorly, become very shallow over the fourth segment, and become slightly narrower and deeper along the anterior part of the terminal piece; the axis becomes a little less vaulted (lateral view); the pleural spines thicken and inflate more, except at the tips, and they spread slightly farther apart.

Discussion. *Ibexaspis coadyi* is compared to *I. brevis* in the discussion of that species. Compared to *I. rupauli* (cf. Pl. 7, fig. 2, Pl. 18, fig. 3), the cranium of *I. coadyi* is relatively wider, and more strongly vaulted (sag., tr.), with much finer, more densely spaced sculpture; less anteriorly bowed anterior border; wider, more parallel-sided glabella with much shallower lateral furrows defining larger lobes; broader interocular fixigenae; longer, narrower palpebral lobes; broader, more strongly downturned posterior fixigenae; LO shorter and more transverse, smaller less prominent tubercles along posterior margin. The hypostome of *I. rupauli* is unknown for comparison. Librigenae differ primarily in the shape of the librigenal field, which is wider and much longer in *I. coadyi*, particularly at mid-width and along the lateral border; the librigenae of *I. coadyi* are wider overall; with a smaller anterior effaced region on the field; wider, deeper lateral border furrow (anteriorly); and slightly wider lateral border. The thoracic segments of *I. coadyi* are considerably larger than the single known thoracic segment of *I. rupauli*, but they seem to differ in possessing much finer sculpture and longer articulating furrows with a cluster of fine tubercles. Pygidia of *I. coadyi* (cf. Pl. 10, figs 3, 14, Pl. 19, fig. 2) have a broader main body, but less splayed spines, and are considerably less vaulted (sag., tr.); with shorter inter-ring furrows and furrows between pleural ribs; shorter, narrower, less vaulted axis with less strongly individually inflated axial rings; much smaller, less inflated terminal piece enclosed posteriorly by pleurae; shorter, thicker pleural spines with blunter tips; and finer, much more densely spaced sculpture.

***Ibexaspis leuppi* n. sp.**

Plates 11–15

2009 *Ibexaspis* sp. nov. 10; Adrain *et al.*, p. 574, fig. 19I, J.

Material. Holotype, cranium, SUI 129837 (Pl. 11, figs 1, 4, 5, 7), and assigned specimens SUI 115372, 115373, 129838–129874, from Section H 251.4 m, Fillmore Formation (Blackhillsian; *Presbynileus ibexensis* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

Etymology. After Clinton Leupp.

Diagnosis. Sagittal glabellar height in anterior view 26.8–28.2% width across posterior projections (excluding genal spines); L2 and L3 conical in outline; interocular fixigena wide, especially anteriorly; librigena with smooth patch on anterior of field extending almost to lateral border furrow.

Description. Cranium long and relatively narrow, with sagittal length 99.8% (98.7–101.2%) width across γ , 71.5% (69.3–74.4%) width across δ , 73.3% (70.1–75.8%) width across ϵ , and 51.9% (50.8–53.2%) maximum width across genal angles, very strongly convex (tr., also sag.) from axial inflation and steep fulcral vaulting, with densely granulate and tuberculate sculpture; anterior border very short medially, longer at exsagittal ends, arcuate and strongly anteriorly bowed, wraps around frontal lobe of glabella, border well inflated, both less inflated and ventrally bowed medially, forming shallow M-shaped curve (anterior view), with densely spaced sculpture of tiny tubercles; doublure expressed as anterior face of border; anterior border furrow short, deep, incised, longer exsagittally along transverse section in front of ocular ridges, median section ventrally bowed to form M-shaped

curve (anterior view), also strongly anteriorly bowed (dorsal view), furrow confluent with axial furrows; ocular ridges short and narrow, weakly independently inflated, contact axial furrows between just anterior to S3 and S4, bounded anteriorly by transverse sections of anterior border furrow and posteriorly by very short, shallow transverse furrow connected to palpebral furrow, ridge sculpture of dense granules and scattered small tubercles, tubercles smaller than those of *fixigena* and more widely spaced; palpebral lobes long, extend from S2 to approximately level with S4, fairly broad, with maximum width a little posterior of mid-length, semi-elliptical, laterodorsally raised, with dense sculpture of granules and tubercles slightly larger and more densely spaced than those of ocular ridge but smaller than those of *fixigenae*; interocular *fixigenae* narrow anteriorly, expanded posteriorly, subtrapezoidal, strongly anteroventrally downturned; posterior *fixigenae* fairly long and broad, adaxial portion roughly horizontal, gently anteroventrally sloped, post-fulcral portion broader than inner part, very strongly ventrolaterally downturned, *fixigenae* with dense granulate sculpture overlain by fairly densely spaced small, pointed tubercles and also very small pits; posterior border furrow deep, short, longer along mid-width, then tapered anterolaterally along curvature at and anterior to genal angle; posterior border short adaxially, expanded almost doubly to maximum length at genal angle, well inflated, with sculpture like that of anterior border, short, thick-based spine extending posterolaterally from genal angle, and with very short transverse furrow on proximal part of posterior margin; doublure turned out posteriorly proximally, rapidly widened post-fulcrum to maximum at genal angle, then cut by facial suture, effaced; axial furrows very deep, except shallow over LO, moderately narrow, widened at junctions with lateral glabellar furrows, weakly anteriorly divergent, tubercles on *fixigenae* and glabella infringe on furrows; glabella lozenge-shaped, long and narrow, weakly anteriorly expanded, with maximum width across L4 81.3% (76.1–85.7%) sagittal length, very strongly vaulted (sag., tr.), with subvertical anterior face (lateral profile), with sculpture of granules overlain by very dense distribution of tubercles slightly smaller than those on rest of cranium; glabellar lateral lobes small and narrow, each distinctly independently inflated; L1 smallest, ovoid, anterolaterally directed; L2 and L3 similar, irregularly semicircular, L3 a little larger; L4 weakly inflated, distinguished mostly as very short lateral bulge even with ocular furrow; LF very large, long medially, almost semicircular in outline, with short, triangular (posteriorly tapered) furrow medially (anterior view); glabellar furrows all narrow (extend only about 25% of distance from axial furrow to sagittal axis), deep (proximal ends abruptly shallowed), long at junction with axial furrows, tapered adaxially; S1 posteromedially directed, S2 and S4 roughly transverse, S3 a little anteromedially angled; SO short, moderately deep to deep, deeper exsagittally behind L1, very shallowly W-shaped, confluent with axial furrows; LO relatively short, 14.6% (13.9–15.2%) sagittal length of cranium, shorter behind mid-width of L1, wide, 30.8% (29.5–31.6%) width across genal angles, well inflated, with sculpture like that of posterior border, and with small median node just posterior to mid-length; doublure long, reaches posterior edge of SO, hardly tapered, pinched out laterally, effaced.

Rostral plate unknown.

Hypostome elongate and narrow, with maximum width across shoulders 83.2% (81.8–84.6%) sagittal length, strongly ventrally convex (tr.), less strongly convex sagittally; anterior border extremely short medially, overhung by middle body in some specimens (Pl. 14, fig. 13; but see Pl. 14, fig. 16), lengthened laterally toward anterior wings; anterior border furrow short, deep, incised, broadly anteriorly bowed; anterior wings roughly trapezoidal, longer than wide, with relatively large wing process pit, very finely tuberculate; middle body long and narrow, posteriorly tapered, with lower convexity posteriorly, poorly separated into lobes; anterior lobe long, wide, ovoid, with densely spaced sculpture of small tubercles and scattered small pits; posterior lobe short to very short, U-shaped, less densely tuberculate with slightly smaller tubercles; middle body furrow mostly not apparent ventrally except far exsagittally as very short, ventromedially angled narrow sections near lateral border furrows (median portion visible as short, somewhat effaced, strongly posteriorly bowed arc on Pl. 14, fig. 13), furrow generally better visible dorsally; lateral border furrow narrow, deep, incised, gently sagittally bowed at about half length of middle body; lateral border fairly narrow, gently ventrolaterally sloped, with dense sculpture of fine tubercles; posterior border furrow very long and shallow medially, abruptly very deep exsagittally where confluent with lateral border furrows, strongly posteriorly bowed; posterior border similar to lateral border, median section gently dorsally bowed (posterior view); doublure poorly preserved, with short lateral notch.

Librigena narrow and elongate, wedge-shaped, gently laterally convex; anterior branch of facial suture long, steep section along field about half length of flat section along anterior projection of border, sections meet at obtuse angle of about 120–130°; posterior branch of facial suture also long, smoothly and steeply sloped along field, slightly upturned along border, cuts posterior projection to expose triangle of doublure; ocular surface large, ovoid,

well inflated, formed from numerous tightly packed lenses (most clearly seen internally, Pl. 14, fig. 11), separated from field by effaced rim, with large smooth patch extending anterolaterally almost to lateral border furrow and extending posteriorly to about 1/3 width of eye; librigenal field subtrapezoidal, narrow anteriorly and broader posteriorly, with width under midpoint of eye 25.2% (24.0–26.3%) exsagittal length, weakly laterally convex (ventrolateral view), with sculpture of granules overlain by small tubercles and small pits on posterior part of field (anterior portion covered by large smooth patch); lateral border furrow narrow, slightly wider anteriorly, very deep, shallower at anterior and posterior extremities; lateral border broad, particularly relative to width of field, strongly inflated, with dense sculpture of small tubercles, larger and less dense near border furrow, with long, anteroventrally directed and out-turned anterior projection, and with fairly long posterior projection tapered to blunt angle; doublure wide, smooth but for a few very fine ridges tracing contour of exsagittal margin, turned out anteroventrally from just a little past the anterior edge of the field to form ventral surface of anterior projection.

Total number of thoracic segments unknown. Segments short and broad, with width of axis 30.5% (28.9–31.8%) width across anterior pleural band, strongly arched axially and due to pleural spines, with sculpture of granules overlain by tubercles; articulating half ring semilunate, long medially, laterally tapered out, raised to equal height of axial ring (lateral view), with transverse band of very tiny tubercles on posterior margin; articulating furrow broadly and shallowly U-shaped, surrounds articulating half ring, very deep, shallower at anterolateral ends, with median sculpture of tiny tubercles in rough transverse row; axial ring short and relatively broad, well inflated, very shallowly U-shaped, with weakly posteriorly bowed anterior margin and weakly anteriorly bowed median posterior margin, ring with sculpture of transverse row of small tubercles along posterior margin, row of slightly smaller tubercles across anterior margin, and intercalated tubercles medially, also with very short furrow along posterior edge above inflation of doublure (posterior view); axial furrows strongly laterally bowed, moderately wide across posterior pleural band, very narrow across anterior band, moderately deep; inner pleurae very broad, outer pleurae very narrow, strongly downturned at subvertical fulcral angle; anterior pleural band very short, equal in width to posterior band, moderately inflated, with extremely short, faint transverse furrow just behind anterior margin of inner pleurae that runs into pleural furrow at exsagittal ends, and with extremely short furrow at very anterior edge of outer pleurae (best observed on Pl. 13, fig. 9); pleural furrow short, shallow adaxially, deep for rest of transverse course; posterior pleural band a little more than twice as long as anterior band, well inflated, with very short articulating furrow setting off short articulating tongue on posterior edge, and with sculpture of transverse row of small, elongate tubercles along anterior and posterior edges which travel down onto pleural spine; pleural spine produced from posterior pleural band, with same length as band adaxially, lengthened abaxially to maximum length just before taper to bluntly pointed tip (at about 90% width of segment), strongly inflated, laterally flattened to produce ovoid cross-section and bluntly bladed anterior edge, spine strongly downturned, with sculpture of tiny tubercles along tapered tip and with small, but slightly elongate tubercles at mid-length and row of tubercles along posterior edge; doublure extremely narrow, just a rim curled medially from base of outer pleurae, slightly wider posteriorly and slightly out-turned anteriorly as part of articulating device, effaced.

Pygidial measurements were made on the specimens of Pl. 13, fig. 34, Pl. 14, figs 26, 29, 32, and Pl. 15, doubling from the sagittal midline as necessary. Pygidium with subtriangular main body, sagittal length 45.9% (43.1–51.2%) width across anterior pleural band of first segment, highly vaulted (sag., tr.), broadest across tips of first pair of pleural spines, formed from four segments with long pleural spines, with dense sculpture of granules overlain by small tubercles on all dorsal surfaces; articulating half ring short, laterally tapered, semilunate, with transverse row of tiny tubercles on posterior margin; articulating furrow long medially, abruptly shorter laterally, deep, shallower medially, with a few very small tubercles at mid-length medially, course anteriorly bowed; axis semi-conical, broad and strongly convex anteriorly, strongly tapered and decreasingly convex posteriorly, first ring 35.9% (33.8–40.1%) width across first segment, fourth ring 53.7% (50.2–58.3%) width across first ring, equal in length (sag.) to main body of pygidium; axial rings well independently inflated, relatively short and broad, transverse to slightly anteriorly bowed, with small median node toward posterior of each ring; terminal piece small, triangular, posteriorly tapered, approximately equilateral; inter-ring furrows long, moderately deep to deep, posterior part of each furrow and exsagittal sections deeper, with a few very small tubercles medially; axial furrows moderately narrow and deep, shallower posteriorly, especially over last segment, but a little deeper again along terminal piece; anterior pleural band present only on first segment, very short, moderately inflated, broad, gently posterolaterally directed, with extremely short, transverse furrow along anterior edge; pleural furrow fairly short, longer exsagittally, shallow adaxially, deeper along rest of gently posterolaterally angled course; posterior pleural

bands strongly inflated, with relatively broad inner pleurae and narrow outer pleurae separated by fulcral angle of about 130°, bands narrower altogether posteriorly, increasingly posteriorly angled, with third pair subparallel and fourth pair parallel or posteromedially angled, inner end evenly rounded on anterior two pairs, tapered on posterior two pairs; pleural spines long, strongly inflated like pleurae, tapered ventrally to blunt points, strongly posteroventrally downturned, splayed with a little less than a spine-width between pairs, with effaced ventral side; interpleural furrows long, deep adaxially, shallower exsagittally, posterolaterally directed like pleurae, granulose; pygidial border expressed ventrally at base of pleural spines, as narrow swollen rim with fine tubercles; doublure strongly upturned (Pl. 15, fig. 11), longest medially, tapered anterolaterally.

Ontogeny. The cranidium (cf. Pl. 11, fig. 1, Pl. 13, fig. 7) elongates and widens slightly overall, decreases in transverse and sagittal convexity; the tuberculate sculpture becomes finer and more densely spaced, particularly on the glabella; the anterior border lengthens, particularly laterally; the anterior border furrow deepens and lengthens, particularly laterally, it develops the M-shaped curvature, and the lateral branches become more transverse rather than anterolaterally directed; the glabella elongates and decreases in convexity (sag., tr.); the lateral furrows lengthen, particularly at the distal ends, and deepen; the axial furrows widen and deepen; LO broadens; the interocular fixigenae widen especially anteriorly; the posterior fixigenae lengthen slightly and widen; the tubercles forming a fringe on the posterior of LO become more effaced, and the genal spines shorten.

The hypostome (cf. Pl. 14, figs 12, 16, 23) becomes more elongate and relatively narrower; the middle body inflates, increasing sagittal convexity; the tuberculate sculpture spreads posteriorly over the rear portion of the anterior lobe of the middle body and over the middle body furrow, obscuring the furrow, and it coarsens on the posterior lobe; the pits on the middle body develop and deepen; the anterior border furrow lengthens and deepens slightly, particularly laterally; the lateral border furrows widen and deepen; the posterior border furrow lengthens and shallows considerably medially; and the posterior border lengthens slightly.

Librigenae (cf. Pl. 14, figs 1, 3) become narrower and relatively more elongate as the librigenal field becomes narrower; the tuberculate sculpture of the field and border becomes finer; the border narrows and deflates slightly; and the anterior projection of the border elongates. The known thoracic segments are too close in size to observe ontogenetic changes.

Pygidia (cf. Pl. 13, fig. 35, Pl. 15, fig. 1) become broader and slightly longer; the tuberculate sculpture becomes slightly finer and slightly more widely spaced, and the median axial tubercles become slightly less prominent; the axis broadens anteriorly and elongates, and increases in transverse convexity, particularly medially; the axial rings become more strongly independently inflated; axial furrows widen and deepen; inter-ring, articulating, and furrows between pleural ribs lengthen considerably and deepen; the pleural spines lengthen slightly, become more tapered and pointed at the tips, and splay further apart.

Discussion. Cranidia of *I. leuppi* differ from those of *I. brevis* in that they possess a much finer and less densely spaced tuberculate sculpture; broader glabella; longer anterior border furrow, with exsagittal transverse portion of furrow especially so and furrow more strongly M-shaped in anterior view; medial portion of anterior border slightly shorter; palpebral lobes longer; interocular fixigena wider. The hypostomes of *I. leuppi* are wider with much wider lateral and posterior borders; the sculpture is generally finer; anterior wings are broader as is the middle body. Librigenae of *I. leuppi* possess less dense sculpture on field with more obvious pits, sculpture on border is also less dense; field is shorter; lateral border furrow deeper; border is longer; smooth patch on anterior portion of field larger. Thoracic segments of *I. leuppi* have a shorter articulating half ring; posterior margin of axial ring is more strongly anteriorly arched; tubercles are slightly taller and more spine like. *Ibexaspis leuppi* pygidia possess shorter ring furrows; larger terminal axial piece; coarser tuberculate sculpture; pleural spines more gently declined with less obvious break in slope (see lateral profile) and generally more slender, with fourth pair of pleural spines longer.

Cranidia of *I. leuppi* compare with those of *I. rupauli* (cf. Pl. 18, fig. 3) as follows: glabella longer and more subrectangular; S1-S4 less clearly incised in lateral profile; fixigena broader; ocular ridge less clearly defined; genal spine shorter; axial furrow, SO, and posterior border furrow generally broader; LO overall shorter and wider, with medial margins more transverse; tuberculate sculpture much finer and less densely spaced on glabella, fixed cheeks, and palpebral lobes, with fewer larger tubercles and more fine tubercles on LO. No hypostome is known for *I. rupauli* and a comparison cannot be made. Librigena of *I. leuppi* differ from those of *I. rupauli* by possessing a broader and longer field with more widely spaced tubercles and clear pits. Only one poorly preserved thoracic segment is known for *I. rupauli*, but those of *I. leuppi* differ from it by possessing smaller tubercles on the axial

ring; a longer articulating furrow with a scattering of small tubercles. Pygidia of *I. leuppi* are broader with the pleural spines more widely splayed laterally; anterior portion of axis broader; fourth pair of pleurae more completely encompassing terminal axial piece; and generally possess a finer tuberculate sculpture.

***Ibexaspis rupauli* n. sp.**

Plates 16–19

Material. Holotype, cranium, SUI 129891 (Pl. 18, figs 3, 5, 6, 11, 14), and assigned specimens SUI 129888–129890, 129892–129904, from Locality YH-J, Yellow Hill Limestone (Blackhillsian; "*Pseudocybele nasuta* Zone"), Yellow Hill, near Pioche, Lincoln County, eastern Nevada, USA. Assigned specimens SUI 129875–129887, from Section J 28T m and J 28.1 m, Wah Wah Formation (Blackhillsian; "*Pseudocybele nasuta* Zone"), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

Etymology. After RuPaul.

Diagnosis. Glabella strongly forwardly expanding; S4 prominently impressed; sparse, transverse row of 4–6 small spines across rear of LO; pygidium with large terminal piece; posterior margin of terminal piece well exposed due to wide median space between fourth pair of pleural spines; terminal piece with rear overhanging posterior margin in dorsal view.

Description. Cranial measurements were made on the large and best preserved specimens of Pl. 16 and Pl. 18. Cranium strongly vaulted (sag., tr.) due to inflation of axis and ventral curvature of fixigenae, relatively long and wide, with sagittal length 110.3% (103.3–114.3%) width across γ , 77.3% (76.3–78.8%) width across δ , 79.9% (76.4–84.3%) width across ϵ , and 55.3% (52.5–57.3%) maximum width across genal angles, with sculpture of coarse tubercles on top of very fine granules, most densely distributed on median part of glabella and on cranial borders; anterior border strongly anteriorly bowed, short and fairly narrow, shallowly M-shaped in anterior view, with median portion depressed; doublure expressed as anterior face, only a rim ventrally; anterior border furrow short and deep, strongly anteriorly arcuate (dorsal view) with narrow subtransverse segments at exsagittal ends, also shallowly M-shaped in anterior view; glabella long, narrow posteriorly, strongly anteriorly expanded, with glabellar maximum width across L4 79.6% (75.8–84.7%) sagittal length, strongly vaulted (sag., tr.), with sculpture of densely spaced small tubercles concentrated medially; glabellar lobes L1–L3 each well independently inflated, L4 less well inflated but still distinct, L1 smallest and anterolaterally angled, remaining lobes slightly larger and progressively more transversely angled; glabellar lateral furrows (S1–S4) very similar, short and very deep, S4 shallower, furrows extend medially to about 1/4 glabellar width, S1 gently posteromedially directed, S2 subtransverse, S3 and S4 gently anteromedially directed; SO very shallowly W-shaped, short and deep, particularly in apodemal pits behind mid-width of L1, confluent with axial furrows; LO short and relatively wide, well inflated, with small median node possessing densely spaced tuberculate sculpture wrapped around it, fringe of 6–8 more spinose small tubercles on posterior margin; doublure of smooth ellipsoid band extending to SO and tapered out laterally; axial furrows very deep, shallowed over posterior border, narrow, wider at intersections with glabellar lateral furrows, gently anteriorly divergent, confluent with all but palpebral furrows; ocular ridges ill-defined, short and narrow; palpebral lobes semi-ellipsoid, widest opposite S3–L4, tuberculate; palpebral furrows narrow and deep, course J-shaped, with anterior part anteromedially angled and posterior part curved around posterior edge of lobe; interocular fixigenae triangular, relatively short and narrow, broader posteriorly, strongly anteriorly downturned, with dense sculpture of small tubercles, interspersed tiny tubercles, and tiny pits, tubercles smaller near axial furrows; posterior fixigenae slightly longer than interocular fixigenae, broad, strongly ventrolaterally downturned, sculpture same as interocular fixigena; posterior border furrow deep, abruptly shallowed at intersection with axial furrows, short, incised, broadly anterolaterally curved; posterior border well inflated, fairly short, with maximum length at genal angle a little shorter than LO, sculpture of moderately densely spaced small tubercles, and with moderately short, broad-based, rapidly tapered, mediolaterally flattened genal spine, and with very short articulating ridge along posterior margin set off by short furrow (e.g., Pl. 16, fig. 3); border doublure short and turned out posteriorly adaxially, slightly lengthened abaxially reaching maximum length at genal angle, smooth.

Rostral plate and hypostome unknown.

Librigenal measurements were made on the specimen of Pl. 18, fig. 20. Librigena narrow and elongate, with

width under midpoint of eye 35.2% length along lateral border; anterior branch of facial suture short and very steep along field, long and gently anteroventrally sloped along border; posterior branch of facial suture steep along field, flat along border, with section along border almost twice as long as section along field; ocular surface poorly preserved, eye raised far above field (ventrolateral view); librigenal field narrow, subtrapezoidal, with extremely narrow extension posteriorly, just along border furrow, extending about half again width of main part of field, extension is part of post-ocular ridge also running along posterior edge of field as slightly swollen margin, field with width under midpoint of eye 22.9% exsagittal length (excluding posterior extension), weakly laterally convex (ventrolateral view), with sculpture of small tubercles and pits on posterior half, anterior half granulose, with effaced patch under anterior part of eye; lateral border furrow narrow and deep, narrower posteriorly, wider and shallower anteriorly; lateral border well inflated, slightly broader than field, anteriorly and posteriorly tapered along long projections, with dense sculpture of small tubercles, tubercles increasingly smaller ventrolaterally; doublure imperfectly preserved, broad and smooth, but with a few fine ridges following contour of outer margin, doublure rotated out anteroventrally along anterior projection of border, inner surface exposed in dorsal view by cut of posterior branch of facial suture at tip of posterior projection of border.

Total number of thoracic segments unknown. Single known segment (Pl. 19, fig. 20) with relatively wide axis 37.1% width across anterior pleural band, strongly vaulted; articulating half ring poorly preserved, raised to same height as axial ring (lateral view); articulating furrow short and deep, shallowly U-shaped, wrapping around half ring, with a few granules; axial ring relatively long compared to width, also shallowly U-shaped, anterolaterally tapered, well inflated, with moderately dense sculpture of small tubercles; doublure moderately short, lens-shaped, smooth but for fine transverse ridge near posterior margin; axial furrows shallow and fairly narrow, bowed laterally around ring; fulcral angle very steep, almost subvertical; anterior pleural band very short, inflated, with extremely short furrow setting off articulating surface on anterior edge; posterior pleural band slightly shorter than axial ring, well inflated, equal in breadth to anterior band, tuberculate; pleural spine poorly preserved, with thick base, tapered exsagittally, slightly laterally compressed, tuberculate dorsally, smooth ventrally; doublure very narrow, just curled under tips of outer pleurae.

Pygidial measurements were made on the larger and more intact specimens of Plates 17 and 19. Pygidium of four segments and terminal piece, strongly vaulted (sag., tr.) mainly from convexity of axis and pleural spines, relatively narrow and long, with sagittal length from articulating furrow 47.9% (45.7–48.8%) width across anterior pleural band, widest across tips of first pleural spines, with moderately densely spaced sculpture of small tubercles; articulating half ring semilunate, short and laterally tapered, smooth; articulating furrow moderately long and deep; axis long, equal to length of pygidium excluding spines, broad anteriorly, 35.6% (35.1–36.1%) pygidial width, strongly posteriorly tapered, strongly convex (sag., tr.), convexity decreases posteriorly; axial rings each well independently inflated, relatively broad and short, each ring slightly longer medially than laterally, with densely spaced sculpture of small tubercles, with four tubercles arranged in a rhombus at midline of second two segments (Pl. 19, fig. 2); terminal piece triangular, large, long and broad anteriorly, strongly posteriorly tapered, posterior tip extends slightly beyond rounded posterior margin; inter-ring furrows short, deep, shallower medially, fourth furrow shorter and shallower; axial furrows moderately wide and shallow (Pl. 19, fig. 2), deeper in smaller specimens, strongly anteriorly divergent; anterior pleural band present only on first segment, very short, swollen, with extremely short transverse articulating furrow along anterior margin; pleural furrow also only on first segment, deep and very short, slightly longer exsagittally; posterior pleural bands well inflated, relatively long and wide, slightly shorter near axial furrows, with sculpture of small tubercles; pleural spines long (oblique), fairly wide, strongly inflated, slightly laterally compressed, tapered to blunt point, tuberculate like pleurae dorsally, granulose ventrally; interpleural furrows moderately long and deep, posterior furrows shallower, furrows increasingly posteromedially directed; pygidial border of very short raised rim at inner base of spines; doublure strongly upturned, best seen in anterior view, moderately long, smooth, upper margin shallowly W-shaped (e.g., Pl. 19, fig. 11).

Ontogeny. Ontogenetic changes in the cranidium and pygidium are well represented in the specimens of *I. rupauli*, but other sclerites are unknown (the hypostome) or known only from single specimens. Cranidia (cf. Pl. 16, fig. 16, Pl. 18, figs 3, 7) become slightly broader relative to sagittal length and therefore a little less vaulted (tr.); the glabella also decreases in convexity (tr., sag. to a lesser extent), it widens slightly anteriorly to S3, and the glabellar furrows become shorter, particularly adjacent to the axial furrows; the axial furrows narrow and become less strongly impressed over LO; SO shortens and becomes more W-shaped rather than transverse in course; LO

deflates slightly, lengthens medially, and its median and posterior fringe tubercles become less prominent while tubercles on the anterior portion increase in size; the palpebral lobes narrow slightly; the interocular fixigenae widen slightly, pushing the posterior end of the palpebral lobes further away from the glabella; the genal spine flattens slightly and develops a wider base; the cranidial sculpture overall becomes much more densely distributed; and the two primary ontogenetic tubercles located anterior to the genal spine and posterior to the palpebral lobe decrease in prominence.

Pygidia (cf. Pl. 17, fig. 18, Pl. 19, figs 1, 2, 19) increase in convexity (tr., also sag.), and the sculpture becomes slightly finer and more densely spaced; the axis broadens, particularly anteriorly, but also becomes less strongly posteriorly tapered, and slightly less vaulted (tr.); the terminal piece enlarges and inflates; the axial nodes weaken and blend more into the rest of the sculpture; the inter-ring furrows and the furrows between the pleural ribs become longer and deeper; the axial furrows widen and deepen; the pleural spines shorten relative to the length of the pygidium, their tips become more sharply pointed, and they splay further apart laterally.

Discussion. *Ibexaspis rupauli* has been compared with its congeners in the species discussions above. The species is by far the youngest member of the genus and of the overall clade treated herein. It occurs approximately 50 m above the next youngest species, *I. leuppi*, which is retrieved as its sister taxon in the phylogenetic analysis.

***Deltapliomera* n. gen.**

Type species. *Deltapliomera humphriesi* n. sp., from the Fillmore Formation (Blackhillsian; *Carolinites nevadensis* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

Other species. *Deltapliomera inglei* n. sp., Fillmore Formation (Tulean; *Heckethornia bowiei* Zone), western Utah; *D. heimbergi* n. sp., Fillmore Formation (Tulean; *Panisaspis sevierensis* Zone), western Utah; *D. eppersoni* n. sp., Fillmore Formation (Blackhillsian; *Bathyrina plicolabeona* Zone), western Utah; *Deltapliomera* n. sp. A, Fillmore Formation (Tulean; *Panisaspis sevierensis* Zone), western Utah.

Etymology. The town of Delta, Utah, and the genus name *Pliomera*. Gender is feminine.

Diagnosis. Sagittal glabellar height in anterior view 29.9–35.0% width across posterior projections (excluding genal spines); anterior course of axial furrows strongly anteriorly divergent; size of librigenal field reduced, trapezoidal in shape; posterior branch of facial suture along lateral border very short; tuberculate sculpture on first pygidial axial ring usually effaced at least medially; distal tips of pygidial pleural spines usually expanded and club-shaped.

Discussion. *Deltapliomera* was recovered as sister to *Millardaspis* in the phylogenetic analysis, and the taxa share a reduction in later ontogeny of clusters of tubercles on the glabellar lateral lobes that are prominent early; librigenal fields with a swollen rim adjacent to the lateral border furrow; and very broad librigenal lateral border furrows.

Species of *Deltapliomera* occur at several horizons with more or less equally common species of *Ibexaspis*. There is little question of correct association of sclerites, however, as species belonging to either genus also occur at some horizons in the absence of any member of the other genus. *Ibexaspis rupauli* and *I. leuppi* do not occur with any other member of the overall clade, nor does *D. inglei*. Reference to the morphology of these species removes any potential confusion when species do co-occur.

***Deltapliomera inglei* n. sp.**

Plate 20, Plate 21, figs 1–21

2009 *Ibexaspis* sp. nov. 3; Adrain *et al.*, p. 567.

Material. Holotype, pygidium, SUI 129565 (Pl. 21, figs 13, 17, 18, 20, 21), and assigned specimens SUI 129553–129564, 129566, from Section H 127.1 m, Fillmore Formation (Tulean; *Heckethornia bowiei* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

Etymology. After Jon Ingle.

Diagnosis. Densely spaced and coarse granulose sculpture all over cranidium, including LO and posterior border; LO without distinct median node in most large specimens; pygidium with sculpture of very coarse granules

or tiny tubercles, blending into smaller granules at tips of pleurae; free tips of pleurae long compared to other species.

Description. *Deltaplomera inglei* is sufficiently similar to *D. humphriesi* that it is treated with an extended comparative discussion. Ratios are given for comparison with other species. Its librigenae and thorax are unknown.

Cranidium with sagittal length 106.7% (104.2–109.5%) width across γ , 74.0% (71.8–75.7%) width across δ , 74.0% (70.8–76.0%) width across ϵ , and 54.8% (54.2–55.9%) maximum width across genal angles; the cranidium of *D. inglei* is broader and slightly less strongly vaulted (sag., especially tr.), with much coarser and more densely spaced tuberculate sculpture; anterior border slightly narrower and less overhung by glabella; glabella narrower and less elongate, maximum width across L3 91.4% (90.0–93.1%) sagittal length, less strongly anteriorly expanded to L3, L3 smaller; axial furrows slightly broader, more laterally bowed and not anteriorly divergent in course; SO slightly shorter and deeper; genal spine shorter, smaller, and blunter; palpebral lobes slightly narrower, longer, and less posterolaterally angled; interocular fixigenae slightly narrower overall; posterior fixigenae longer and broader, a little less strongly downturned.

Hypostome shorter and narrower overall, with smaller, shorter, narrower, more strongly posteriorly tapered middle body; lateral border broader, particularly at shoulders, and more strongly downturned; posterior border longer, and without median dorsal inflection; hypostome in general with slightly finer sculpture.

Pygidium slightly narrower and shorter, with sagittal length from articulating furrow 45.6% width across anterior pleural band of first segment; more strongly vaulted (sag., tr.); axis relatively longer and narrower, width across first ring 41.2% width across anterior band of first segment, and width across fourth ring 50.0% width across first ring, more convex (sag., tr.); axial rings more strongly independently inflated, shorter and more densely tuberculate, especially medially; no terminal piece; inter-ring furrows shorter and deeper; axial furrows deeper and more strongly anteriorly divergent; pleurae slightly wider, with tubercles extending to edge of pleura; pleural spines slightly longer and thinner, with many more tubercles, especially near tips; doublure of even length and shorter medially than that of *D. humphriesi*.

Ontogeny. Cranidial ontogenetic changes (cf. Pl. 20, figs 1, 3 and Pl. 21, fig. 1) include overall broadening of the cranidium; fining of the sculpture, particularly on the glabella and LO, and addition of smaller tubercles increasing density of its distribution; anterior expansion of the glabella; slight decrease in glabellar vaulting; inflation of lateral glabellar lobes; lengthening, deepening, and slight adaxial extension of lateral glabellar furrows; slight enlargement of L3 relative to L2; effacement of median LO node to blend in with other LO tubercles; and the genal spine shrinks to a rounded nub.

Hypostomal changes include overall elongation; the middle body also becomes longer and narrower, with a better defined (laterally) middle body furrow; the lateral and posterior border furrows become much shallower; and the lateral and posterior borders widen/lengthen considerably. It also appears that the lateral and posterior border sculpture becomes much more dense and finer, although the border area of the smallest specimen (Pl. 21, fig. 4) is obscured by detritus.

The pygidium of *D. inglei* is known from only two specimens, but the high size disparity (Pl. 21, fig. 16 is a transitory pygidium with a single thoracic segment attached) demonstrates a number of ontogenetic changes. The pygidium becomes wider overall; the sculpture becomes finer but denser, with more small tubercles intercalated; the inter-ring and furrows between pleural ribs lengthen and shallow slightly; the median axial nodes shrink and blend in with the other tubercles; and the pleural spines splay out anterolaterally with increased space between them.

Discussion. Cranidia of *D. heimbergi* and *D. inglei* are very similar, but the latter have a more parallel sided glabella that is less strongly inflated; S3 more deeply incised; the palpebral lobes are more slender overall; the posterior fixigenae are wider; the row of tubercles along posterior margin of LO and posterior borders is composed of much smaller and more subdued tubercles; sculpture is generally coarser with more fine granules interspersed between the tubercles. The hypostomes of *D. inglei* have much broader lateral and posterior borders, are less posteriorly tapered so that their outline posteriorly is more gently rounded rather than pointed, and generally finer sculpture. A comparison of the librigenae and thorax cannot be made as they are unknown for *D. inglei*. The largest pygidium of *D. inglei* is overall longer and wider; with longer more widely splayed pleural spines; longer axis; and much more prominently tuberculate sculpture, especially along the central portion of axis, which possesses prominent clusters of larger tubercles, and along the pleural spines, which also exhibit loose rows of prominent tubercles.

A comparison of *D. eppersoni* with *D.inglei* is as follows. Cranidia of *D.inglei* possess glabellae that are narrower and do not overhang the median portion of the anterior border as seen in *D. eppersoni*; the interocular and posterior fixigenae are longer, with the abaxial portion of the posterior fixigenae especially so; the palpebral furrows and sutures are less strongly posteriorly divergent; SO and posterior border furrows are shorter and more deeply incised; the sculpture is much coarser and densely spaced, especially on LO (which is mostly effaced medially in *D. eppersoni*). The hypostomes of both species are very similar, but those of *D.inglei* are less convex, with a more posteriorly tapered middle body that is also narrower. The pygidium of *D.inglei* possesses larger more prominent tubercles overall with a cluster of prominent tubercles running along the sagittal axis; the pleural spines are more widely splayed with the distal tips directed obliquely and not posteriorly in dorsal view as in *D. eppersoni*, with the fourth pair of pleural spines much longer in dorsal view; first and second axial rings are slightly pinched out abaxially rather than maintaining a constant length (sag., exsag.).

***Deltapliomera heimbergi* n. sp.**

Plates 22–27

2009 *Ibexaspis* sp. nov. 4; Adrain *et al.*, p. 569, fig. 16D, H.

2009 *Ibexaspis* sp. nov. 5 (*partim*); Adrain *et al.*, p. 569, fig. 16P (only; fig. 16L = *Ibexaspis* sp. nov. C herein).

Material. Holotype, cranidium, SUI 129568 (Pl. 22, figs 2, 3, 6, 9, 12), from Section H 178.2 m, and assigned specimens SUI 115304, 115305, 115308, 129567, 129569–129616, from Section H 166.2–173.2 m, Fillmore Formation (Tulean; *Panisaspis sevierensis* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

Etymology. After Alex Heimberg.

Diagnosis. Cranidium with densely spaced coarse sculpture including common punctate tubercles and pitted fixigenae, but sculpture more effaced on LO and posterior border; hypostome rhombic, very broad at shoulders and very strongly posteriorly tapered; librigena with elongate anterior branch of facial suture compared to congeners; pygidial doublure elongate medially but tapered laterally, coming to a distinct point at midline.

Description. *Deltapliomera heimbergi* is similar enough to *D. humphriesi* that it is described with a list of all morphological differences. The cranidium is of similar dimensions with sagittal length 51.5% (49.1–55.2) width across genal angles, 104.5% (96.1–113.0%) width across γ , 69.4% (63.7–72.6%) width across δ , 68.2% (65.0–70.9%) width across ϵ , but slightly less vaulted (tr.), and slightly more vaulted (sag.), with coarser sculpture overall; the anterior border is usually almost fully visible vs. medially overhung in *D. humphriesi*; the glabella is shorter, narrower and less anteriorly expanded (sagittal length 106.6% (100.8–111.7%) width across L3).

Hypostomes of *D. heimbergi* differ from those of *D. humphriesi* in being shorter (width across shoulders 112.9% (111.3–114.8%) length), more strongly posteriorly tapered (shoulders very wide compared to posterior border), and with less densely spaced sculpture of tiny tubercles, a little finer in size on middle body and a little coarser on borders; the anterior border is less overhung medially by the middle body; the anterior wings are smaller (shorter and narrower) and turned more anterodorsally, so that the wing process pit is less visible (it is also smaller); the middle body is much less ventrally vaulted (sag., tr.), shorter and more posteriorly tapered, with a smaller, shorter anterior lobe and larger, longer posterior lobe that wraps further around the anterior lobe; the lateral and posterior border furrows are slightly deeper; the lateral border is narrower; and the posterior border is shorter.

Librigenae of *D. heimbergi* are narrower and much more elongate, with width under midpoint of eye 35.4% (33.7–37.9%) length along lateral border; the smooth spot at the anterolateral margin of the eye is smaller; the librigenal field is considerably narrower and a little shorter, width 33.5% (30.4–37.0%) length, with coarser and more sparsely distributed tubercles and pits; the lateral border furrow is shallower and less anteriorly widened; the lateral border is more elongate, with a much longer anterior projection, slightly broader, and has much coarser tuberculate sculpture, particularly adaxially.

Thoracic segments differ mainly in that those of *D. heimbergi* are coarsely tuberculate and those of *D. humphriesi* are nearly effaced, and also the line of tubercles on the anterior edge of the axial ring is made of fewer, larger tubercles.

Pygidia of *D. heimbergi* are of similar dimensions to those of *D. humphriesi* with sagittal length from articulating furrow 55.7% (52.5–58.4%) width across anterior pleural band of first segment, a little less strongly

vaulted (sag., particularly tr.), and have much coarser tuberculate sculpture, compared to lightly tuberculate or nearly effaced; the axis is more strongly posteriorly tapered (width of fourth ring 44.6% (40.1–53.5%) width of first ring); the axial rings are slightly longer compared to their width and more inflated; the terminal piece is small (Pl. 27, figs 12, 18, 27) or absent (Pl. 27, figs 1, 13, 26); the pleurae and pleural spines are more inflated; the spines are shorter and they are less splayed, particularly the fourth pair; the doublure is shorter laterally and longer medially, coming to a point at the midline (Pl. 27, fig. 14).

Ontogeny. Ontogenetic changes in the cranidia of *Deltapliomera heimbergi* are well represented. Cranidia (cf. Pl. 23, figs 1, 9) become relatively shorter and narrower overall, and more strongly vaulted (tr., sag.), while the sculpture changes from granules overlain by sparse large tubercles to small densely spaced tubercles; the anterior border shortens, deflates slightly, and becomes overhung medially by the glabella, as does the anterior border furrow; the glabella inflates to become strongly convex, the lateral furrows lengthen and shallow, and the lobes become independently inflated; LO shortens and inflates, the median node shrinks dramatically, and the tubercles on the posterior margin also shrink to blend in with finely tuberculate sculpture; the axial furrows narrow and shallow; the interocular fixigenae broaden, particularly posteriorly; the palpebral furrows broaden slightly and shallow; the palpebral lobes broaden; the posterior fixigenae broaden, and the distal portions become more steeply downturned; the posterior border furrow lengthens and shallows, particularly proximally; the posterior border inflates a bit more; the genal spine shortens to a nub; and the ontogenetic tubercles on the border and the anterolateral edge of the posterior fixigenae reduce to blend in with the rest of the sculpture.

The hypostome (cf. Pl. 25, figs 1, 19) elongates relative to the width across the shoulders; the sculpture becomes slightly coarser all over; the middle body inflates, the anterior lobe becomes more strongly posteriorly tapered and the posterior lobe lengthens medially while shortening laterally and wrapping further anteriorly around the anterior lobe; the middle body furrow becomes more strongly impressed (although still only expressed anterolaterally); the posterior border furrow lengthens and deepens; and the lateral border narrows and the posterior border shortens.

Librigenae (cf. Pl. 24, figs 16, 22) broaden; the field broadens and narrows slightly, and the pits deepen; the lateral border furrow narrows and deepens; the lateral border broadens, deflates very slightly, and its tuberculate sculpture becomes finer and more densely packed, and the anterior projection lengthens. Thoracic segments are insufficiently well known to observe ontogenetic changes.

The pygidium (cf. Pl. 26, fig. 15, Pl. 27, fig. 27) broadens slightly overall and becomes more strongly vaulted (sag., tr.); the tuberculate sculpture becomes larger in size and more sparsely distributed; the axis also increases in convexity and broadens, particularly anteriorly; the axial rings each become more independently inflated; the inter-ring furrows lengthen and shallow; the axial furrows broaden and shallow somewhat; the pleurae inflate more; the pleural spines also inflate, and spread further apart from each other.

Discussion. *Deltapliomera heimbergi* is compared with *D. humphriesi* in the differential description above, and is compared with *D. inglei* and *D. eppersoni* in discussions of those species.

Two poorly preserved cranidia (Pl. 23, figs 3, 6, 11; Pl. 26, figs 17, 19, 22) have distinctly wider and shallower axial furrows. The cranidia are also less vaulted (tr.), with a less inflated (sag., tr.) glabella. They may represent another species, or possibly a new species of *Millardaspis*, but the poor preservation of the palpebral lobes and sculpture limits more precise assessment.

***Deltapliomera eppersoni* n. sp.**

Plates 28–33

- 1953 *Protopliomerops? quattuor* Hintze, pl. 21, fig. 10 [only; pl. 21, figs. 9, 12–14 = *Panisaspis quattuor* (Hintze, 1953); pl. 10, fig. 11 = *Ibexaspis brevis* (Young, 1973)].
2009 *Ibexaspis* sp. nov. 6; Adrain *et al.*, p. 570, fig. 17T, U.

Material. Holotype, cranidium, SUI 115337 (Pl. 28, figs 1, 2, 4, 6, 9)), from Section H 191.7 m, and assigned specimens SUI 115338, 129617–129673, from Section H 185.6–191.7 m, Fillmore Formation (Blackhillsian; *Bathyrina plicolabeona* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

Etymology. After John Epperson.

Diagnosis. Cranidial axial furrows wide, especially adjacent to L3 and shallow compared to congeners;

cranial sculpture with infrequent punctate tubercles and lightly pitted fixigenae; librigena more strongly pitted with common punctate tubercles; space between proximal ends of pygidial pleural spines rounded, keyhole-shaped.

Description. *Deltapliomera eppersoni* is sufficiently similar to *D. humphriesi* that it is described through extended and detailed comparison with that taxon. Measurements are given for better comparison to other species. Cranidia of *D. eppersoni* are shorter and relatively broader overall (length 51.7% (50.1–54.3%), maximum width across genal angles, 102.1% (94.6–104.3%) width across γ , 72.1% (67.8–76.4%) width across δ , 68.1% (64.3–72.6%) width across ϵ); the sculpture is of coarser and more widely spaced tubercles on both the glabella and fixigenae; the anterior border is only slightly overhung by the frontal lobe of the glabella; the glabella is less vaulted (sag., especially tr.), slightly shorter, broader at the base and less anteriorly expanded (sagittal length 111.4% (103.1–117.4%) maximum width across mid-length of L3, sagittal length 79.8% (76.8–81.9%) cranial length, maximum width 37.0% (35.5–39.5%) maximum cranial width); L1 is slightly larger; L3 is wider; the glabellar furrows extend further sagittally; S3 is deeper but S1 and S2 are shallower, and S2 is shorter at the junction with the axial furrows; SO is slightly longer and shallower; LO is broader and slightly longer (length 15.6% (14.7–17.0%) sagittal cranial length, maximum width 34.5% (28.3–39.6%) cranial width), more shallowly W-shaped (longer medially and shorter behind the inner end of L1), and tuberculate, with a row of tiny tubercles on the anterior margin, slightly larger tubercles posteriorly, and a larger median node; the axial furrows are wider (particularly across from L3), shallower (moderately deep compared to very deep in *D. humphriesi*), less laterally bowed around L3, and less anteriorly divergent in general; the interocular fixigenae are broader, particularly posteriorly; the palpebral lobes are located slightly further anteriorly, and the sculpture is tuberculate rather than effaced; the posterior fixigenae are a little less strongly downturned and the outer portion (exsagittal to the edge of the post-ocular ridge) is narrower; the posterior border furrow is longer, particularly adaxially, and shallower, and a little less anterolaterally curved; the posterior border is shorter at the genal angle, and the tubercles lining the anterior margin are slightly larger, while the genal spine has a smaller base, and there are small tubercles near the posterior margin and one small tubercle just posterior to the cut of the facial suture.

Hypostomes of *D. eppersoni* are slightly broader than those of *D. humphriesi* (maximum width across shoulders 92.5% (89.8–100.0%) sagittal length); they possess smaller anterior wings set further abaxially and with smaller wing process pits; the middle body is wider anteriorly, shorter, and less strongly posteriorly tapered; the anterior lobe is more rounded posteriorly, rather than tapered, it is slightly more inflated (sag.), and it has finer tuberculate sculpture; the posterior lobe is longer medially, with narrower, longer anterolateral arms; and the lateral and posterior borders are slightly wider/longer; and the lateral notch is shorter and deeper, with less upturned doubleure.

Librigenae differ in being overall narrower and more elongate (width opposite midpoint of eye 39.3% (35.8–43.1%) length along lateral border); the ocular surface is less inflated and less elevated above the field; the platform is narrower and the anterior effaced area is smaller; the librigenal field is narrower, with more tuberculate sculpture and fewer closely spaced pits; the lateral border furrow is shallower, particularly anteriorly, and more upturned anteriorly; the lateral border is slightly narrower, with a longer anterior projection, less densely spaced tuberculate sculpture, with scattered punctate tubercles, and more robust fine ridges on the ventral side of the anterior projection (ventrolateral view).

Thoracic segments are compared based on similar proportions (indicating similar position in thorax; those of Pl. 31 compared with Pl. 42, figs 4, 19, 27). They differ mainly in that those of *D. eppersoni* are more tuberculate, with very small tubercles lining the posterior margin of the articulating half ring, lining the anterior margin of the axial ring and on its abaxial posterior margin, and slightly larger tubercles arranged transversely across the posterior of the ring, as well as tiny tubercles on the anterior and posterior edges of the inner pleurae (mostly effaced on segments of *D. humphriesi*) and increasing in size ventrally down the spine (smaller and more closely spaced on *D. humphriesi*); the axis also appears to be slightly wider (with width of axis 53.0% (50.1–55.9%) width across anterior pleural band); the axial furrows are broader, deeper.

Pygidia of *D. eppersoni* are shorter and relatively wider with sagittal length from articulating furrow 53.8% (50.1–59.4%) width across anterior pleural band of first segment; the sculpture is much more tuberculate, with the entire axial ring covered and pleurae sculptured at least adaxially; the tubercles are slightly elongate and spinose, rather than flat; the axial nodes persist at larger pygidial sizes; the axis is narrower, more strongly posteriorly tapered (width of fourth ring 41.7% (34.0–53.2%) width of first ring), and more strongly vaulted (tr.); axial rings

are shorter; the terminal piece is smaller and more sharply posteriorly tapered; inter-ring, pleural, and interpleural furrows are shallower; and the pleural spines are shorter, thinner, and less strongly downturned, and the space between the proximal ends of the pleural spines is rounded (space between bases of spines forms keyhole shape).

Ontogeny. Cranidia (cf. Pl. 28, figs 1, 15, Pl. 29, figs 3, 11) become wider overall, and slightly less strongly vaulted (tr., sag. to a lesser degree), and the sculpture becomes smaller and slightly more sparsely distributed on the fixigenae; the anterior border broadens and becomes medially overhung by the glabella; the glabella widens and decreases slightly in convexity (sag., tr.), the lateral furrows lengthen and shallow abaxially while deepening adaxially, and the glabellar lobes increase in individual inflation; the axial furrows widen and shallow; the interocular fixigenae widen, particularly posteriorly, pushing the posterior end of the palpebral lobes out further laterally; the posterior fixigenae widen adaxially; the posterior border furrow lengthens and shallows; and the genal spine shortens.

The hypostome (cf. Pl. 31, figs 10, 25) lengthens and becomes relatively narrower; the middle body overall lengthens and narrows (especially the anterior lobe; the posterior lobe lengthens but does not narrow as noticeably), and inflates, and the tubercles on the anterolateral edges of the anterior lobe efface away while pits develop on the posteromedian portion; the middle body furrows narrow and deepen, but the posteromedian ends efface so that the furrows end just past the shoulder; the lateral border furrows broaden and shallow far anteriorly, but deepen significantly posteriorly; the posterior border furrow shallows; the lateral border broadens considerably; the posterior border lengthens to match it; and the sculpture of both borders becomes more effaced.

Librigenae (cf. Pl. 30, figs 3, 13, 14) broaden overall; the eye enlarges; the librigenal field broadens, particularly posteriorly, and the smaller background tubercles become more effaced; the lateral border furrow shallows posteriorly; the lateral border broadens, the posterior and especially anterior projections lengthen, and the tubercles become slightly smaller. The known thoracic segments are too close in size to demonstrate ontogenetic change.

The pygidium (cf. Pl. 30, fig. 22, Pl. 33, fig. 4) becomes broader overall (including spines), but the main body of the pygidium narrows and lengthens, and it becomes slightly less vaulted (sag., tr.) overall; the axis broadens anteriorly and becomes less strongly posteriorly tapered; the axial rings slightly decrease in individual inflation, the sculpture of densely spaced tubercles becomes more clearly developed, but the median tubercles shrink and become less apparent; the inter-ring furrows lengthen (particularly the anterior ones) and shallow, as does the articulating furrow; the axial furrows narrow, and shallow far anteriorly and posteriorly; the pleurae inflate slightly, and the tubercles become slightly smaller and more closely spaced; the furrows between pleural ribs lengthen and shallow considerably; the pleural spines splay apart, and the tips become slightly more tapered and pointed.

Discussion. Compared to *D. heimbergi*, cranidia of *D. eppersoni* possess a less strongly inflated glabella, which is broader across the posterior margin and less laterally expanded around L3; the axial furrows are shallower and slightly broader; the posterior fixigenae are shorter and narrower; and they generally have a sculpture of finer tubercles, with LO and posterior border much more effaced, and a smaller median node on LO. Hypostomes of *D. eppersoni* are much less strongly tapered posteriorly, with broader lateral and posterior borders, and a finer tuberculate sculpture. Librigenae are slightly shorter and the tuberculate sculpture is finer with more isolated tubercles (compared to the coarse densely spaced tubercles present on *D. heimbergi*), less obvious background sculpture of densely spaced granules. Thoracic segments with broader axis, and lacking prominent coarse tubercles. Pygidia of *D. heimbergi* and *D. eppersoni* are very similar, but the latter have shorter axial rings with shallower ring furrows, smaller terminal piece, thinner pleural spines, a finer tuberculate sculpture.

Some specimens represent transitory pygidia or earliest holaspid. One (Pl. 32, fig. 27) has five pairs of pleural spines and four axial rings. It likely represents a last-stage meraspid, with the anterior segment representing an as yet unreleased posteriormost thoracic segment. A specimen of similar overall size (Pl. 32, fig. 32) has four pairs of spines, but only three axial rings. It likely represents the earliest holaspid stage following release of the last thoracic segment, and prior to the development of a fourth axial ring associated with the fourth pair of spines.

***Deltapliomera humphriesi* n. sp.**

Plates 34–43

1953 *Protopliomerops* sp. 4; Hintze, p. 210, pl. 21, fig. 4 [only; pl. 21, fig. 8 =*Panisaspis quattuor* (Hintze)].

2009 *Ibexaspis* sp. nov. 7; Adrain *et al.*, p. 573, fig. 18I, M.

2009 *Ibexaspis* sp. nov. 8; Adrain *et al.*, p. 573, fig. 18J.

Material. Holotype, pygidium, SUI 129755 (Pl. 43, figs 1, 2, 5, 8, 11), and assigned specimens SUI 115358, 129674–129704, from Section H 208.2 m, and SUI 115357, 129705–129752, 129756–129761, from Section H 222.1 m, Fillmore Formation (Blackhillsian, *Carolinites nevadensis* Zone), southern Confusion Range, Ibox area, Millard County, western Utah, USA.

Etymology. After Barry Humphries.

Diagnosis. Cranidium with anterior border furrow and most or all of border overhung medially by glabella; long and narrow interocular fixigenae (including frontal area); strongly anteriorly expanded glabella; palpebral lobes located in a relatively posterior position on cranidium; inner margins of lobes/palpebral furrows almost parallel to sagittal axis (in large specimens); librigena with wide field relative to congeners; pygidium with axial sculpture concentrated on anterior half of rings; sculpture of large cranidia and pygidia generally finely granular and densely spaced to dorsally effaced (see discussion); pygidial pleural spines thicker, more rounded in cross section than those of congeners; terminal piece well expressed in most specimens.

Description. Cranidial measurements were made on the sufficiently complete large specimens of Plates 34, 35, 38–40. Measurements were doubled from the sagittal midline where necessary. Cranidium very strongly vaulted (sag., tr.), with anterior face subvertical (see sagittal profile), long and broad, increasingly wide posteriorly, with sagittal length 99.8% (93.4–105.6%) width across γ , 73.4% (68.8–78.8%) width across δ , 69.3% (66.0–74.4%) width across ϵ , and 52.3% (50.7–56.3%) maximum width across posterior projections; anterior border very short, slightly longer (oblique) at exsagittal ends, a little wider than LO, strongly anteriorly bowed in dorsal view and nearly overhung medially by glabella on most specimens, lateral portions of border slightly downturned in anterior view, with densely spaced sculpture of very fine tubercles; doublure expressed as very short anterior face of border, just a rim ventrally; anterior border furrow short and deep, incised, strongly anteriorly bowed, with narrow transverse section anterior to frontal areas; glabella very large, long, very broad, anteriorly expanded, with sagittal length 111.3% (101.8–122.3%) maximum width across mid-length of L3, sagittal length 81.1% (77.0–84.1%) cranidial length, maximum width 38.3% (35.4–42.8%) maximum cranidial width, strongly inflated, with three well-defined lateral lobes, sculpture of small densely spaced tubercles (some specimens more effaced medially), with small, low tubercles on lobes; all lateral lobes narrow (tr.), L1 smallest, short and slightly more anteriorly directed than L2 and L3; L2 and L3 similar in appearance, L3 a little longer and bigger, both lobes approximately transversely oriented, LF semilunate, broad and anteriorly convex; glabellar furrows all fairly short, expanded exsagittally toward axial furrows, deep, except innermost ends abruptly shallowed, S3 always shallower than S1 and S2, S1 gently posteromedially directed, S2 transverse, S3 gently anteromedially directed; SO moderately long, lengthened in all specimens behind mid-width of L1, deep (shallower when longer), course subtransverse; LO fairly long, 14.2% (11.9–16.6%) sagittal cranidial length, broad, with maximum width 32.7% (30.6–35.0%) cranidial width, independently well inflated, mostly effaced (in large specimens), with a few small tubercles near corners; doublure broad, long, pinched out laterally, effaced; axial furrows very deep except over LO, a little wider at intersections with other cranidial furrows, meet all but palpebral furrows, course gently anteriorly divergent, more laterally bowed from L3 anteriorly; frontal areas subequant, short and narrow, subvertical, effaced but for a few scattered fine tubercles; palpebral lobes a little independently inflated, long, about 1/3 sagittal cranidial length, downturned anteriorly and posteriorly, held horizontally at about half-length, lobes narrow, a little wider posteriorly, inner margin straight except curved around posterior end, lateral margin unevenly arcuate, with strongest curvature posteriorly, lobes generally semi-elliptical to half-teardrop shaped, with short, posteriorly tapered postaxial ridge, and with sculpture of fine granules to effaced; palpebral furrows narrow (exsag.), deeply incised except at anteriormost edge of palpebral lobe, course roughly J-shaped, anteromedially angled along main part of palpebral lobe, hooked around posterior end and postocular ridge; interocular fixigenae long, subtriangular, narrowed anteriorly, roughly horizontal at palpebral lobes, very strongly downturned anteriorly, with sculpture of densely spaced small tubercles overlying scattered small pits; posterior fixigenae wide and relatively short, subrectangular, very strongly ventrolaterally sloped from fulcrum, about 50° below horizontal, with rounded anterior margin from cut of facial suture, sculpture like that of interocular fixigenae; posterior border furrow deep, fairly short, course gently anterolaterally directed, with exsagittal ends a little anteromedially curved; posterior border well inflated, wide, adaxial ends short, border rapidly expanded to maximum length at genal angle, then tapered slightly toward cut of facial suture, effaced except for rim of fine tubercles on anterior edge extending

into posterior border furrow; doublure forming a rim ventrally adaxial to fulcral angle, turned out posteriorly, rapidly expanded abaxial to fulcral angle to maximum length just adaxial to genal angle, cut by facial suture at genal angle, effaced.

Hypostomal measurements were made on the specimens of Plates 36, 41. Hypostome ovoid and oblong, with width across shoulders (approximately equal to width across anterior wings) 90.1% (84.1–96.6%) sagittal length, densely covered in very fine tubercles except for posterior lobe of middle body, sculpture a little coarser and slightly sparser on anterior lobe of middle body than on borders; anterior border vanishingly short medially, also mostly overhung by middle body, drawn out laterally into anterior wings; wings small, triangular, about as wide as long, directed posterolaterally, with very deep wing process pit just inside outer edge; middle body relatively narrow, elongate, width across anterior tips of posterior lobe (even with shoulders) 68.9% (62.1–74.3%) sagittal length of middle body, strongly ventrally vaulted (sag., tr.), decreasing over posterior lobe to posterior border furrow, body poorly differentiated into anterior and posterior lobes on most specimens by almost totally effaced middle body furrow; middle body furrow only apparent anterolaterally where it meets lateral border furrow as notch in margin of middle body, particularly in large specimens (Pl. 36), otherwise represented by effacement of sculpture; anterior lobe makes up most of body, oblong, subtriangularly posteriorly tapered, sculpture of coarse densely spaced granules; posterior lobe U- or V-shaped, short and curved around anterior lobe, lateral arms pinched out at lateral border furrow, effaced; lateral border furrow deep, narrow, overlies middle body furrow anteriorly, then slightly wider toward confluence with posterior border furrow; lateral border narrow anteriorly, rapidly widens toward shoulder, then gradually narrows a little toward posterior border, gently ventrolaterally downturned at edges, rim slightly inflated, very finely tuberculate like anterior lobe of middle body, but tubercles slightly smaller and more densely distributed; posterior border furrow moderately shallow and a little longer than width of lateral border furrows, gently posteriorly arcuate; posterior border similar to lateral border; doublure of a short and narrow rim around posterolateral margin (likely longer, but not well preserved), with long, shallow lateral notch between wings and shoulder, effaced.

Librigenal measurements were made on the large, intact specimens of Plate 41, and on Plate 36, figure 23. Librigena wedge-shaped, with width under midpoint of eye 42.4% (38.8–47.5%) length along lateral border, gently laterally bowed and convex; eye fairly large, strongly inflated, domed with subrounded outline; eye adjacent to (and poorly differentiated from) elevated smooth area on field; anterior branch of facial suture long, section along anterior projection of lateral border slightly longer than portion along field, sections form angle of about 110–120° at lateral border furrow, with posterior section subvertical along field and anterior section gently anteroventrally sloped along projection; posterior branch of facial suture long, very steeply sloped along field, a little less so than anterior branch, then gently posteroventrally curved along short posterior projection of border, cuts border so that small sliver of underside of doublure is exposed; librigenal field subtrapezoidal, moderately wide and long, wider posteriorly, with width under midpoint of eye 42.3% (39.3–57.3%) length along lateral border furrow, with sculpture of very fine granules overlain by scattered small tubercles, and with small pits concentrated along posterior part of field, effaced except for granules opposite lateral border furrow; lateral border furrow deep and moderately wide, slightly shallower and wider anteriorly (e.g., Pl. 41, figs 5, 14); lateral border wide, narrower anteriorly toward long, anteroventrally directed anterior projection, narrower and tapered posteriorly on short, bluntly terminated posterior projection, border well inflated, less so posteriorly and slightly compressed to form sharper edge ventrolaterally (Pl. 41, fig. 4), with dense sculpture of small tubercles, tubercles finer and more densely spaced ventrolaterally; doublure broad, reaches almost to lateral border furrow, tapered to sharp point posteriorly, smooth but for a fine ridge or two along exsagittal margin (Pl. 36, fig. 32), turned ventrally along anterior projection.

Thoracic measurements were made on the specimens of Plate 42. Thoracic segments highly vaulted in axis and pleurae, short, moderately wide to wide (narrower segments, e.g., Pl. 42, figs 1, 3, 22 positioned more posteriorly in thorax), with moderately wide axis, axial width 52.4% (50.0–54.8%) width across anterior pleural band, maximum segmental width occurs across or near tips of pleural spines; segments with dense sculpture of fine granules all over, overlain by small tubercles; articulating half ring semilunate (Pl. 42, fig. 4), longer medially and gradually laterally tapered, relatively long, with densely spaced rim of very fine tubercles or coarse granules on posterior margin (shown well on Pl. 42, fig. 25); articulating furrow deep, slightly shallower medially, deepest anterolaterally, long, with very shallowly U-shaped course, broad median section very slightly anteriorly bowed, lateral sections more strongly anterolaterally directed; axial ring moderately independently inflated, short and

relatively wide, very shallowly U-shaped, with broad, roughly transverse median section and shorter anterolaterally curved lateral sections, with posteriorly convex (e.g., Pl. 42, figs 1, 3, 22) or slightly medially anteriorly bowed (e.g., Pl. 42, figs 4, 17, 19) posterior margin, with line of small tubercles on anterior rim (effaced medially and only present on lateral sections of some specimens, e.g., Pl. 42, figs 17, 19), and with 3–4 larger tubercles on posterolateral ends of some specimens (Pl. 42, figs 2, 14); doublure of similar shape and size as articulating half ring, semilunate, pinched out laterally, effaced, anterior edge reaches posterior edge of articulating furrow; axial furrows moderately wide, deep, subparallel along posterior pleural band, with wider anterior and posterior ends due to curvature of adaxial end of pleural band, course deflected anteromedially around lateral edge of axial ring, then subparallel along very short edges of articulating half ring; anterior pleural band very short, a little longer exsagittally, slightly inflated, more inflated exsagittally to form articulating structure set off posteriorly by extremely short furrow, band equal in width to posterior band (excluding pleural spine), horizontal, except exsagittal tips curled under into very narrow doublure, effaced or very finely granulose; pleural furrow short, deep, incised, transverse to gently posterolaterally directed; posterior pleural band long, strongly inflated, fairly narrow, sculpture densely granulose, with transverse line of many small tubercles on anterior edge; pleural spine long, very strongly downturned, thick, tip tapered to blunt point, with sculpture of dense granules, and small tubercles continuing along anterior edge from pleural band, tubercles bigger ventrally, also with tiny tubercles along anterior edge of spine tip, and with short, more effaced articulating facet on exsagittal anterior edge defined posteriorly by very short furrow; doublure extremely narrow, only a rim curled under end of inner pleurae, best visible in anterior and posterior views.

Pygidial measurements were made on the most complete specimens of Plates 37, 43. Pygidium of four segments and terminal piece with spinose pleurae, strongly vaulted (sag., tr.), mostly from convexity of axis and curvature of pleural spines, semi-elliptical in outline, with sagittal length excluding articulating half ring and pleural spines 57.2% (53.0–63.8%) maximum width across anterior pleural band of first segment, and with sculpture of small tubercles concentrated near edges of furrows; articulating half ring short and wide, semilunate (but anterior curvature often not well preserved), effaced but for granules along posterior edge; articulating furrow deep, slightly shallower medially, long medially and tapered toward axial furrows, granulose; axis very broad anteriorly, with maximum width 52.3% (50.1–54.6%) pygidial width across anterior pleural band of first segment, strongly posteriorly tapered, with width of fourth ring 50.0% (46.1–57.7%) width of first ring, long, equal in length to main body of pygidium, very strongly vaulted anteriorly, decreasingly convex posteriorly to flat terminal piece; axial rings each strongly independently inflated, short, progressively shorter posteriorly, relatively wide, rings effaced in some specimens (Pl. 37, figs 1, 3), or with closely spaced tubercles along anterior margin or anterior half on others (Pl. 43, figs 1, 4); inter-ring furrows deep, short in most specimens, long and shallower medially in large specimens, transverse; terminal piece triangular, short and narrow, moderately inflated, with very small tubercles at least along anterior margin; axial furrows strongly anteriorly divergent, slightly laterally bowed, deep, moderately narrow, narrower along terminal piece and shallower, almost effaced posteriorly in some specimens (Pl. 37, figs 3, 14), furrows meet (or almost meet) at tip of terminal piece; anterior pleural band present only on first segment, wide, very short, slightly expanded exsagittally, moderately inflated, with extremely short furrow near anterior edge of outer pleurae for articulation; pleural furrow also only present on first segment, short, deep, incised, gently posterolaterally directed; posterior pleural bands strongly independently inflated, long and wide, bands increasingly posteriorly directed, with fourth pair subparallel to sagittal axis, mostly effaced, with a few small tubercles along margins and adjacent to axial furrows; pleural spines very long (oblique), strongly inflated, posterolaterally to posteriorly directed like pleurae, widely splayed, very strongly ventrolaterally curved, tapered along ventral margin from about half-length to blunt point, with dense sculpture of small tubercles (larger than main body sculpture) on posterior face, slightly smaller tubercles on lateral faces and at tips, inner face granulose or effaced; interpleural furrows long and deep, posterior furrows shorter, directed like pleurae; border expressed ventrally just inside base of pleural spines, narrow, moderately inflated; doublure held subvertically, but fully visible only in anterior view, slightly peaked medially, gently tapered anterolaterally, effaced.

Ontogeny. The cranium (cf. Pl. 34, fig. 1, Pl. 38, fig. 1, Pl. 40, figs 3, 15, 18) overall becomes broader (excluding genal spines), more elongate, and more strongly vaulted (sag., tr.), and the sculpture changes from fairly closely spaced medium-sized tubercles to either almost totally effaced (specimens from H 208.2 m) or to very densely spaced small tubercles (specimens from H 222.1 m); the anterior border shortens and becomes overhung medially by the glabella; the glabella widens posteriorly more than it expands anteriorly, creating a bulbous but less

posteriorly tapered outline, it inflates to become more vaulted (sag., tr.), the lateral furrows lengthen and deepen, and the lobes become more strongly independently inflated; SO lengthens and deepens; LO widens, and the median node and the tubercles on the posterior margin become more effaced; the palpebral lobes become effaced and move further posteromedially and lengthen; the interocular fixigenae broaden; the posterior fixigenae become more strongly downturned; the posterior border furrow lengthens; the posterior border lengthens at the genal angle; and the genal spine becomes reduced to a short spine (H 222.1 m) or to a nub (H 208.2 m).

The hypostome (cf. Pl. 36, figs 2, 26) becomes narrower and more elongate overall; the middle body inflates further, the anterior lobe also elongates and narrows, and the sculpture spreads posteriorly; the middle body furrow deepens and widens, but does not extend as far medially, giving the outline of the middle body a less hourglass-like shape in large specimens; the lateral border furrows widen and deepen; the posterior border furrow lengthens and shallows considerably; and the lateral border develops less prominent shoulders by widening more anterior and posterior to them.

Librigenae (cf. Pl. 41, figs 1, 15) are fairly close in size, but it is apparent that they become broader overall; the librigenal field broadens, particularly anteriorly, and develops pits more anteriorly while the tuberculate sculpture becomes finer and less densely distributed; the lateral border furrow broadens considerably and deepens; and the lateral border sculpture becomes larger. Thoracic segments are either too close in size, or not comparable in thoracic position (Pl. 42, fig. 3), and therefore cannot be evaluated for ontogenetic change.

The pygidium (cf. Pl. 37, figs 1, 27, Pl. 43, fig. 1) becomes narrower and more elongate overall; less strongly vaulted (sag., tr.); and effaced except for tubercles near edges of furrows and on pleural spines, although specimens from H 222.1 m usually also retain tubercles along the anterior portion of the axial rings; the axis becomes more elongate and less strongly posteriorly tapered; the axial rings become more strongly individually inflated; the axial furrows widen and deepen; the articulating and inter-ring furrows and the furrows between pleurae lengthen and shallow (particularly median sections of the articulating and inter-ring furrows); the pleural spines lengthen and splay further apart, and the tips become slightly more pointed.

Discussion. *Deltapliomera humphriesi* is compared to *D.inglei*, *D.heimbergi*, and *D.eppersoni* in the differential descriptions of those taxa.

Specimens of *D. humphriesi* from H 208.2 m differ slightly from those from H 222.1 m in that comparably large specimens are more effaced (see especially pl. 34, figs 1, 8, 14). It is difficult to know whether this effacement is taphonomic or biological, but we have observed a similar situation in common sclerites of species of *Dimeropygiella* Ross, 1951, from H 208.2 m, which suggests post-mortem abrasion may have acted on this sample. Given that some sclerites from H 208.2 are not effaced (e.g., Pl. 34, fig. 11) and occasional specimens from H 222.1 m are at least partially effaced (e.g., Pl. 38, fig. 10) and that the samples do not otherwise seem to differ morphologically, we are confident that they represent the same species.

***Deltapliomera* n. sp. A**

Plate 21, figs 22–26

2009 *Ibexaspis* sp. nov. 5 (*partim*); Adrain *et al.*, p. 569, fig. 16L (only; fig. 16P = *Deltapliomera heimbergi* n. sp.).

Material. Assigned specimen SUI 115308 from Section H 172.5T m, Fillmore Formation (Floian; Tulean; *Paniaspis severiensis* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

Discussion. A single cranidium differs from the co-occurring species *D. heimbergi* (cf. Pl. 21, fig. 22 with Pl. 23, fig. 1) by being broader, less strongly vaulted (tr., sag.) both axially and from less strongly downturned fixigenae; in possessing considerably finer, denser tuberculate sculpture; narrower interocular fixigenae; narrower palpebral lobes; a more parallel-sided, not forwardly-expanding, glabella that is broader at the base and has a larger, more transversely oriented L1, and a slightly smaller L3 and shallower S3; slightly shorter SO; longer, wider, more effaced LO; longer (especially adaxially) and a less tuberculate posterior border.

Deltapliomera heimbergi occurs separately from *Deltapliomera* n. sp. A at H 166.2 m and at H 173.2 m.

Tuleaspis n. gen.

Type species. *Tuleaspis jeneki* n. sp., from the Fillmore Formation (Tulean, low *Protopliomerella contracta* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

Other species. *Tuleaspis* n. sp. A, Fillmore Formation, western Utah and Garden City Formation, southeastern Idaho (both Tulean; low *Psalikilopsis cuspidicauda* Zone); *Tuleaspis?* n. sp. B, Fillmore Formation (Tulean; low *Protopliomerella contracta* Zone), western Utah.

Etymology. From the Tule Valley, and Greek *aspis*, shield. Gender is feminine.

Diagnosis. Diagnostic characters are not present in the cladistic analysis, because they would be represented as autapomorphies of *T. jeneki*. Members of *Tuleaspis* possess a long, broad, low-vaulted (tr., sag.) glabella with straight sides and a broadly, evenly bowed anterior margin; palpebral lobes lacking palpebro-ocular ridge and situated with broadest part opposite L2; hypostome with long posterior border of even length (not tapered and pointed medially and without marginal spines); and coarse tuberculate sculpture, particularly along axial furrows and on pygidium, with some small spiny tubercles at corners of LO and inner margin of posterior border.

Discussion. Other characteristics which set *Tuleaspis* apart from the other members of the *Ibexaspis* group are mainly plesiomorphic, and shared with species of *Hintzeia* or plesiomorphic species of *Paniaspis*: large, evenly shaped glabellar lobes; a broad, subtriangular librigenal field; a pygidium with a wide axis and posteriorly swept pleurae.

Tuleaspis jeneki n. sp.

Plates 44–46

1973 *Protopliomerops* sp. I; Demeter, p. 53, pl. 3, figs 3, 8.

2009 *Ibexaspis* sp. nov. 1; Adrain *et al.*, p. 563, fig. 13Y.

Material. Holotype, cranium, SUI 129505 (Pl. 44, figs 1, 4, 5, 7, 10), and assigned specimens SUI 115250, 129506–129532, from Section G 210.2, Fillmore Formation (Tulean, low *Protopliomerella contracta* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. The species has also been sampled from the high *P. contracta* Zone at HC6 224.5 m, Garden City Formation, west side of Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho, USA.

Etymology. After Shane Jenek.

Diagnosis. Cranium with long glabella compared to congeners, parallel-sided, and not highly convex (tr.), with wide lateral lobes; L1 only a little smaller in area than L2 and L3; genal spine very small and nub-like. Hypostome with longer posterior border than width of lateral border at shoulders (border not tapered posteriorly as in other members of *Ibexaspis*-group). Pygidium with five axial rings and four pairs of pleurae; narrow and deep axial furrow; short and deep inter-ring furrows; short, very deep interpleural furrows; and pleural spines closely spaced and backswept, not splayed.

Description. Cranium strongly vaulted (sag., tr.), sub-semicircular in outline, with sagittal length 104.1% (97.9–107.1%) width across γ , 75.1% (71.3–77.0%) width across δ , 70.7% (65.6–74.5%) width across ϵ , and 50.0% (44.9–52.9%) maximum width across genal angles; anterior border lightly inflated, short, with length 4.4% (4.0–5.2%) sagittal cranial length, broad, gently anteriorly bowed, densely covered in small tubercles; doublure only a rim ventrally, mainly expressed as anterior face of border; anterior border furrow very short, deep, incised, with small (narrow) lateral sections intersecting S3 and main part of furrow following arc of border; palpebral lobe situated with posterior margin slightly anterior from S1 and anterior portion of palpebral lobe level with mid-L3, with less distinct (better expressed in small specimens, e.g., Pl. 45, figs 22, 23), lobe elongate, fairly narrow, with broadest curvature approximately level with S2, sharply dorsolaterally elevated (anterior view), with sculpture of small tubercles and some effacement posteriorly and along lateral rim particularly in larger specimens, and with very narrow post-ocular ridge tapering down to fulcrum of fixigena; palpebral furrow narrow, very deep, anteromedially directed, sinuous, with very slight lateral flexure along main body of lobe, then curled sharply around posterior edge, not well-defined anteriorly; interocular fixigena subtriangular, fairly narrow, anteriorly tapered to a point at mid-L3, flat to slightly ventrolaterally sloped, densely tuberculate, with underlying granules and slightly longer tubercles opposite axial furrows; posterior fixigena short and very wide, with anteriorly curved

anterolateral margin, very steeply downturned, with sculpture like that of interocular fixigena, and with some small pits on lateral portions and smaller tubercles near posterior border furrow; posterior border furrow short, deep, roughly transverse in course until anteriorly curved at genal angle; posterior border shortest adaxially, length approximately doubles to maximum at genal angle, moderately inflated, increasing toward genal angle and then slightly deflated again, finely granulose, with slightly larger granules lining border furrow and anterior from nub-like small genal spine, with small cluster of spiny tubercles near axial furrow and scattered tubercles roughly following posterior margin; doublure only a rim until abruptly widened at genal angle, then anteriorly expanded until cut off by facial suture, smooth; axial furrows moderately narrow, very deep, roughly parallel, only very slightly laterally bowed, intersect all but palpebro-ocular furrows; LO broad, long medially, with sagittal length 14.7% (12.7–16.1%) sagittal cranial length, shorter at exsagittal ends (mainly in larger specimens), moderately inflated, finely granulose, with small cluster of spinose tubercles on lateral margin extending into axial furrows, 4–7 scattered small tubercles along posterior edge, and small median node at mid-length (effaced in larger specimens); doublure broad, long, pinched out laterally, elliptical; SO deep, very deep laterally, long medially, then shorter and overhung by posterior edge of L1, with broadly W-shaped course, middle portion anteriorly bowed in most specimens and lateral portions posteriorly bowed; glabella long and broad, parallel-sided with moderately anteriorly bowed anterior margin, posterior margin more weakly anteriorly bowed (especially on smaller specimens), subrectangular, with length excluding LO 107.2% (99.6–114.5%) maximum width across L2, mildly vaulted (sag., tr.), with distinct, independently inflated lateral lobes, and with dense sculpture of small tubercles; L2 and L3 very similar in shape and size, subrectangular, broader than long, occupy about 1/3 cranial width, L2 slightly longer than L3 in most specimens, lobes nearly transverse to somewhat anterolaterally directed; L1 a little smaller, shorter and narrower, more ellipsoidal, more anterolaterally directed, with a few elongate tubercles extending into SO from posterior edge; LF wedge-shaped, long medially and short laterally; S1–S3 short (sag.), deep, incised, S1 a little longer and shallower at sagittal end, all furrows gently anterolaterally directed.

Rostral plate and thorax unknown.

Hypostome with sagittal length 118.4% (113.7–123.2%) maximum width (excluding anterior wings) across posterior lobe of middle body; hypostomal suture broad, strongly anteriorly bowed, anterolaterally redirected along anterior wings; anterior border extremely short, just a rim along middle body, expanded laterally into small, posterolaterally placed, strongly upturned anterior wings; anterior border furrow short, incised, overhung medially by anterior margin of middle body in some specimens; middle body elliptical, moderately ventrally inflated anteriorly, much less inflated over posterior lobe, with large, ovoid, posteriorly tapered anterior lobe and short, U-shaped posterior lobe; anterior lobe densely covered in small tubercles except near posterior margin, posterior lobe effaced medially, but with small tubercles on lateral arms; middle body furrow mostly effaced medially, visible as indentation in lateral view, narrow and incised anterolaterally (with overlap of lateral border furrows); lateral border furrows strongly posteromedially directed along anterior lobe of middle body, wider, deeper, and less medially angled along posterior lobe; lateral border narrowest at lateral notch, abruptly widened just past notch and very slightly expanded posteriorly, moderately downturned, densely covered in small tubercles dorsally, with very fine granules on rim; posterior border furrow strongly posteriorly bowed, deep but slightly shallower than lateral furrows; posterior border long, with sculpture like that of lateral border; doublure incompletely preserved, but about half length/width of borders, smooth, sloped, with long, shallow lateral notch.

Librigena with width at midlength of eye 40.8% (37.9–43.5%) length of lateral border; ocular surface almost entirely unknown, with only raised adaxial margin of eye area preserved, with very narrow effaced patch extending onto anterior part of field (Pl. 46, fig. 4); anterior branch of facial suture short and very steep along field, longer with nearly flat slope along anterior projection of lateral border, sections form approximately 120° angle at anterior terminus of lateral border furrow; posterior branch of facial suture long and sloped along field, with slope decreasing after mid-width of field, short and nearly flat along posterior projection of border, with sections forming approximately 130° angle; librigenal field trapezoidal, widest under posterior end of eye, narrower anteriorly and posteriorly, with width at mid-length of eye 38.2% (35.4–40.3%) length along lateral border furrow, shallowly ventrolaterally sloped, somewhat laterally convex, with dense sculpture of mixed very small and tiny tubercles, and with small pits concentrated abaxially; lateral border furrow narrow, deeply incised, gently laterally bowed; lateral border almost as wide as anterior edge of field, narrower along anterior projection, tapered to a blunt point along posterior projection, moderately well inflated anteriorly, gradually deflated posteriorly, with very dense sculpture of very small tubercles, laterally bowed, with lateral margin more convex than border furrow, and with anterior

projection anteroventrally rotated; doublure broad and smooth, discontinued along anterior projection, tapered to a point posteriorly, with triangular section of inner face visible externally (Pl. 46, fig. 1).

Pygidium with sagittal length from articulating furrow 67.7% width across anterior pleural band (ratio may be slightly distorted due to poor preservation); articulating half ring broad, short, with line of very fine granules on posterior edge; articulating furrow moderately long, very deep; axis composed of five rings and terminal piece, broad and well vaulted anteriorly, with width across first ring 55.3% pygidial width across anterior pleural band, strongly posteriorly tapered and flattened, with width across fifth ring 46.5% width across first ring; axial rings moderately long, fifth ring only slightly shorter than first ring, each ring independently well inflated, widest at mid-length, with lateral margins rounded around dense sculpture of medium tubercles, with mix of smaller tubercles and granules dorsally and lining anterior and posterior margins; inter-ring furrows moderately long (more posterior furrows shorter), very deep; terminal piece small, triangular, less inflated than rings, with sculpture of small tubercles; axial furrows narrow (except at intersections with inter-ring and interpleural furrows), shallower along terminal piece, then merged with fourth interpleural furrow as single median furrow behind terminal piece; anterior pleural band present only on first segment, very short, effaced, with small anteriorly curved prong at tip; interpleural furrow very short and deep, slightly overhung by first posterior pleural band in dorsal view; four posterior pleural bands long (measured obliquely), well inflated, each more posteromedially directed, with second bands essentially parallel, with sculpture of medium tubercles and smaller tubercles at margins on first half of length (first band more sparsely sculptured), then effaced, then with collection of medium tubercles near tips of (posterior view) moderately long, blunt spines; posterior border expressed ventrally as V-shaped, raised posterolateral rim with fine terrace lines; doublure seen only in anterior view, not well preserved, but appears longest (tallest) medially, anterolaterally tapered, smooth.

Ontogeny. Ontogenetic differences in the known cranidia of *T. jeneki* are not dramatic, but comparison of the largest (Pl. 44, fig. 1) and smallest (Pl. 45, fig. 23) specimens show that they become broader overall; fixigenae develop pitting, and the tubercles along the axial furrows elongate into the furrows; the glabella broadens and deflates slightly while the lateral lobes inflate slightly; glabellar furrows lengthen (sag.) and shallow slightly at adaxial ends; glabellar sculpture becomes slightly finer; SO lengthens and shallows, particularly medially; LO changes mainly in sculpture: the median node becomes effaced, the tubercles on the posterior edge become finer, and the tubercles on the lateral edges grow into the axial furrows; tubercles on the posterior border become effaced, and the genal spine decreases to a nub.

The known hypostomes and librigenae are too close in size for meaningful ontogenetic comparison, except to note that the librigenal sculpture becomes slightly less dense and finer, and tubercles on the anterior lobe of the middle body of the hypostome decrease in size and number so that only fine tubercles remain on the anterior part of the lobe (cf. Pl. 46 fig. 10 with other specimens). The slight median indentation in the posterior margin of the hypostomal posterior border may also be an ontogenetic development, or it may be unique to the specimen of Pl. 46, fig. 10.

Notable ontogenetic changes in the pygidia of *T. jeneki* include finer tuberculation overall in the larger specimen, but with the addition of intercalated finer tubercles increasing the density of sculpture; and the terminal piece becomes much larger. Further comparison is hindered by the small sample size and incomplete preservation of the specimens.

Discussion. *Tuleaspis jeneki* is compared with *Tuleaspis* n. sp. A and *Tuleaspis?* n. sp. B in the discussions of those taxa.

***Tuleaspis* n. sp. A**

Plate 42, figs 35–41

Material. Assigned specimen SUI 129753 from Section G 155.6 m, Fillmore Formation, southern Confusion Range, Ibex area, Millard County, western Utah, USA, and SUI 129754 from Section HC5 203.7–204.2T m, Garden City Formation, east side of Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho, USA. Both are from the Tulean (low *Psalikilopsis cuspidicauda* Zone).

Discussion. One cranidium and one pygidium are assigned to *Tuleaspis* n. sp. A. Although the pygidium is from Section G in Utah and the cranidium is from Section HC5 in Idaho, we feel justified that they represent a

single species because each sclerite clearly represents an *Ibexaspis* group pliomereid, and the only known co-occurring pliomereids are well-known species of *Paniaspis* McAdams and Adrain, 2011b, and *Protopliomerella* Ross, 1951 (revised by McAdams and Adrain [2011c]). Additionally, both horizons are from the same biostratigraphic zone, and share many species in common. The pygidium overall is rather different to that of *T. jeneki*, but *Tuleaspis* n. sp. A is also a considerably older taxon, and the additional segment and terminal piece of *T. jeneki* likely represent a derived condition. The sculpture of the pygidium is coarser and more widely spaced than that of the cranidium, but this is also true of *T. jeneki*, and therefore does not indicate that the sclerites might represent different species.

The cranidium of *Tuleaspis* n. sp. A differs from those of *T. jeneki* (cf. Pl. 42, fig. 40, Pl. 44, fig. 3) in being much more strongly vaulted (sag., particularly tr.) and narrower relative to sagittal length; with sculpture of slightly larger tubercles, evenly distributed on the glabella rather than concentrated on the lateral lobes; a slightly longer, more inflated, and more strongly anteriorly bowed anterior border; slightly shorter, wider, and considerably more inflated glabella with a smaller L1 relative to the other lobes; longer SO; LO with a more prominent median tubercle and fewer tubercles at the lateral corners; wider axial furrows; shorter, slightly wider, more anterolaterally positioned palpebral lobes; posterior portion of the palpebro-ocular suture describing a much less acute angle opposite the posterior fixigenae; longer, narrower posterior fixigenae; and a posterior border with more tubercles on the posterior margin.

The pygidium of *Tuleaspis* n. sp. A is quite different from that of *T. jeneki* (cf. Pl. 42, fig. 41, Pl. 46, figs 24, 29) because it possesses four segments and lacks a terminal piece, compared to five segments and a large terminal piece; it is relatively shorter, wider, and less posteriorly tapered in outline, as well as slightly more vaulted (sag., particularly tr.); the axis is shorter and broader, with more strongly inflated and medially shortened axial rings, and longer articulating and inter-ring furrows; the axial furrows are wider and shallower; the pleural spines are narrower and more closely spaced; and the sculpture is generally smaller, more sparsely distributed tubercles, with effaced areas along the midlength of the first axial ring and on the pleural spines.

Tuleaspis n. sp. A is compared to *Tuleaspis?* n. sp. B in the discussion of the latter species.

***Tuleaspis?* n. sp. B**

Plate 54, figs 21–24.

- 1973 *Protoliomerops quattuor* Hintze; Demeter, p. 53, pl. 3, fig. 1 [only; pl. 3, fig. 6 =*Paniaspis quattuor* (Hintze)].
2009 *Ibexaspis* sp. nov. A; Adrain *et al.*, p. 563, fig. 13Z.
2011b *Ibexaspis* n. sp.; McAdams and Adrain, p. 44.

Material. Assigned specimen SUI 115251, from Section G 210.2 m, Fillmore Formation (Tulean; low *Protopliomerella contracta* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

Discussion. *Tuleaspis?* n. sp. B is represented by a single cranidium that differs from the co-occurring species *T. jeneki* (cf. Pl. 44, fig. 24 with Pl. 54, fig. 22) in possessing more densely spaced tuberculate sculpture; a wider, slightly more inflated anterior border; shorter, narrower, more strongly vaulted (sag., especially tr.) glabella with smaller, narrower lateral lobes (particularly L1) and shallower furrows; a tuberculate LO without an obvious median node; shorter, wider palpebral lobes; wider interocular fixigenae (especially anteriorly), longer posterior fixigenae with a wider inner portion and narrower outer portion; and a tuberculate (rather than mostly effaced) posterior border with small genal spines.

Compared to that of *Tuleaspis* n. sp. A, the cranidium of *Tuleaspis?* n. sp. B is broader relative to its length, and less strongly vaulted (sag., tr.); with a less strongly anteriorly bowed anterior border; narrower, more strongly inflated glabella with shorter and shallower lateral furrows; shorter SO; densely tuberculate LO; larger (wider and longer) palpebral lobes; and posterior border lacking obvious isolated tubercles along posterior portion. Some of these differences, e.g., furrow length and LO sculpture, may be due to the larger size of the *Tuleaspis* n. sp. A cranidium, but this cannot be determined without more specimens of both species.

***Millardaspis* n. gen.**

Type species. *Millardaspis milsteadi* n. sp., from the Garden City Formation (Floian; Tulean; *Heckethornia hyndae* Zone), Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho, USA.

Other species. *Millardaspis knoxi* n. sp., Fillmore Formation (Tulean; *Panisaspis sevierensis* Zone), western Utah.

Etymology. From Millard County, and Greek *aspis*, shield. Gender is feminine.

Diagnosis. Cranidium strongly (sag.) and moderately (tr.) vaulted, with low glabellar inflation; axial furrows relatively wide and shallow; palpebral lobe broad; dorsal tuberculate sculpture dense all over exoskeleton (pygidia partially effaced in large specimens), granulose to tuberculate; pygidial pleural ribs laterally compressed and blade-like; pygidial pleural spines with strong ventral curvature.

Discussion. *Millardaspis* is proposed for a pair of species with highly distinctive pygidia which feature laterally compressed pygidial pleural ribs and spines that are strongly down-curved. This results in a plan view shape completely unlike any other member of the overall clade, all of which have rounded ribs and spines which splay laterally in plan view.

***Millardaspis milsteadi* n. sp.**

Plates 47–53, Plate 54, figs 1–20

? 1973 *Protopliomerops* sp. II; Demeter, p. 54, pl. 3, fig. 4.
2009 *Ibexaspis* sp. nov. 2; Adrain *et al.*, p. 567, fig. 14K.

Material. Holotype, cranidium, SUI 135528 (Pl. 47, figs 1, 3, 4, 6, 8), and assigned specimens SUI 135529–135563, from Section HC6 226.5 m, Garden City Formation (Tulean; *Heckethornia hyndae* Zone), west side of Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho, USA; assigned specimens SUI 115262, 129533–129543, from Section YH 128.9 m, Yellow Hill Limestone (Tulean; *Heckethornia hyndae* Zone), Yellow Hill, near Pioche, Lincoln County, Nevada, USA.

Etymology. After Glenn Milstead.

Diagnosis. Prominent punctate tubercles on cranidium, librigenae, and thorax (of articulated specimen); punctae without tubercles on thoracic and pygidial pleural spines; glabella very short; wide and somewhat shallow axial furrows in large specimens; short, roughly triangular-based genal spine extending almost laterally from genal angle; librigenal lateral border furrow approximately doubling in width from posterior to anterior ends; lateral border wide and strongly inflated; pygidium long, with strongly independently inflated axial rings separated by long inter-ring furrows; tall, spinose small tubercles in about 2 transverse rows on pygidial axial rings (effaced in larger specimens), with cluster of large tubercles at proximal end of pleurae, but effaced spines; large and well-expressed terminal piece.

Description. Measurements were made on the large and well-preserved specimens of Plates 47–54 and were doubled from the sagittal midline if necessary due to incomplete preservation. Cranidium moderately vaulted (tr.), more strongly sagittally vaulted, broad and relatively short, sagittal length 99.1% (96.3–103.4%) width across γ , 68.2% (64.9–72.0%) width across δ , 63.5% (59.7–66.7%) width across ϵ , and 47.2% (44.9–49.5%) maximum width across genal angles, with fairly densely spaced sculpture of small tubercles all over dorsal surface; anterior border short, of even length all along course, fairly broad, extends in front of narrow anterior interocular fixigena to edge of palpebro-ocular ridge, broadly anteriorly bowed, well inflated, tubercles a little smaller than on rest of cranidium; doublure turned down and expressed as anterior face, just a rim ventrally; anterior border furrow moderately short, deep, incised, gently anteriorly bowed medially, roughly transverse to weakly posterolaterally directed exsagittally anterior to fixigena; palpebro-ocular ridge poorly expressed on small specimens, ridge effaced on larger specimens, leaving palpebral lobe; lobe located across from nearly S3–mid-L2, narrow anteriorly and expanded posteriorly, irregularly half-teardrop shaped, tapered into very narrow post-ocular ridge, lobes laterally raised above horizontal, strongly anteroventrally sloped, finely tuberculate; palpebral furrow narrow, deep, incised, J-shaped; interocular fixigena broad and held horizontal posteriorly, anteriorly tapered and strongly downturned, subvertical far anteriorly, with sculpture of small pits underlying tubercles, less tuberculate adjacent to axial furrows in large specimens; posterior fixigena short, very wide, portions proximal and distal to fulcrum about

evenly wide, inner half gently anteroventrally sloped, outer part moderately strongly lateroventrally downturned, sculpture like interocular fixigena; glabella subrectangular, sagittal length 102.7% (96.2–108.4%) maximum width, moderately vaulted (sag., tr.), with distinctly independently inflated lateral lobes, glabellar tubercles a little larger medially, with a scattering of larger isolated tubercles present on median portion of specimens from HC6; L1 small, elliptical, anterolaterally angled, sometimes effaced on a few specimens from HC6; L2 and L3 similar in size, subquadrate, but L2 with angled posterior margin and a little more anteriorly angled, L3 more transversely directed; LF short and broad, semilunate; glabellar furrows short and deep, extend to a little less than 1/3 width of glabella, S1 posteromedially angled, S2 and S3 approximately transverse; SO moderately short, deep, incised, slightly longer posterior to adaxial end of L1, very gently anteriorly arched medially, with distal portions deflected around posterior margins of L1; LO moderately short, strongly inflated, with rim of very small tubercles on anterior margin, transverse row of slightly larger tubercles on posterior margin, and scattered small tubercles medially (effaced on some larger specimens); doublure lens-shaped, nearly reaches SO, pinched out laterally, with sculpture of fine transverse ridges; posterior border furrow moderately short, deep, roughly transverse adaxially, anterolaterally curved abaxially; posterior border short adaxially, expanded laterally to about double length at genal angle, tapered to facial suture, well inflated, with small tubercles lining anterior margin, and slightly larger, more widely spaced tubercles on posterior margin, effaced at mid-length, and with very short, broad-based spine; doublure just a rim on inner fixigena, turned out posteriorly to articulate with thorax, and with a very short, shallow transverse furrow, abruptly expanded near genal angle, then cut by facial suture anteriorly in small arc.

Hypostome elongate and relatively narrow, with sagittal length 107.8% (measured on Pl. 54.4) maximum width across anterior wings, moderately strongly ventrally convex (sag., tr.); anterior border extremely short medially, expanded laterally toward small, triangular, posterolaterally set anterior wings with small, deep wing process pits; anterior border furrow also extremely short, incised medially, poorly expressed laterally behind raised rim of border at anterior edge of wings; middle body long, posteriorly tapered, long (sag.) densely tuberculate (Pl. 50.2) anterior lobe, with short (sag.) more effaced posterior lobe; middle body furrow poorly expressed, shallow; lateral border furrows narrow and somewhat shallow; lateral border very narrow anteriorly, expanded to maximum width a little posterior to shoulders, then tapered to posterior border, with densely tuberculate sculpture a little finer than that of anterior lobe; posterior border furrow shallow; posterior border slightly shorter (sag.) than lateral border, gently dorsally bowed (Pl. 54, fig. 8) medially; doublure smooth, reaches border furrows, with depressed lateral notch.

Rostral plate unknown.

Librigena roughly wedge-shaped, with width under midpoint of eye 34.1% (31.8–37.6%) length along lateral border; anterior branch of facial suture very long, very steep, subvertical and slightly anteriorly bowed along field, then approximately flat along anterior projection of border, slightly downturned near tip of projection; posterior branch of facial suture shorter, steeply sloped and bowed along field, less steeply sloped exsagittally, very gently posterodorsally sloped along posterior projection of border, cut across border exposes triangular sector of doublure; ocular surface ovoid, well vaulted, situated on top of raised smooth platform, platform extends anteriorly and exsagittally in effaced, slightly swollen rounded area on field; librigenal field subtrapezoidal, longer posteriorly, with width under mid-length of eye 31.6% (25.2–38.8%) exsagittal length, gently laterally convex and ventrolaterally declined, with granulose sculpture overlain by dense distribution of small tubercles concentrated posteriorly near eye, with small pits interspersed; lateral border furrow deep, narrow posteriorly and approximately doubling in width anteriorly, finely granulose; lateral border very broad, strongly inflated, with dense sculpture of small tubercles, sculpture slightly less dense, with larger and longer tubercles sagittally near border furrow and posteriorly on projection, denser and finer ventrolaterally, posterior projection of border short and tapered to blunt angle, anterior projection very long, curved anteroventrally; doublure wide, nearly reaches border furrow, rotated outward along anterior projection to form ventral surface, smooth except for fine ridges running along exsagittal margin.

Thorax known from small articulated specimen (Pl. 50, figs 1, 2, 6, 8); each segment with strong independent dorsal inflation; axis of nearly equal width (tr.) from first to sixth segment, then gently tapered (tr.) posteriorly, with strong independent inflation; pleurae also progressively tapered posteriorly, distal portion from fulcrum abaxially flexed ventrally, pleurae terminate in free, bluntly tipped spines, similar to those on pygidium; pleurae largely smooth except for single row of small tubercles along anterior margin between axial furrow and fulcrum, and a patch of small tubercles present along the anterior margin of the distal tips of the pleural spines (see Pl. 50, fig. 8);

axis with more prominent tubercles across median portion of each ring, middle most of these tubercles stand tall (see Pl. 50, fig. 8).

Pygidium of four segments and terminal piece, subrhombic in outline, very strongly vaulted (sag., tr.) mainly due to strongly downwardly deflected pleural spines, but also dorsally inflated axis, widest across tips of first pleural spines, sagittal length excluding articulating half ring 76.2% (70.5–82.1%) width across anterior band of first segment; articulating half ring short (sag.), slightly shorter abaxially, anterior and posterior margins gently anteriorly arched, with line of very fine granules along posterior margin; articulating furrow deep, moderately long (sag., exsag.); axis roughly equal in length to main body of pygidium, very strongly vaulted, strongly posteriorly tapered, width (tr.) of first ring 56.1% (53.2–60.6%) pygidial width across anterior band of first segment, width of fourth ring 51.0% (45.3–55.9%) width of first ring; axial rings with very strong independent inflation, short and relatively broad, posterior rings only a little shorter than first, first ring may be slightly anteriorly bowed with second–fourth rings generally transverse, anterior margins of second–fourth rings wider (tr.) than respective posterior margins so that the rings have a sub trapezoidal outline, sculpture of granules overlain by prominent spinose tubercles roughly organized transversely along anterior portion of each ring, although some specimens possess some extra tubercles intercalated medially; terminal piece small, less inflated than rings, triangular, generally smooth (see Pl. 51, fig. 13), but some specimens possess a cluster of spinose tubercles along anterior margin (see Pl. 54, fig. 11); inter-ring furrows fairly long, with median portion slightly longer, furrows progressively shorter (sag., exsag.) posteriorly, furrow overall deep, slightly shallower medially, transverse; axial furrows moderately wide and deep (shallower on larger specimen), narrower and shallower opposite terminal piece, confluent behind terminal piece, strongly posteriorly convergent; anterior band of first pleurae very short, posterolaterally directed about 30° below horizontal, moderately inflated, smooth, with short furrow at anterior rim for articulation with thorax; pleural bands strongly posterolaterally directed, strongly inflated, extended into strongly downturned spines, first and second pleurae obliquely directed in dorsal view, with third nearly subparallel to sagittal axis and fourth slightly medially convergent in dorsal view, in posterior view fourth pair subparallel to medially bowed (Pl. 52, fig. 5), in lateral view first and second pair obliquely directed (Pl. 52, fig. 7) compared to third and fourth pair which are more strongly downturned, with fourth pair most strongly downturned, cluster of small spinose tubercles on pleurae between axial furrow and fulcrum; pleural spines slightly laterally compressed, subtriangular cross-section, tapered to blunt point, with dense sculpture of very fine tubercles on anterolateral face of distal tips of some specimens; many specimens with punctae on pleural spines; interpleural furrows moderately long, posterolaterally directed like pleurae, deep; pygidial border expressed ventrally as swollen rim at base of spines (Pl. 52, fig. 11), describing broad U-shaped curve with anterolateral tips flared laterally, sculpture of fine, closely spaced, concentric ridges following curvature of margin; doublure strongly upturned and subvertical (anterior view, Pl. 52, fig. 12), longest medially and tapered anterolaterally, smooth except for a few fine transverse ridges at base like those on pygidial border.

Ontogeny. Cranidia become slightly more strongly vaulted, with posterolateral corners becoming more strongly downturned; anterior border furrow lengthens slightly; posterior border furrow and SO lengthen slightly; the axial furrows widen, and become more laterally bowed in course; the glabella becomes wider, shorter, and more rounded (especially anteriorly); S1 broadens (especially adaxially); large prominent tubercles on the glabella and LO become more subdued, with those on LO becoming nearly effaced on some larger specimens.

The known librigenae and the pygidia of *M. milstedi* are too similarly sized to assess ontogenetic changes.

Discussion. Compared to *Millardaspis knoxi*, the cranidium of *M. milstedi* (cf. Pl. 53, fig. 20, Pl. 55, fig. 8) is less vaulted (sag., tr.); the anterior border is longer and broader; the glabella is slightly more elongate, less inflated and does not overhang the anterior border (cf. Pl. 47, figs 4, 5, Pl. 55, fig. 7), has more clearly incised lateral furrows (especially S3), with S1 longer, and generally possesses sculpture of finer tubercles; the axial furrows are slightly narrower and deeper; LO is shorter (sag.) relative to sagittal length of the glabella. The librigenae of *M. milstedi* are slightly longer; the field is slightly narrower, but longer, with a more gradually sloped posterior margin, and with the tubercles concentrated posteromedially; the lateral border furrow is longer overall, especially anteriorly; and the lateral border is slightly narrower, with finer sculpture and lacking fine ridges along ventrolateral margin of border. No hypostomes are known for *Millardaspis knoxi* so a comparison cannot be made. The thoracic segments of *M. milstedi* are less tuberculate with smooth pleurae; the pleurae lack a prominent anteriorly directed process located distally (cf. Pl. 50, fig. 8, Pl. 55, fig. 9). The pygidium of *M. milstedi* is longer and narrower overall; the axis is longer, more strongly posteriorly tapered, with a prominent and elongate terminal

piece, overall less inflated (especially anteriorly); the axial rings are smoother with finer and fewer tubercles; the axial furrows are shallower and broader; the pleurae are more strongly backswept; and the pleural spines are slightly less strongly downturned, longer, effaced but for granules, and also more laterally compressed to a sharper tip.

Millardaspis milsteadi is known from two widely separate geographic occurrences: the well preserved type material from southeastern Idaho (HC6 226.5 m) and the somewhat less well preserved sample from eastern Nevada (YH 128.9 m). There are obvious differences in the range of intrasample variation in each collection which must be addressed. The sample from YH 128.9 m is relatively small, but cranidial tuberculation is on most specimens dense and fairly coarse, in some cases with tubercles on the rear of LO posteriorly overhanging the posterior margin. Cranidia from HC6 226.5 m, comprising a much larger sample, tend to have generally smaller cranidial tubercles, and no non-juvenile specimens are known in which tubercles on LO overhang the posterior margin. Nevertheless, there is variation in the size of the tubercles, and some specimens (e.g., Pl. 49, figs 2, 8) seem directly comparable to the YH 128.9 m sample. The two pygidia known from YH 128.9 m have prominent tubercles on all of the axial rings, the terminal piece, and the adaxial parts of the pleural ribs. None of the pygidia from HC6 226.5 m have tuberculate terminal pieces and two have nearly smooth axial rings, with only tiny tubercles along the anterior margins. However one pygidium from HC6 226.5 (Pl. 51, fig. 18) has prominent tubercles on the rings, nearly as coarse as those on the YH 128.9 specimens, and another (Pl. 51, fig. 21) is approximately intermediate in sculpture. Hence, while there are quite striking differences in pairwise comparisons of certain sclerites, the situation appears to reflect one smaller sample (YH 128.9 m) with a narrowly circumscribed range of variation and a larger sample (HC6 226.5 m) with a broader range, but one which encompasses, or nearly encompasses that of the former.

A small articulated specimen (Pl. 50, figs 1, 2, 6, 8) appears to have 11 thoracic segments. This is a low number for a pliomereid. Among contemporary taxa in the faunas, *Hintzeia parafirmimarginis* McAdams and Adrain, 2011a, has 15 segments. Work in progress has shown that species of *Lemureops* McAdams and Adrain, 2009 have 14 segments, and those of *Pseudocybele* have 15. Given its size and low segment count, the *M. milsteadi* specimen is probably a meraspid. The segment count is not known, however, for any other species described herein, nor for any member of the presumptive sister group, *Panisaspis*.

***Millardaspis knoxi* n. sp.**

Plate 55

Material. Holotype, pygidium, SUI 129548 (Pl. 55, figs 12, 17, 18) and assigned specimens SUI 129544–129547, 129549–129552 from Section H 163.3 m, Fillmore Formation (Tulean; *Panisaspis sevierensis* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

Etymology. After Benjamin Knox.

Diagnosis. Librigena with short posterior branch of facial suture; pygidium with very coarse tuberculate sculpture and line of large tubercles running down the middle of each pygidial pleura and onto the spine; shallow and wide pygidial axial furrow; lacks terminal piece.

Discussion. *Millardaspis knoxi* is compared to *Millardaspis milsteadi*, noting all morphological differences, in the discussion of that species. Compared to the stratigraphically nearest species of the *Ibexaspis* group, *Deltapliomera heimbergi*, *Millardaspis knoxi* (cf. Pl. 24, fig. 1, Pl. 55, fig. 2) has a narrower, more strongly vaulted (sag., tr.) cranidium; a more anteriorly bowed anterior border; a shorter, slightly more inflated glabella with slightly longer and shallower lateral furrows; a longer, more laterally tapered LO; more laterally directed palpebral lobes; shorter and narrower posterior fixigenae; and more densely spaced sculpture.

Librigenae (cf. Pl. 24, figs 16, 17, Pl. 55, fig. 3) of *Millardaspis knoxi* possesses a shorter librigenal field with more tubercles, and a lateral border with a relatively longer anterior projection and coarser sculpture near the border furrow.

Thoracic segments (cf. Pl. 25, fig. 27, Pl. 55, fig. 11) mainly differ in that the specimen assigned to *Millardaspis knoxi* has a more inflated axial ring and pleurae than that of *D. heimbergi*; the axial ring is longer; the axial furrows are shallower; there is a transverse line of granules on the posterior margin of the articulating half ring; and the sculpture is also more densely spaced, particularly on the pleural spine. The longer pleural spines of

Millardaspis knoxi may be attributable to a different position in the thorax, or may be another difference, but more thoracic segments from both species are needed for comparison.

The pygidia (cf. Pl. 26, fig. 2, Pl. 27, fig. 13, pygidia of Pl. 55) are slightly narrower and much more strongly vaulted (sag., tr.) in both the axis and the pleurae; the pleurae are more strongly backswept, much more strongly downturned, and less splayed; the axial rings are more strongly independently inflated, as are the pleural ribs; the axial furrows are wider, especially across the first and second pleurae; the sculpture is composed of larger, more closely spaced tubercles; and the terminal piece is apparently never expressed, as opposed to its presence in about half of the *D. heimbergi* pygidia.

Millardaspis knoxi uniquely (among all members of the *Ibexaspis* group) possesses a line of large tubercles running down the middle of each pygidial pleura and onto the spine.

Acknowledgements

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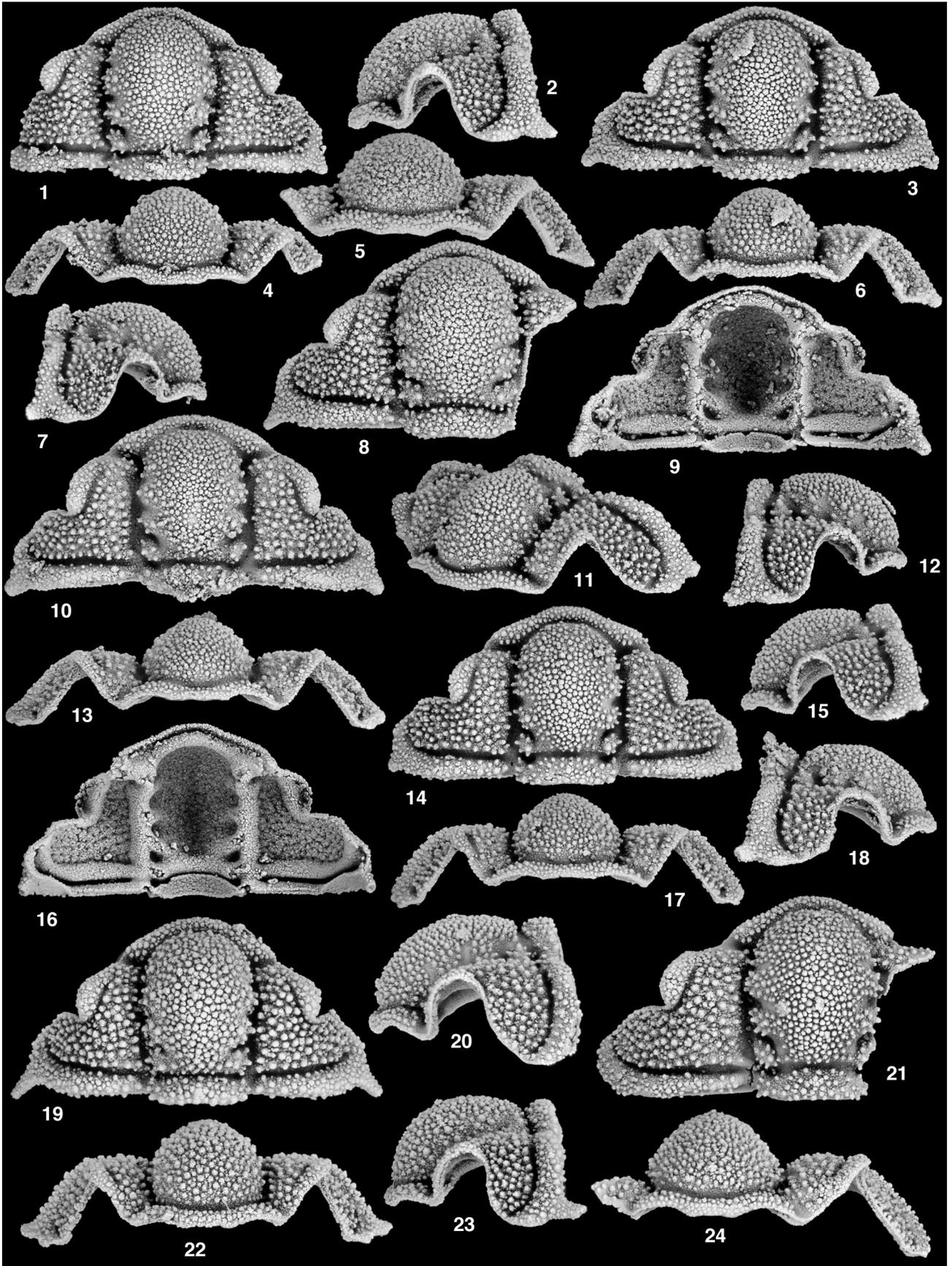


PLATE 1.



PLATE 1. *Ibexaspis brevis* (Young, 1973), from Section H 186.2 m, Fillmore Formation (Floian; Blackhillsian; *Bathyrina plicolabeona* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

- 1, 4, 7. Cranidium, SUI 129762, dorsal, anterior, and right lateral views, x12.
- 2, 5, 8. Cranidium, SUI 129763, left lateral, anterior, and dorsal views, x12.
- 3, 6, 9, 12. Cranidium, SUI 129764, dorsal, anterior, ventral, and right lateral views, x12.
- 10, 13, 18. Cranidium, SUI 129765, dorsal, anterior, and right lateral views, x12.
- 11, 14, 15, 16, 17. Cranidium, SUI 129766, oblique, dorsal, left lateral, ventral, and anterior views, x12.
- 19, 22, 23. Cranidium, SUI 129767, dorsal, anterior, and left lateral views, x15.
- 20, 21, 24. Cranidium, SUI 129768, left lateral, dorsal, and anterior views, x12.

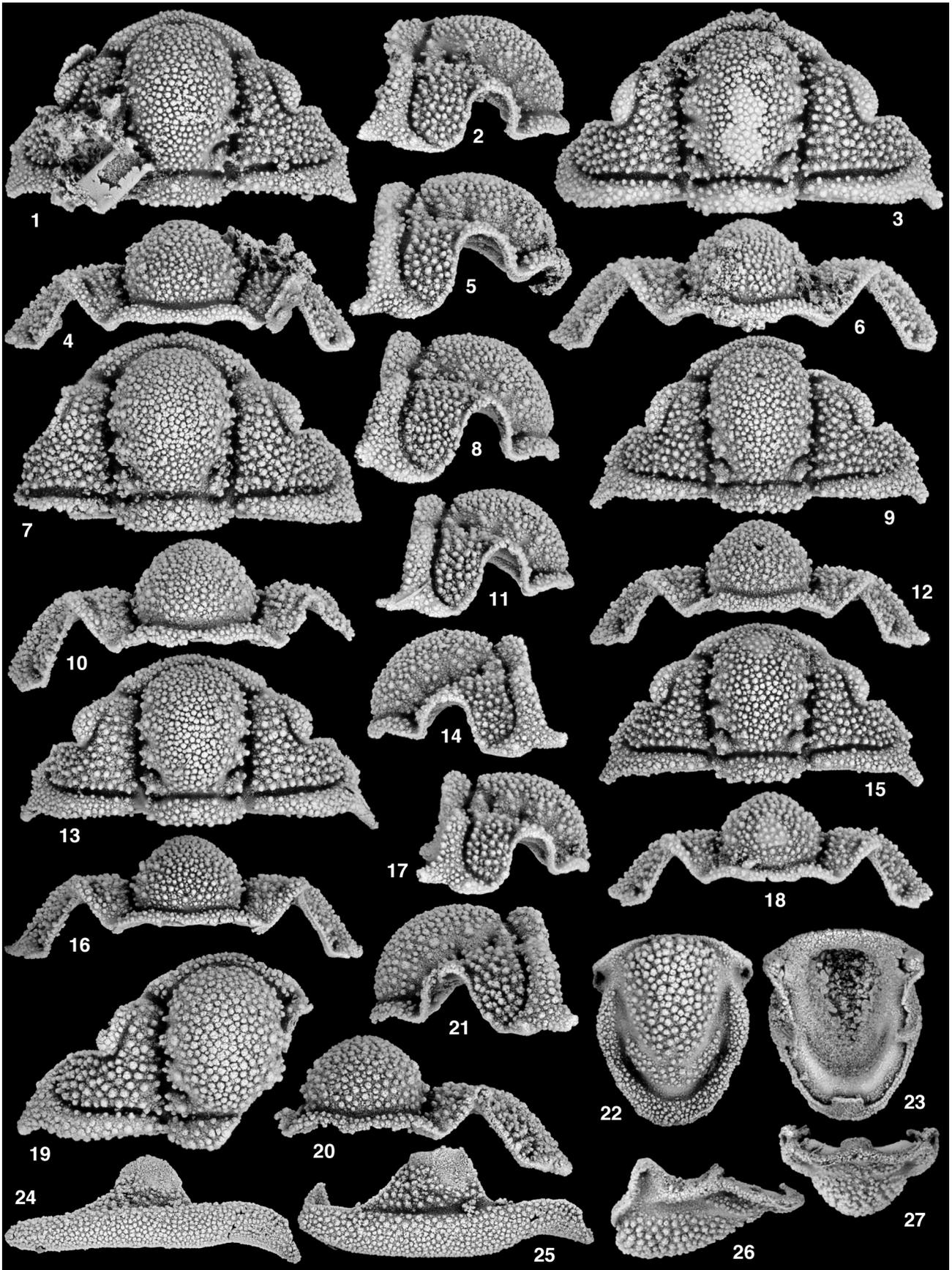


PLATE 2.



PLATE 2. *Ibexaspis brevis* (Young, 1973), from Section H 186.2 m, Fillmore Formation (Floian; Blackhillsian; *Bathyrina plicolabeona* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

- 1, 2, 4. Cranidium, SUI 129769, dorsal, right lateral, and anterior views, x15.
- 3, 5, 6. Cranidium, SUI 129770, dorsal, right lateral, and anterior views, x15.
- 7, 8, 10. Cranidium, SUI 129771, dorsal, right lateral, and anterior views, x15.
- 9, 12, 14. Cranidium, SUI 129772, dorsal, anterior, and left lateral views, x15.
- 11, 13, 16. Cranidium, SUI 129773, right lateral, dorsal, and anterior views, x15.
- 15, 17, 18. Cranidium, SUI 129774, dorsal, right lateral, and anterior views, x15.
- 19-21. Cranidium, SUI 129775, dorsal, anterior, and left lateral views, x15.
- 22, 23, 26, 27. Hypostome, SUI 129776, ventral, dorsal, left lateral, and posterior views, x20.
- 24, 25. Right librigena, SUI 129777, ventrolateral and external views, x15.

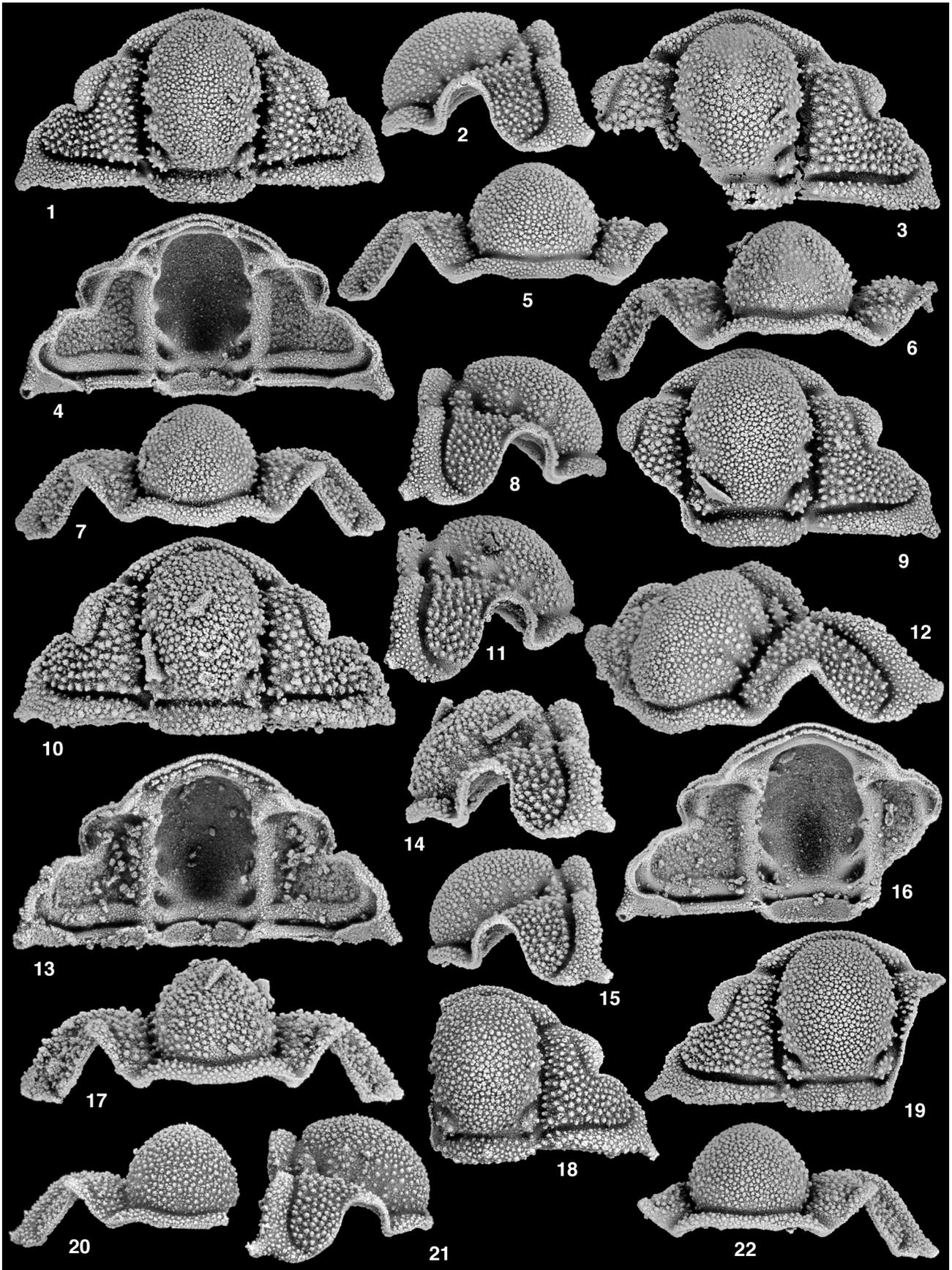


PLATE 3.

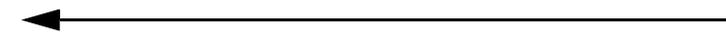


PLATE 3.*Ibexaspis brevis* (Young, 1973), from Section H 191.7 m, Fillmore Formation (Floian; Blackhillsian; *Bathyrina plicolabeona* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

- 1, 2, 4, 7, 12. Cranidium, SUI 129778, dorsal, left lateral, ventral, anterior, and oblique views, x14.
3, 6, 11. Cranidium, SUI 129779, dorsal, anterior, and right lateral views, x12.
5, 8, 9, 16. Cranidium, SUI 129780, anterior, right lateral, dorsal, and ventral views, x12.
10, 13, 14, 17. Cranidium, SUI 129781, dorsal, ventral, left lateral, and anterior views, x14.
15, 19, 22. Cranidium, SUI 129782, left lateral, dorsal, and anterior views, x12.
18, 20, 21. Cranidium, SUI 115330, dorsal, anterior, and right lateral views, x15.

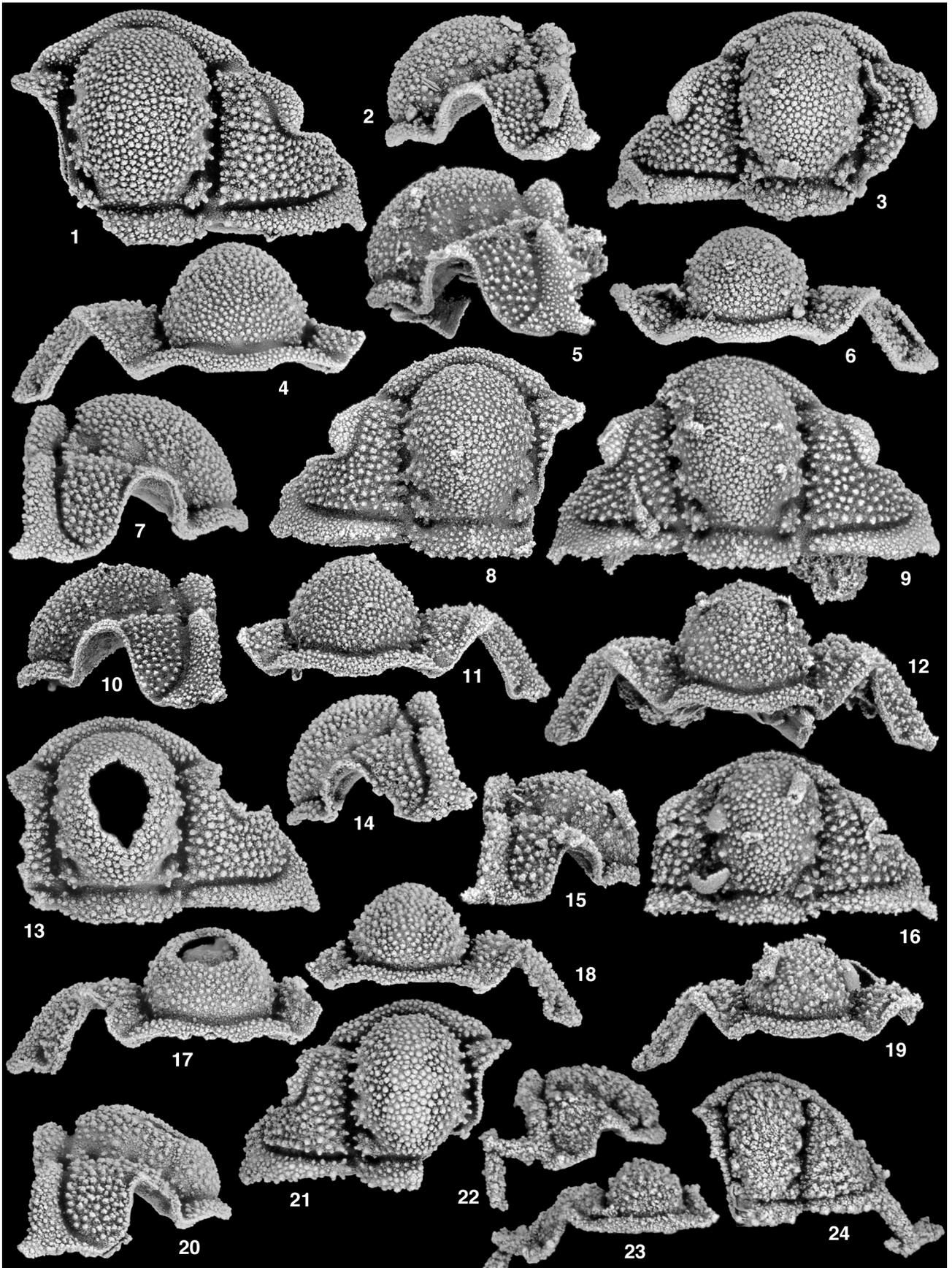


PLATE 4.



PLATE 4. *Ibexaspis brevis* (Young, 1973), from Section H 191.7 m, Fillmore Formation (Floian; Blackhillsian; *Bathyrina plicolabeona* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

- 1, 4, 7. Cranidium, SUI 129783, dorsal, anterior, and right lateral views, x15.
- 2, 3, 6. Cranidium, SUI 129784, left lateral, dorsal, and anterior views, x15.
- 5, 9, 12. Cranidium, SUI 129785, left lateral, dorsal, and anterior views, x15.
- 8, 10, 11. Cranidium, SUI 129786, dorsal, left lateral, and anterior views, x15.
- 13, 17, 20. Cranidium, SUI 129787, dorsal, anterior, and right lateral views, x15.
- 14, 18, 21. Cranidium, SUI 129788, left lateral, anterior, and dorsal views, x15.
- 15, 16, 19. Cranidium, SUI 129789, right lateral, dorsal, and anterior views, x15.
- 22–24. Cranidium, SUI 129790, right lateral, anterior, and dorsal views, x25.

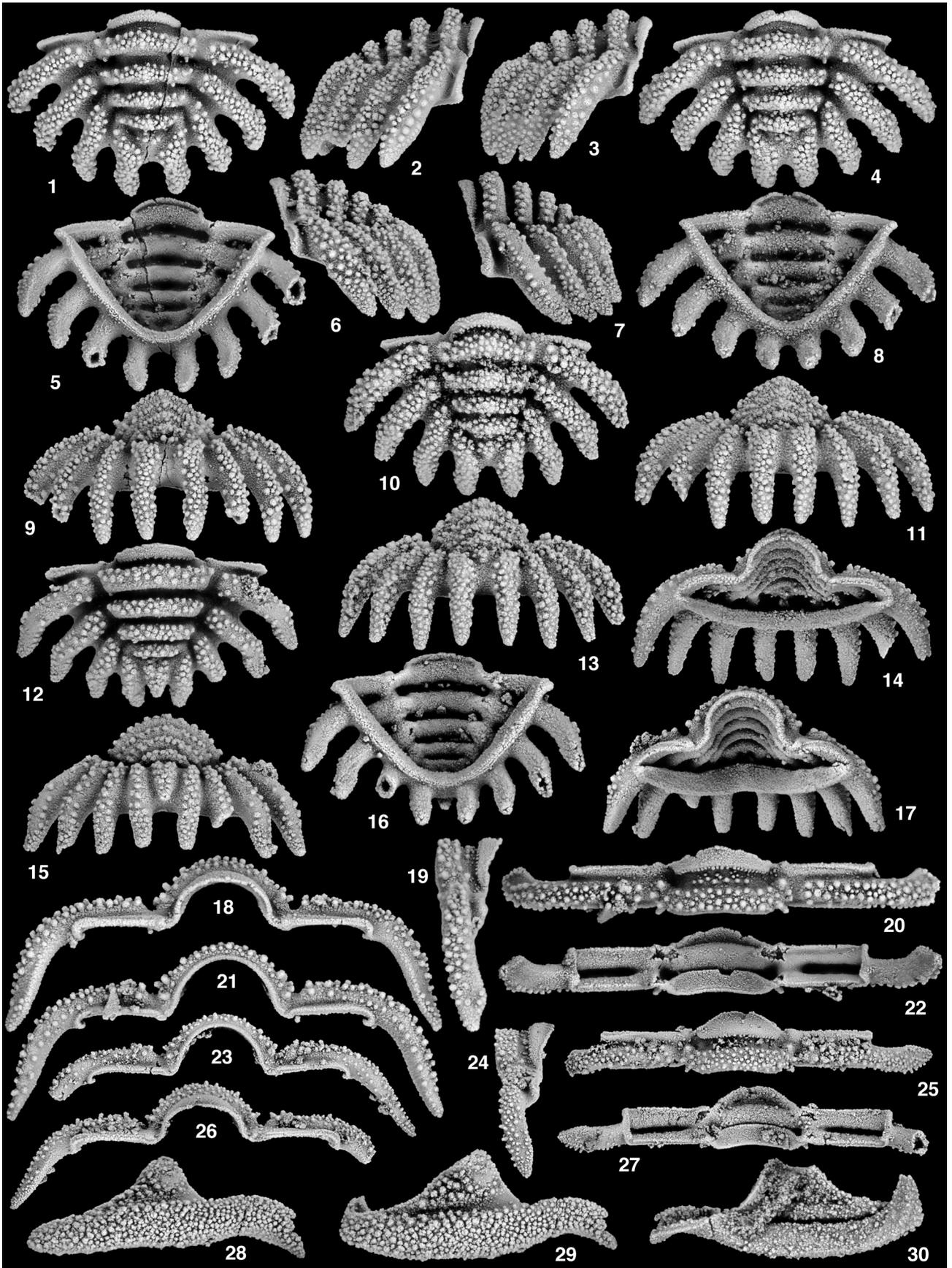


PLATE 5.



PLATE 5. *Ibexaspis brevis* (Young, 1973), from Section H 185.6, H 186.2, and H 191.7 m, Fillmore Formation (Floian; Blackhillsian; *Bathyrina plicolabeona* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

- 1, 2, 5, 9. Pygidium, SUI 129791, dorsal, right lateral, ventral, and posterior views, x14 (H 186.2 m).
3, 4, 8, 11, 14. Pygidium, SUI 129792, right lateral, dorsal, ventral, posterior, and anterior views, x14 (H 186.2 m).
6, 10, 13. Pygidium, SUI 129793, left lateral, dorsal, and posterior views, x15 (H 186.2 m).
7, 12, 15-17. Pygidium, SUI 129794, left lateral, dorsal, posterior, ventral, and anterior views, x15 (H 185.6 m).
18-22. Thoracic segment, SUI 129795, anterior, right lateral, dorsal, posterior, and ventral views, x15 (H 186.2 m).
23-27. Thoracic segment, SUI 129796, posterior, right lateral, dorsal, anterior, and ventral views, x12 (H 191.7 m).
28-30. Right librigena, SUI 129797, ventrolateral, external, and internal views, x17 (H 186.2 m).

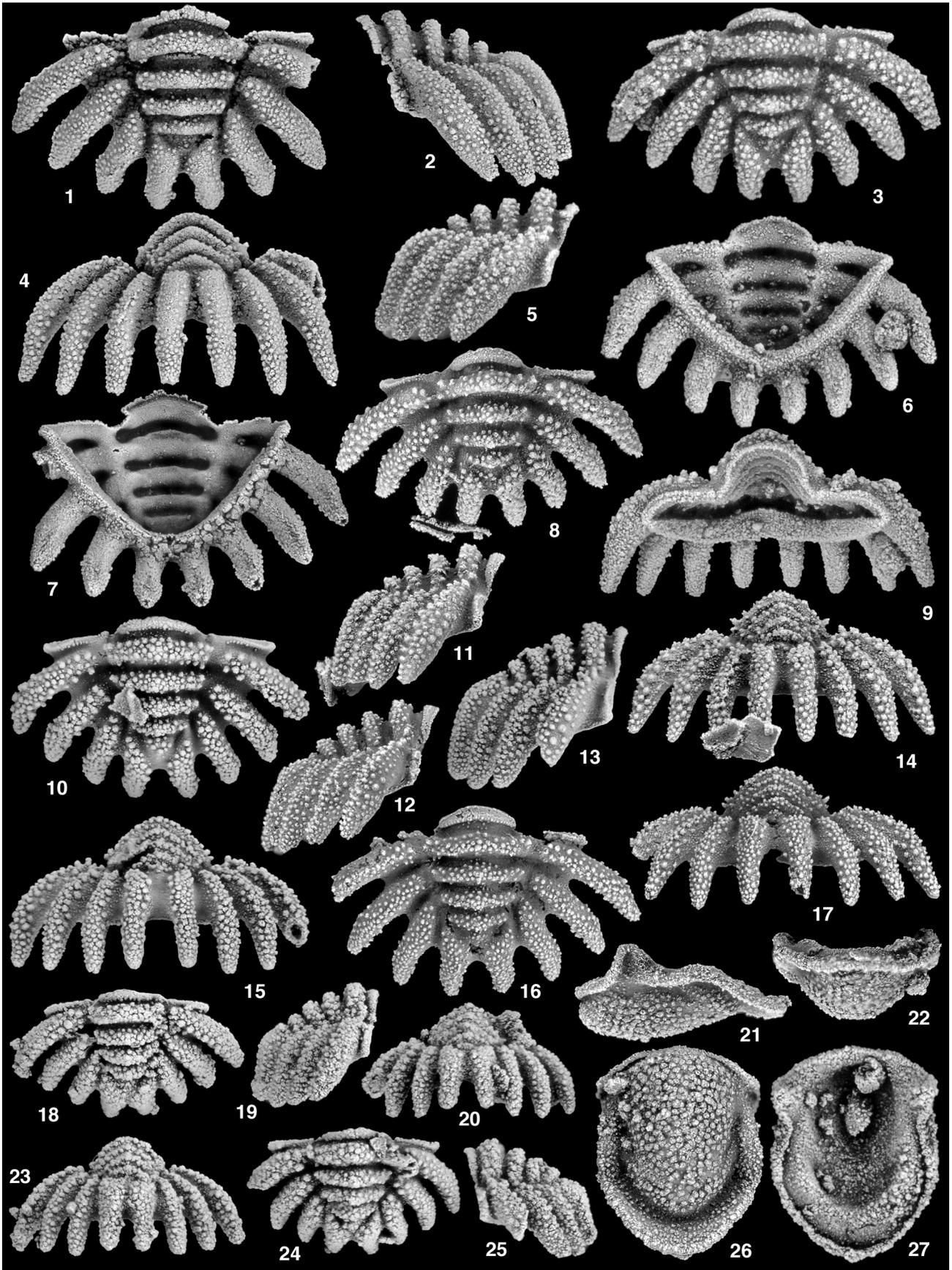


PLATE 6.



PLATE 6. *Ibexaspis brevis* (Young, 1973), from Section H 191.7 m, Fillmore Formation (Floian; Blackhillsian; *Bathyrina plicolabeona* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

- 1, 2, 4, 7. Pygidium, SUI 129798, dorsal, left lateral, posterior, and ventral views, x15.
3, 5, 6, 9. Pygidium, SUI 129799, dorsal, right lateral, ventral, and anterior views, x20.
8, 11, 14. Pygidium, SUI 129800, dorsal, right lateral, and posterior views, x20.
10, 13, 15. Pygidium, SUI 129801, dorsal, right lateral, and posterior views, x17.
12, 16, 17. Pygidium, SUI 115331, right lateral, dorsal, and posterior views, x15.
18, 19, 23. Pygidium, SUI 129802, dorsal, right lateral, and posterior views, x17.
20, 24, 25. Pygidium, SUI 129803, posterior, dorsal, and left lateral views, x20.
21, 22, 26, 27. Hypostome, SUI 129804, left lateral, posterior, ventral, and dorsal views, x20.

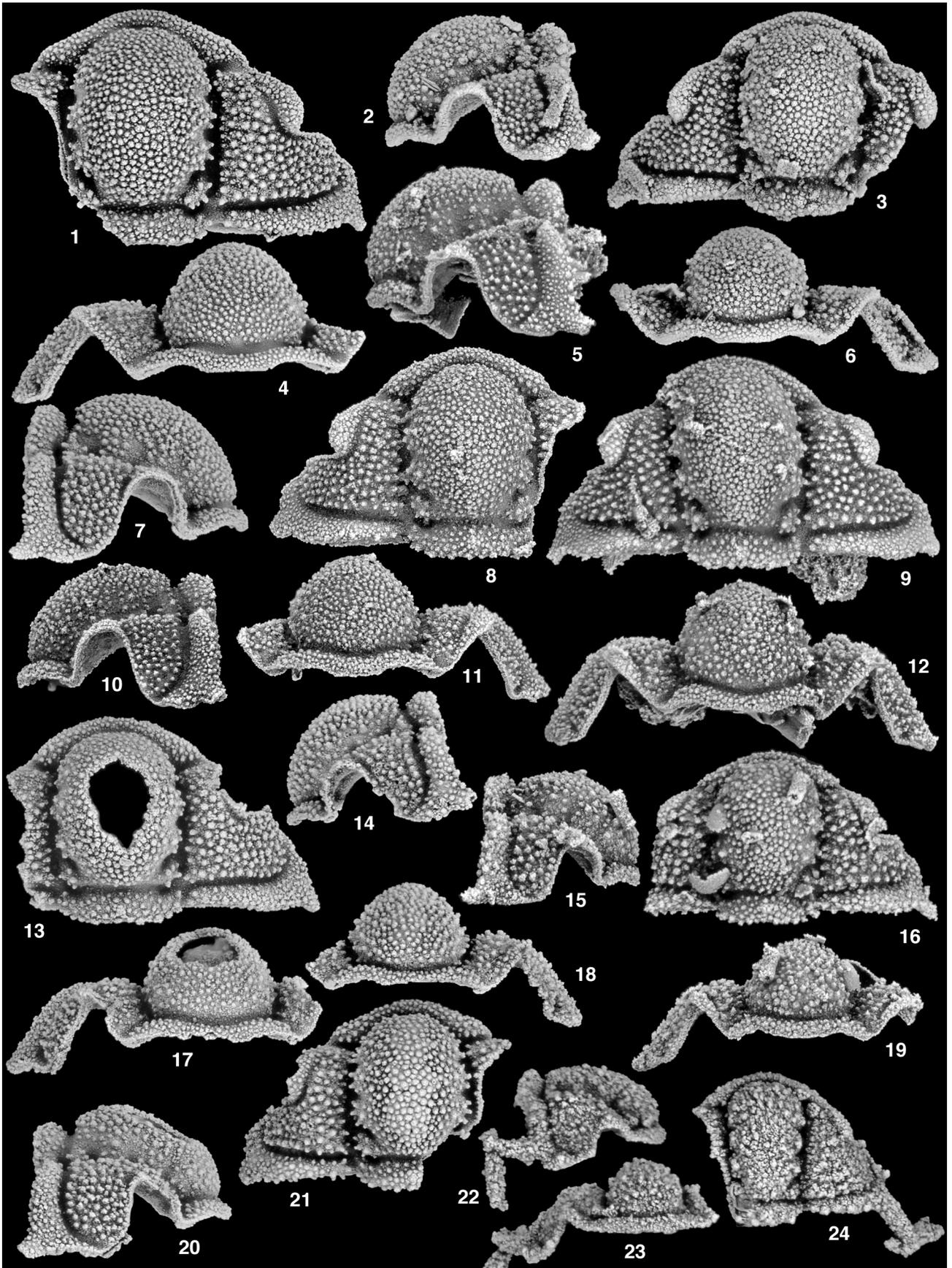


PLATE 7.



PLATE 7. *Ibexaspis coadyi* n. sp., from Section H 222.1 m, Fillmore Formation (Floian; Blackhillsian; *Carolinites nevadensis* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. All magnifications are x15.

1, 3, 5, 7. Cranidium, SUI 129805, dorsal, anterior, ventral, and left lateral views.

2, 4, 6, 9. Cranidium, SUI 129806, dorsal, anterior, oblique, and right lateral views.

8, 10, 17. Cranidium, SUI 129807, right lateral, anterior, and dorsal views.

11, 13, 16. Cranidium, SUI 129808, right lateral, anterior, and dorsal views.

12, 14, 15, 18. Cranidium, SUI 129809, dorsal, left lateral, anterior, and ventral views.

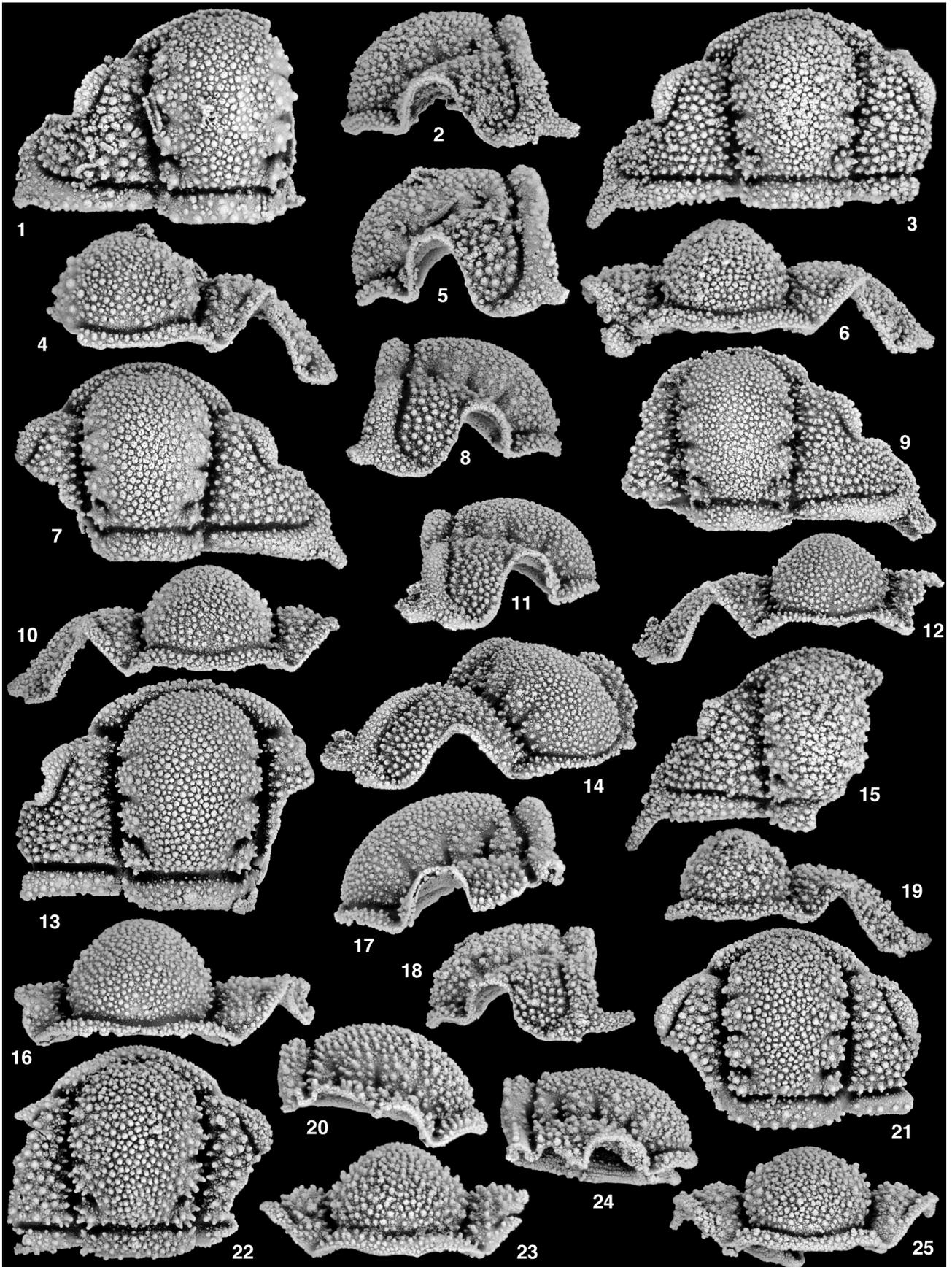


PLATE 8.

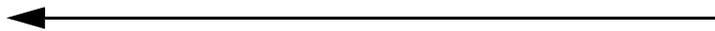


PLATE 8. *Ibexaspis coadyi* n. sp., from Section H 222.1 m, Fillmore Formation (Floian; Blackhillsian; *Carolinites nevadensis* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

- 1, 4, 5. Cranidium, SUI 129810, dorsal, anterior, and left lateral views, x15.
2, 3, 6. Cranidium, SUI 129811, left lateral, dorsal, and anterior views, x15.
7, 8, 10. Cranidium, SUI 129812, dorsal, right lateral, and anterior views, x15.
9, 11, 12, 14. Cranidium, SUI 129813, dorsal, right lateral, anterior, and oblique views, x12.
13, 16, 17. Cranidium, SUI 129814, dorsal, anterior, and left lateral views, x15.
15, 18, 19. Cranidium, SUI 129815, dorsal, anterior, and left lateral views, x17.
20, 22, 23. Cranidium, SUI 129816, right lateral, dorsal, and anterior views, x17.
21, 24, 25. Cranidium, SUI 129817, dorsal, right lateral, and anterior views, x15.



PLATE 9.

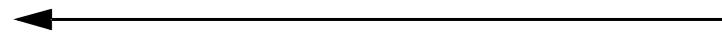


PLATE 9. *Ibexaspis coadyi* n. sp., from Section H 222.1 m, Fillmore Formation (Floian; Blackhillsian; *Carolinites nevadensis* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

1, 4, 7. Left librigena, SUI 129818, external, internal, and ventrolateral views, x17.

2, 5, 8. Left librigena, SUI 129819, external, internal, and ventrolateral views, x20.

3, 6. Left librigena, SUI 129820, external and internal views, x17.

9, 13. Right librigena, SUI 129821, external and ventrolateral views, x17.

10-12. Right librigena, SUI 129822, ventrolateral, internal, and external views, x17.

14, 19, 23. Hypostome, SUI 129823, ventral, right lateral, and posterior views, x17.

15, 20, 24. Hypostome, SUI 129824, ventral, right lateral, and posterior views, x17.

16, 17, 21, 28. Hypostome, SUI 129825, ventral, dorsal, left lateral, and posterior views, x17.

18, 22, 31, 41. Hypostome, SUI 129826, ventral, left lateral, posterior, and dorsal views, x17.

25-27, 30. Thoracic segment, SUI 129827, anterior, right lateral, posterior, and dorsal views, x12.

29, 32, 33, 36, 38. Thoracic segment, SUI 129828, dorsal, ventral, left lateral, anterior, and posterior views, x12.

34, 35, 37, 39, 40. Thoracic segment, SUI 129829, dorsal, ventral, anterior, right lateral, and posterior views, x12.

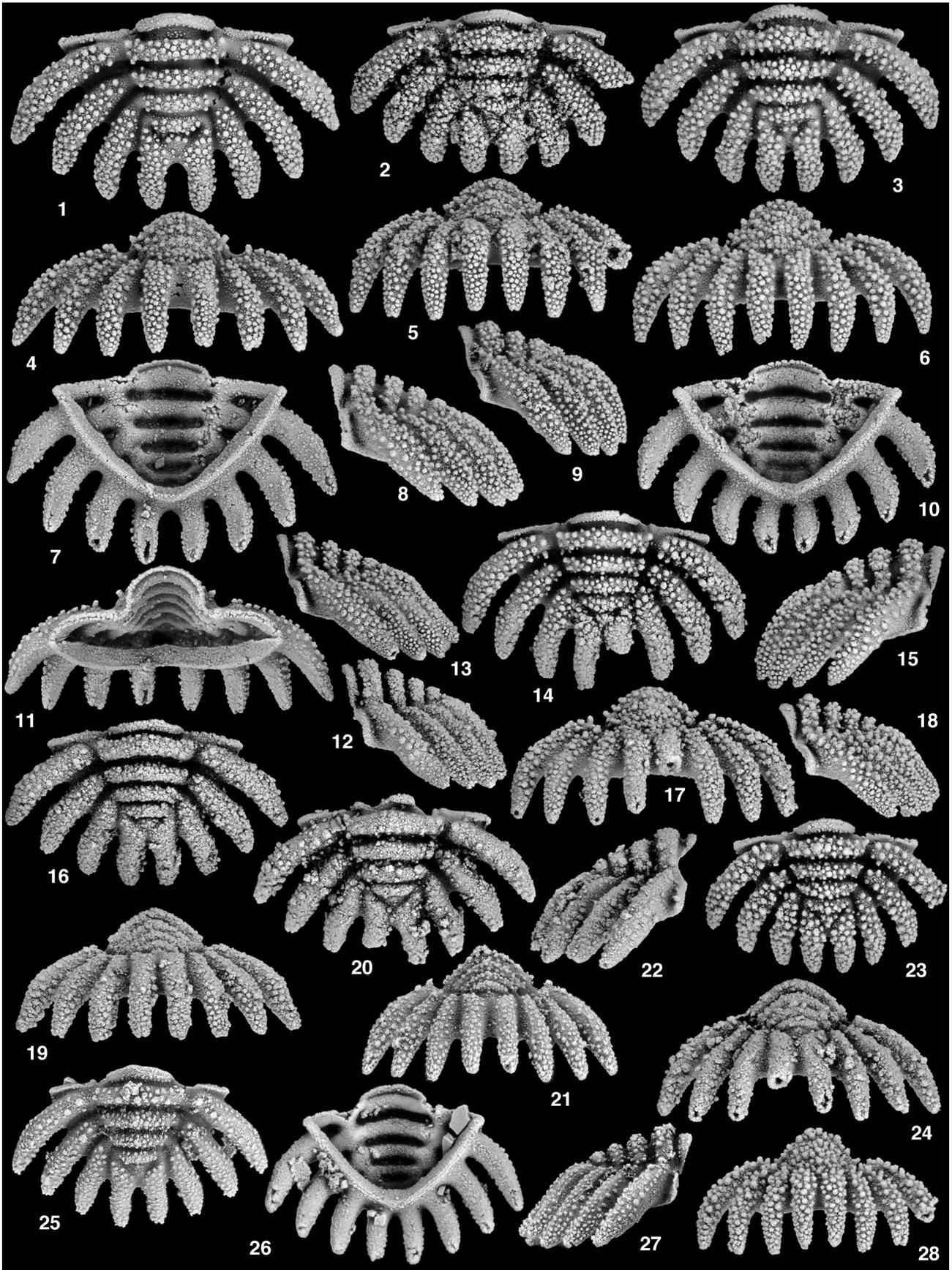


PLATE 10.



PLATE 10. *Ibexaspis coadyi* n. sp., from Section H 222.1 m, Fillmore Formation (Floian; Blackhillsian; *Carolinites nevadensis* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

1, 4, 7, 8, 11. Pygidium, **holotype**, SUI 129830, dorsal, posterior, ventral, left lateral, and anterior views, x15.

2, 5, 9. Pygidium, SUI 129831, dorsal, posterior, and left lateral views, x15.

3, 6, 10, 15. Pygidium, SUI 129832, dorsal, posterior, ventral, and right lateral views, x15.

12, 16, 19. Pygidium, SUI 129833, left lateral, dorsal, and posterior views, x15.

13, 14, 17. Pygidium, SUI 129834, left lateral, dorsal, and posterior views, x15.

18, 23, 28. Pygidium, SUI 129835, left lateral, dorsal, and posterior views, x15.

20, 22, 24. Pygidium, SUI 129836, dorsal, right lateral, and posterior views, x15.

21, 25–27. Pygidium, SUI 115362, posterior, dorsal, ventral, and right lateral views, x20.

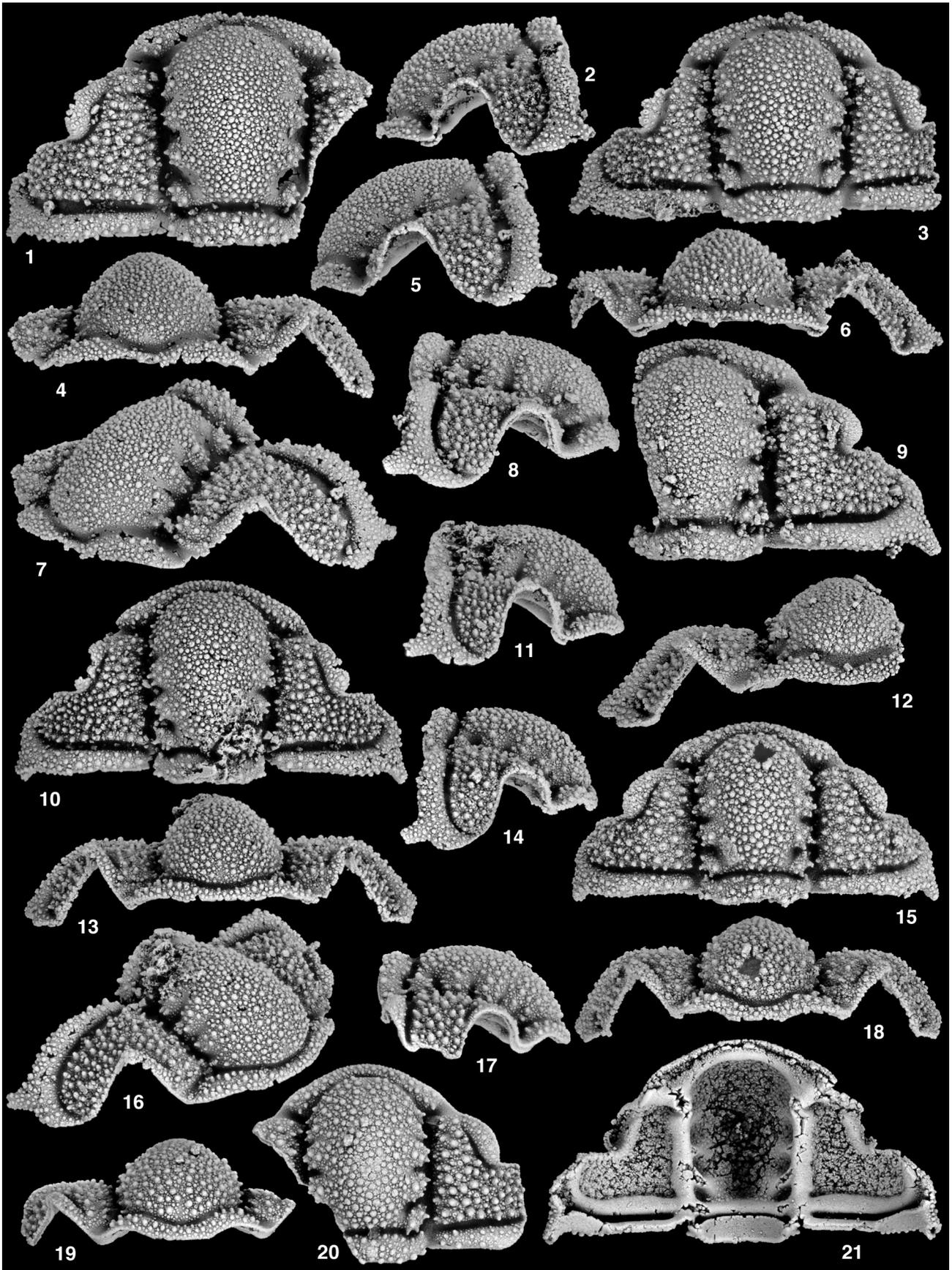


PLATE 11.



PLATE 11. *Ibexaspis leuppi* n. sp., from Section H 251.4 m, Fillmore Formation (Floian; Blackhillsian; *Presbynileus ibexensis* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. All magnifications are x15.

- 1, 4, 5, 7. Cranidium, **holotype**, SUI 129837, dorsal, anterior, left lateral, and oblique views.
2, 3, 6. Cranidium, SUI 129838, left lateral, dorsal, and anterior views.
8, 9, 12. Cranidium, SUI 129839, right lateral, dorsal, and anterior views.
10, 11, 13, 16. Cranidium, SUI 129840, dorsal, right lateral, anterior, and oblique views.
14, 15, 18, 21. Cranidium, SUI 129841, right lateral, dorsal, anterior, and ventral views.
17, 19, 20. Cranidium, SUI 129842, right lateral, anterior, and dorsal views.

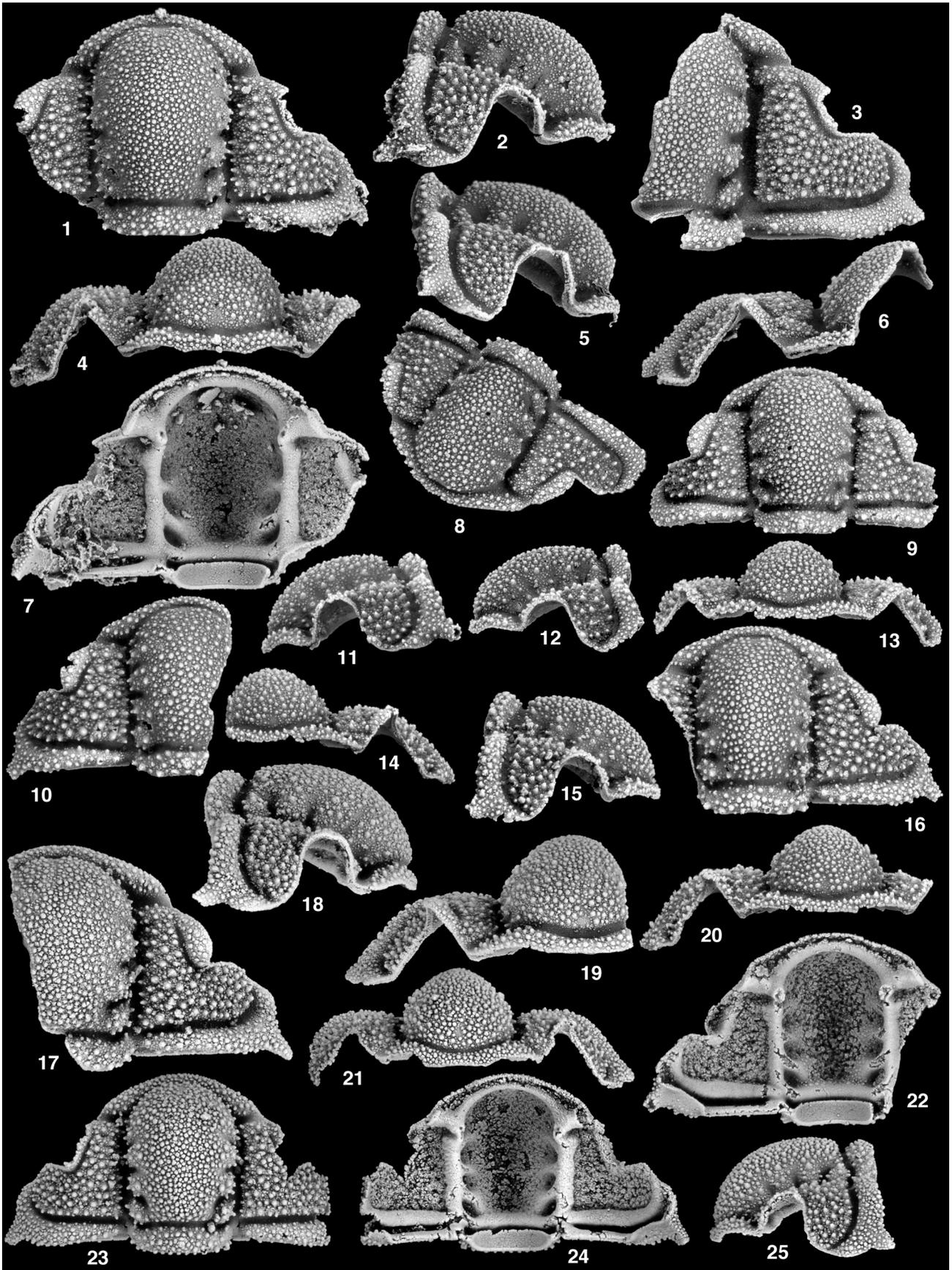


PLATE 12.



PLATE 12. *Ibexaspis leuppi* n. sp., from Section H 251.4 m, Fillmore Formation (Floian; Blackhillsian; *Presbynileus ibexensis* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. All magnifications are x15.

- 1, 2, 4, 7. Cranidium, SUI 129843, dorsal, right lateral, anterior, and ventral views.
- 3, 5, 6. Cranidium, SUI 129844, dorsal, right lateral, and anterior views.
- 8, 9, 12, 13. Cranidium, SUI 115372, oblique, dorsal, left lateral, and anterior views.
- 10, 11, 14. Cranidium, SUI 129845, dorsal, left lateral, and anterior views.
- 15, 16, 20, 22. Cranidium, SUI 129846, right lateral, dorsal, anterior, and ventral views.
- 17–19. Cranidium, SUI 129847, dorsal, right lateral, and anterior views.
- 21, 23–25. Cranidium, SUI 129848, anterior, dorsal, ventral, and left lateral views.

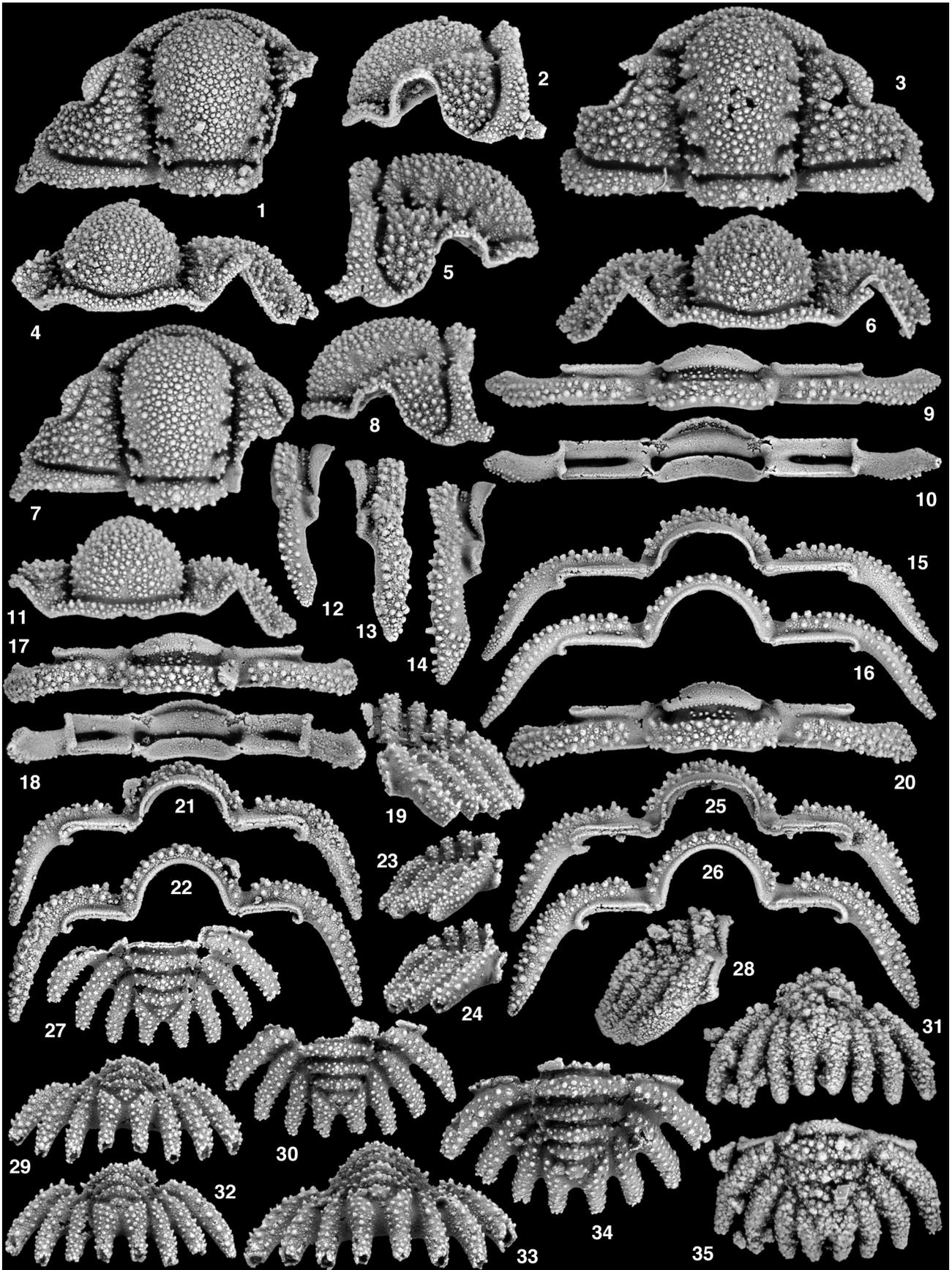


PLATE 13.



PLATE 13. *Ibexaspis leuppi* n. sp., from Section H 251.4 m, Fillmore Formation (Floian; Blackhillsian; *Presbynileus ibexensis* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

- 1, 2, 4. Cranium, SUI 129849, dorsal, left lateral, and anterior views, x15.
3, 5, 6. Cranium, SUI 129850, dorsal, right lateral, and anterior views, x20.
7, 8, 11. Cranium, SUI 129851, dorsal, left lateral, and anterior views, x20.
9, 10, 12, 15, 16. Thoracic segment, SUI 129852, dorsal, ventral, right lateral, anterior, and posterior views, x15.
13, 17, 18, 21, 22. Thoracic segment, SUI 129853, left lateral, dorsal, ventral, anterior, and posterior views, x15.
14, 20, 25, 26. Thoracic segment, SUI 129854, right lateral, dorsal, anterior, and posterior views, x15.
19, 33, 34. Pygidium, SUI 129855, left lateral, posterior, and dorsal views, x20.
23, 30, 32. Pygidium, SUI 129856, right lateral, dorsal, and posterior views, x15.
24, 27, 29. Pygidium, SUI 129857, right lateral, dorsal, and posterior views, x15.
28, 31, 35. Pygidium, SUI 129858, right lateral, posterior, and dorsal views, x25.

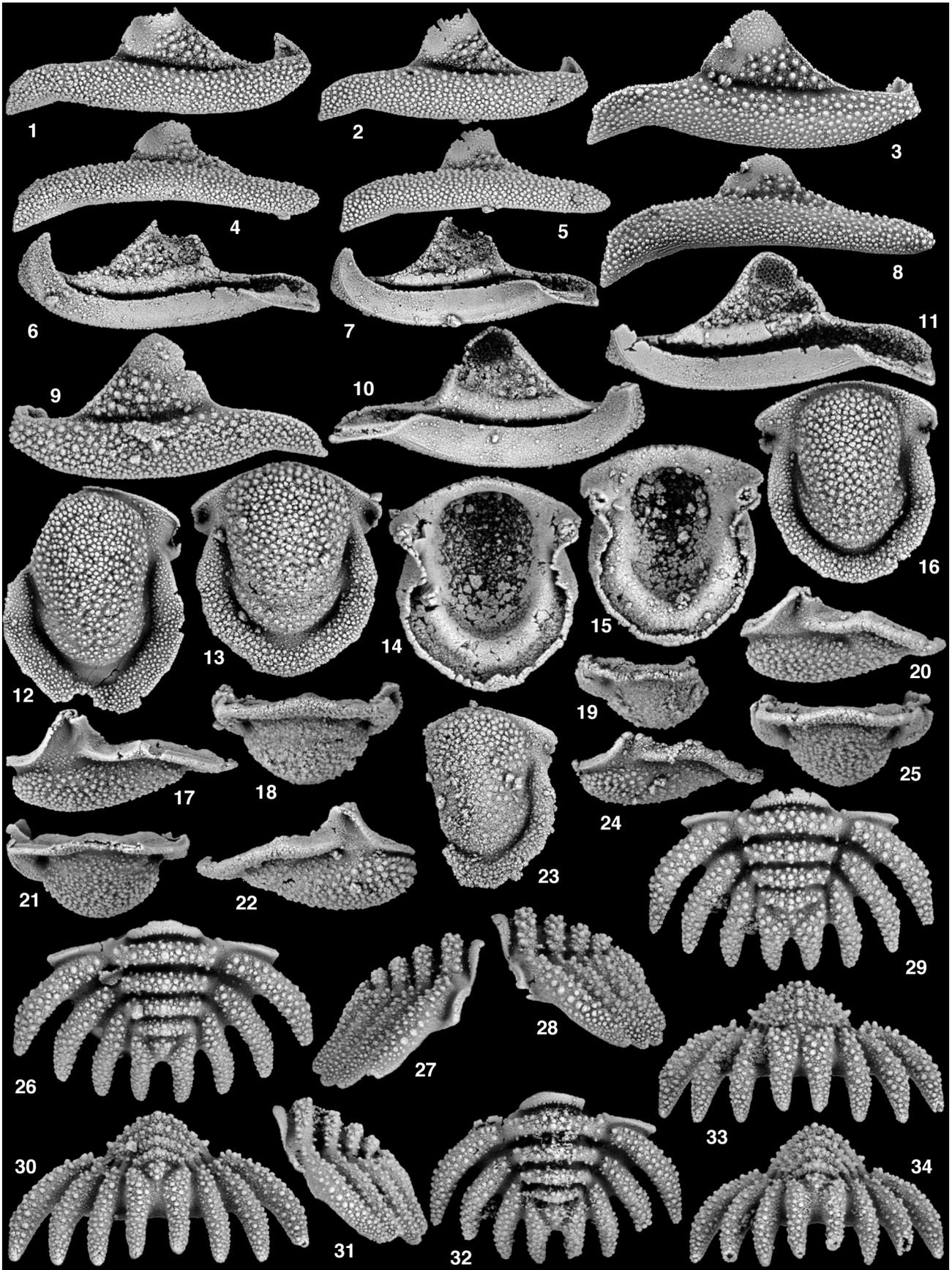


PLATE 14.



PLATE 14. *Ibexaspis leuppi* n. sp., from Section H 251.4 m, Fillmore Formation (Floian; Blackhillsian; *Presbynileus ibexensis* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

- 1, 4, 6. Left librigena, SUI 129859, external, ventrolateral, and internal views, x15.
2, 5, 7. Left librigena, SUI 129860, external, ventrolateral, and internal views, x15.
3, 8, 11. Left librigena, SUI 129861, external, ventrolateral, and internal views, x20.
9, 10. Right librigena, SUI 129862, external and internal views, x20.
12, 17, 21. Hypostome, SUI 129863, ventral, left lateral, and posterior views, x17.
13, 14, 18, 22. Hypostome, SUI 129864, ventral, dorsal, posterior, and right lateral views, x20.
15, 16, 20, 25. Hypostome, SUI 129865, dorsal, ventral, left lateral, and posterior views, x20.
19, 23, 24. Hypostome, SUI 129866, posterior, ventral, and left lateral views, x20.
26, 27, 30. Pygidium, SUI 129867, dorsal, right lateral, and posterior views, x20.
28, 29, 33. Pygidium, SUI 129868, left lateral, dorsal, and posterior views, x20.
31, 32, 34. Pygidium, SUI 129869, left lateral, dorsal, and posterior views, x20.

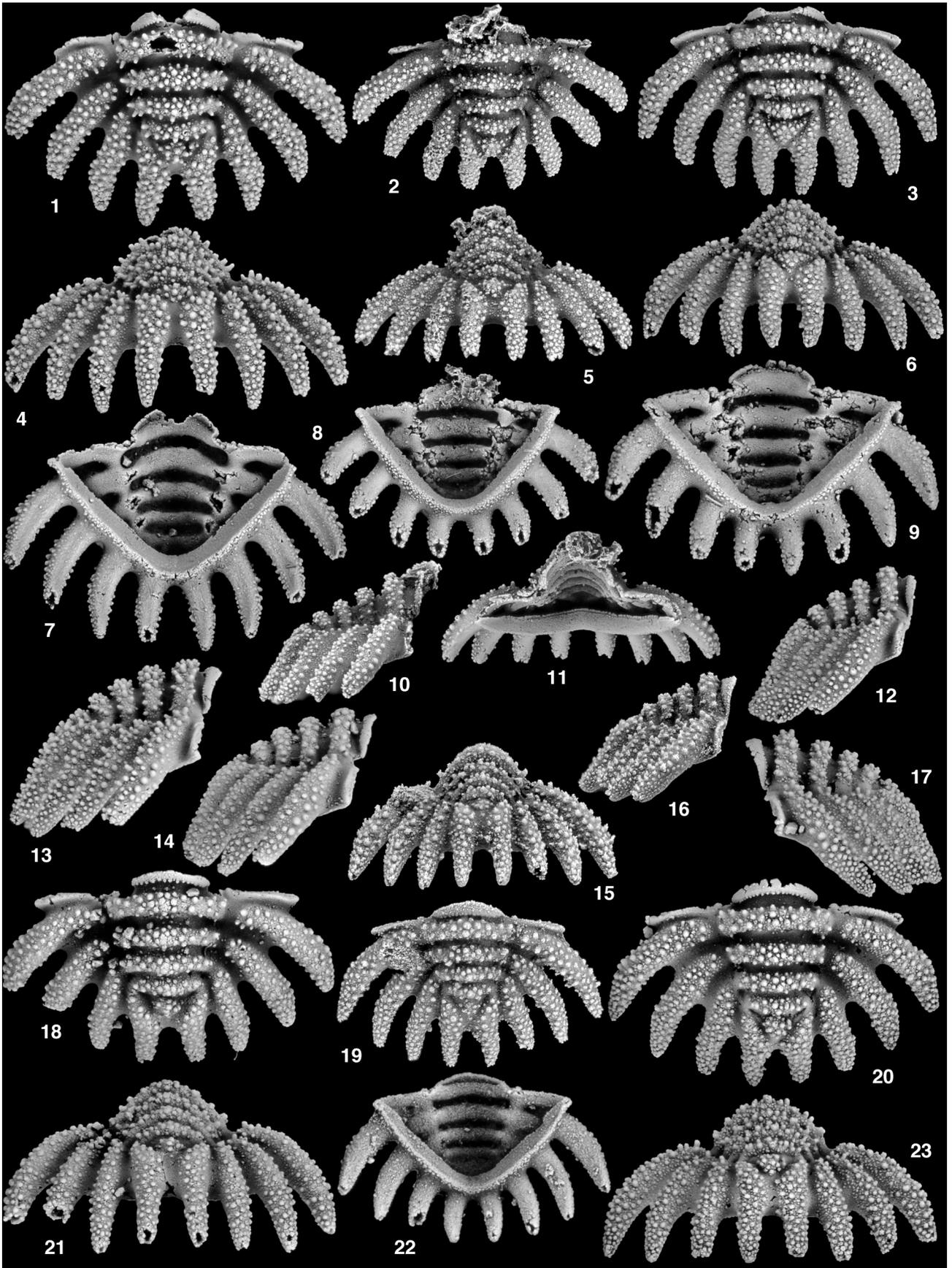


PLATE 15.



PLATE 15. *Ibexaspis leuppi* n. sp., from Section H 251.4 m, Fillmore Formation (Floian; Blackhillsian; *Presbynileus ibexensis* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

1, 4, 7, 13. Pygidium, SUI 129870, dorsal, posterior, ventral, and right lateral views, x17.

2, 5, 8, 10, 11. Pygidium, SUI 115373, dorsal, posterior, ventral, right lateral, and anterior views, x15.

3, 6, 9, 12. Pygidium, SUI 129871, dorsal, posterior, ventral, and right lateral views, x17.

14, 18, 21. Pygidium, SUI 129872, right lateral, dorsal, and posterior views, x17.

15, 16, 19, 22. Pygidium, SUI 129873, posterior, right lateral, dorsal, and ventral views, x20.

17, 20, 23. Pygidium, SUI 129874, left lateral, dorsal, and posterior views, x17.

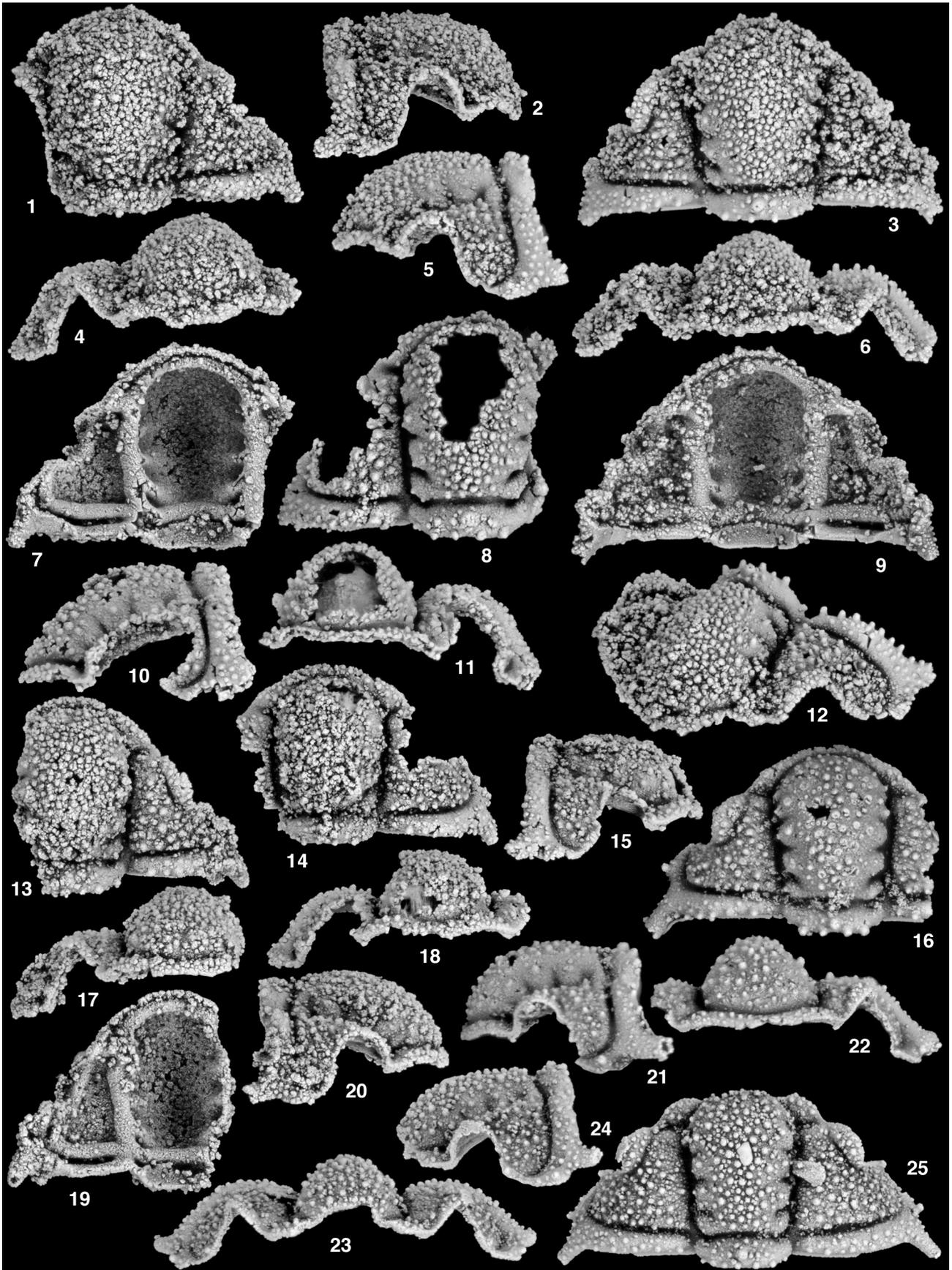


PLATE 16.



PLATE 16. *Ibexaspis rupauli* n. sp., from Section J 28T m and J 28.1 m, Wah Wah Formation (Floian; Blackhillsian; "Pseudocybele nasuta Zone"), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

1, 2, 4, 7. Cranidium, SUI 129875, dorsal, right lateral, anterior, and ventral views, x17 (J 28.1 m).

3, 5, 6, 9, 12. Cranidium, SUI 129876, dorsal, left lateral, anterior, ventral, and oblique views, x20 (J 28.1 m).

8, 10, 11. Cranidium, SUI 129877, dorsal, left lateral, and anterior views, x20 (J 28.1 m).

13, 17, 19, 20. Cranidium, SUI 129878, dorsal, anterior, ventral, and right lateral views, x17 (J 28.1 m).

14, 15, 18. Cranidium, SUI 129879, dorsal, right lateral, and anterior views, x17 (J 28.1 m).

16, 21, 22. Cranidium, SUI 129880, dorsal, left lateral, and anterior views, x25 (J 28.1 m).

23–25. Cranidium, SUI 129881, anterior, left lateral, and dorsal views, x20 (J 28T m).

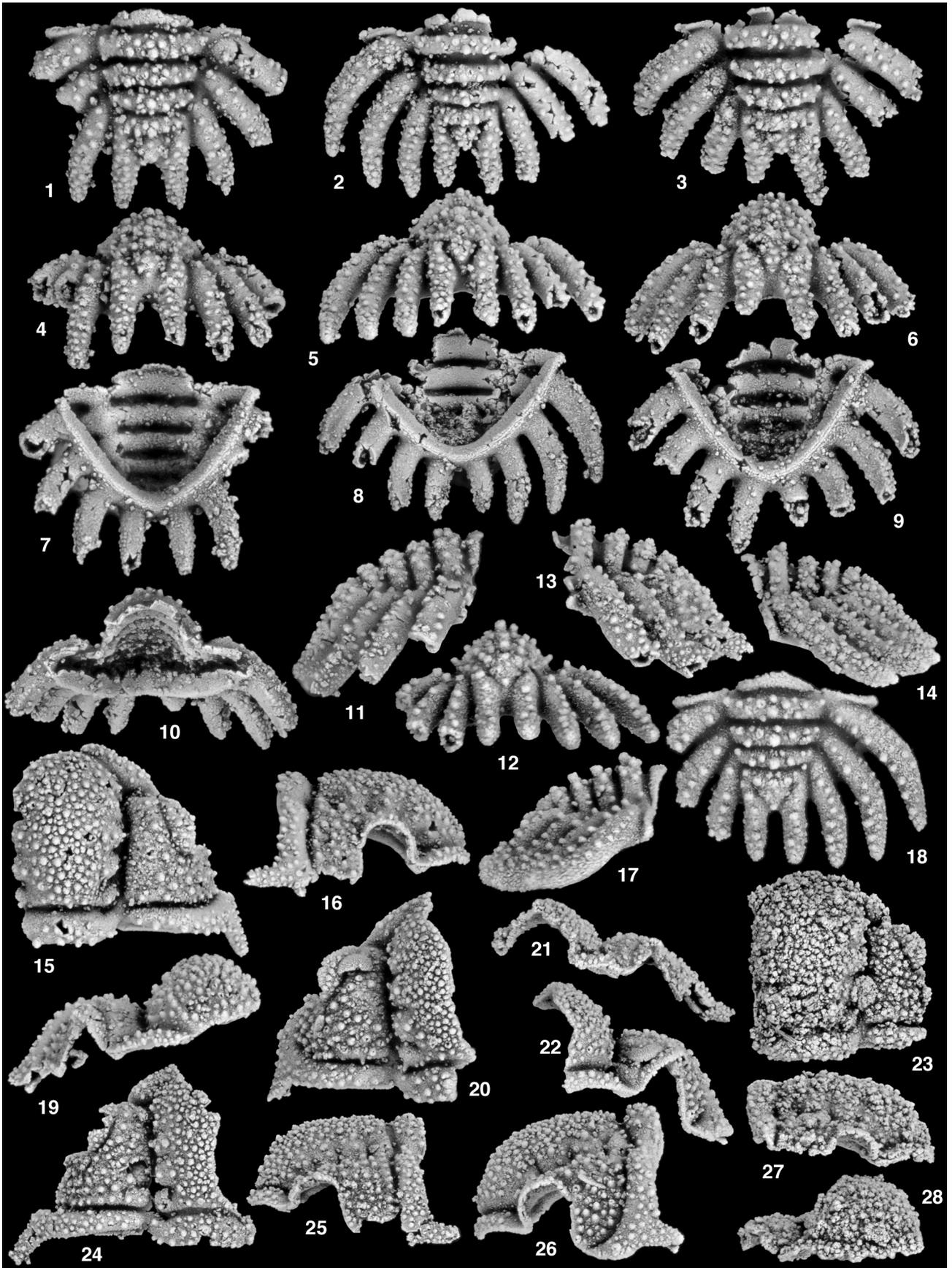


PLATE 17.



PLATE 17. *Ibexaspis rupauli* n. sp., from Section J 28T m and J 28.1 m, Wah Wah Formation, southern Confusion Range, Ibex area, Millard County, western Utah, USA, and Locality YH-J, Yellow Hill Limestone, Yellow Hill, near Pioche, Lincoln County, eastern Nevada, USA. All are Floian (Blackhillsian; "*Pseudocybele nasuta* Zone").

- 1, 4, 7, 10, 11. Pygidium, SUI 129882, dorsal, posterior, ventral, anterior, and right lateral views, x25 (J 28.1 m).
- 2, 5, 8, 13. Pygidium, SUI 129883, dorsal, posterior, ventral, and left lateral views, x20 (J 28.1 m).
- 3, 6, 9, 14. Pygidium, SUI 129884, dorsal, posterior, ventral, and left lateral views, x20 (J 28.1 m).
- 12, 17, 18. Pygidium, SUI 129885, posterior, right lateral, and dorsal views, x30 (J 28T m).
- 15, 16, 19. Cranidium, SUI 129886, dorsal, right lateral, and anterior views, x20 (J 28.1 m).
- 20, 22, 26. Cranidium, SUI 129887, dorsal, anterior, and left lateral views, x17 (J 28T m).
- 21, 24, 25. Cranidium, SUI 129888, anterior, dorsal, and left lateral views, x17 (YH-J).
- 23, 27, 28. Cranidium, SUI 129889, dorsal, right lateral, and anterior views, x17 (YH-J).

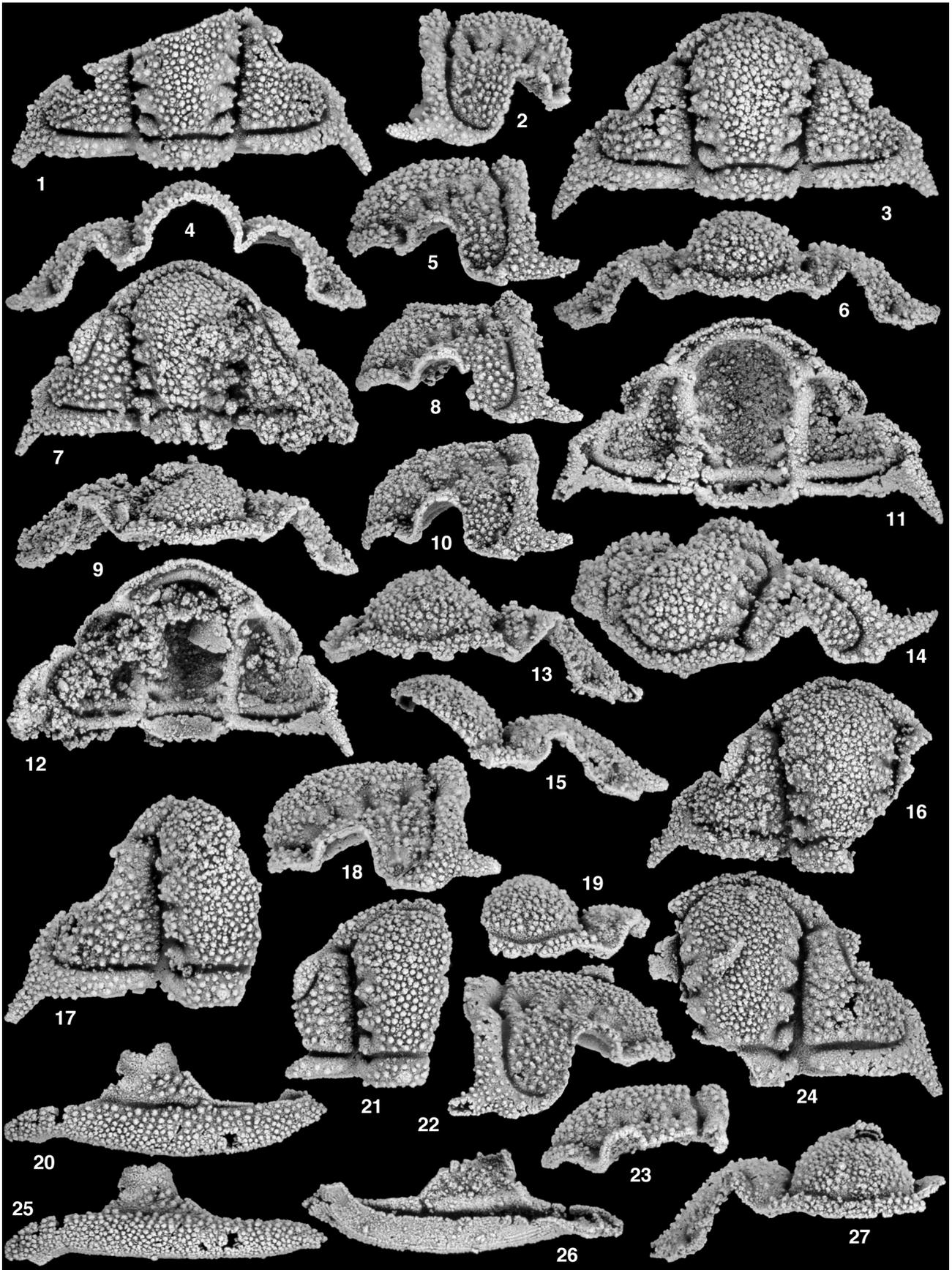


PLATE 18.

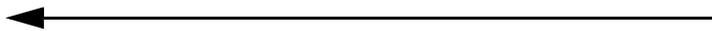


PLATE 18. *Ibexaspis rupauli* n. sp., from Locality YH-J, Yellow Hill Limestone (Floian; Blackhillsian; "*Pseudocybele nasuta* Zone"), Yellow Hill, near Pioche, Lincoln County, eastern Nevada, USA.

- 1, 2, 4. Cranidium, SUI 129890, dorsal, right lateral, and anterior views, x17.
3, 5, 6, 11, 14. Cranidium, **holotype**, SUI 129891, dorsal, left lateral, anterior, ventral, and oblique views, x17.
7, 8, 9, 12. Cranidium, SUI 129892, dorsal, left lateral, anterior, and ventral views, x15.
10, 13, 16. Cranidium, SUI 129893, left lateral, anterior, and dorsal views, x15.
15, 17, 18. Cranidium, SUI 129894, anterior, dorsal, and left lateral views, x17.
19, 21, 23. Cranidium, SUI 129895, anterior, dorsal, and left lateral views, x17.
20, 25, 26. Left librigena, SUI 129896, external, ventrolateral, and internal views, x20.
22, 24, 27. Cranidium, SUI 129897, right lateral, dorsal, and anterior views, x17.

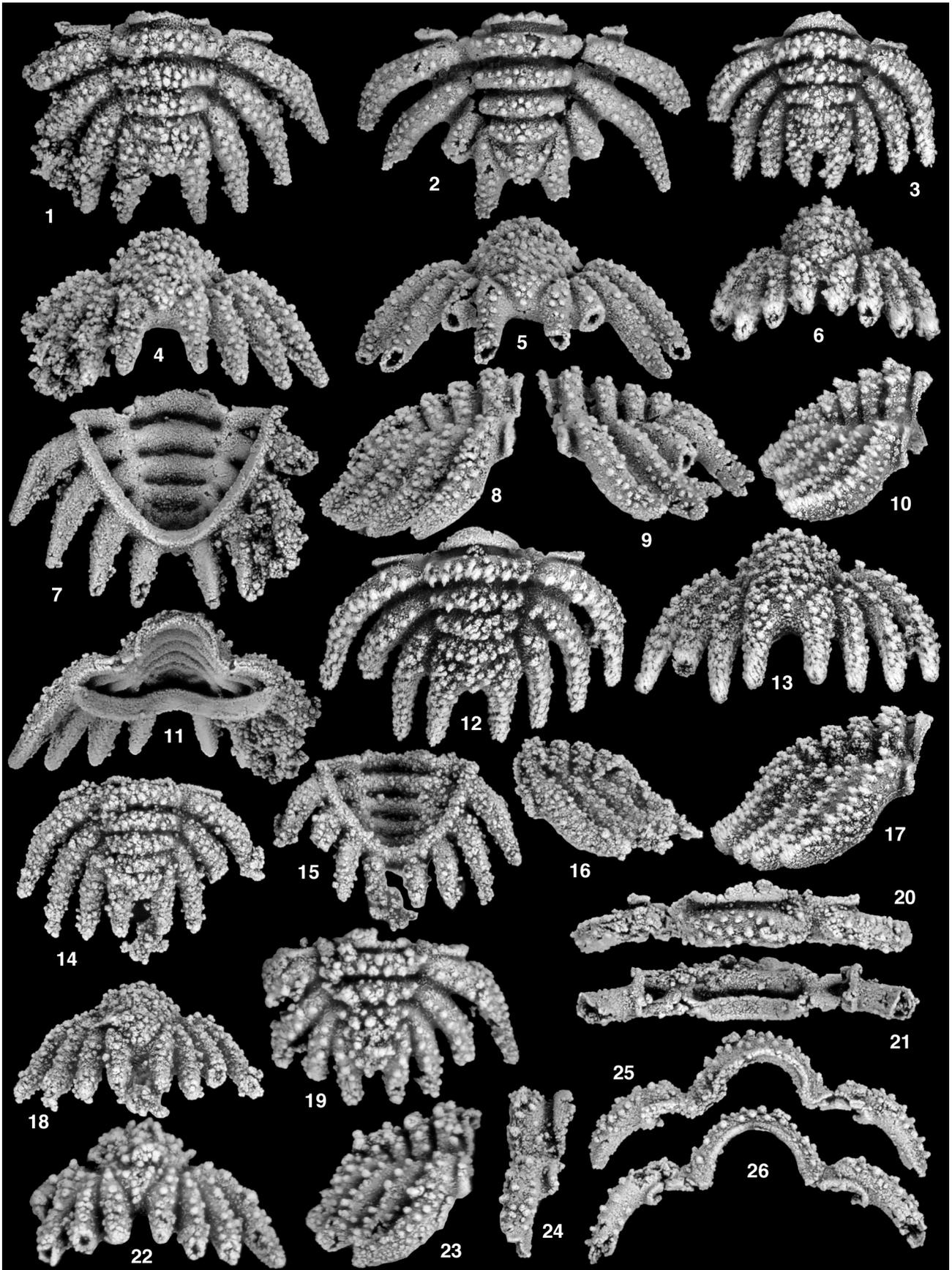


PLATE 19.



PLATE 19. *Ibexaspis rupauli* n. sp., from Locality YH-J, Yellow Hill Limestone (Floian; Blackhillsian; "*Pseudocybele nasuta* Zone"), Yellow Hill, near Pioche, Lincoln County, eastern Nevada, USA.

- 1, 4, 7, 8, 11. Pygidium, SUI 129898, dorsal, posterior, ventral, right lateral, and anterior views, x20.
2, 5, 9. Pygidium, SUI 129899, dorsal, posterior, and left lateral views, x20.
3, 6, 10. Pygidium, SUI 129900, dorsal, posterior, and right lateral views, x25.
12, 13, 17 Pygidium, SUI 129901, dorsal, posterior, and right lateral views, x20.
14–16, 18. Pygidium, SUI 129902, dorsal, ventral, left lateral, and posterior views, x20.
19, 22, 23. Pygidium, SUI 129903, dorsal, posterior, and right lateral views, x30.
20, 21, 24, 25, 26. Thoracic segment, SUI 129904, dorsal, ventral, right lateral, anterior, and posterior views, x20.

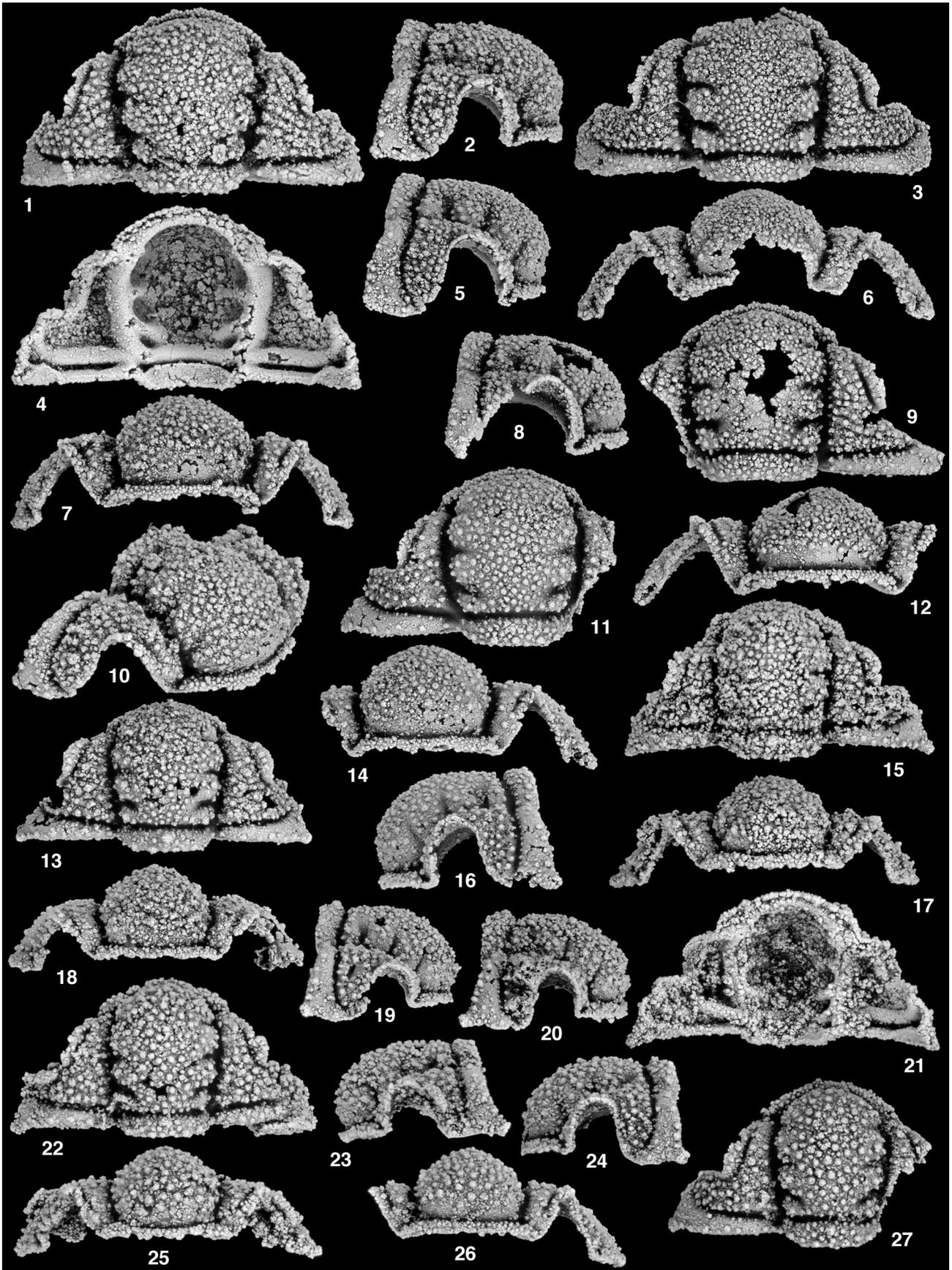


PLATE 20.



PLATE 20. *Deltapliomera inglei* n. sp., from Section H 127.1 m, Fillmore Formation (Floian; Tulean; *Heckethornia bowiei* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

- 1, 2, 4, 7, 10. Cranidium, SUI 129553, dorsal, right lateral, ventral, anterior, and oblique views, x15.
3, 5, 6. Cranidium, SUI 129554, dorsal, right lateral, and anterior views, x12.
8, 9, 12. Cranidium, SUI 129555, right lateral, dorsal, and anterior views, x12.
11, 14, 16. Cranidium, SUI 129556, dorsal, anterior, and left lateral views, x15.
13, 18, 19. Cranidium, SUI 129557, dorsal, anterior, and right lateral views, x15.
15, 17, 20, 21. Cranidium, SUI 129558, dorsal, anterior, right lateral, and ventral views, x15.
22, 23, 25. Cranidium, SUI 129559, dorsal, left lateral, and anterior views, x17.
24, 26, 27. Cranidium, SUI 129560, left lateral, anterior, and dorsal views, x17.

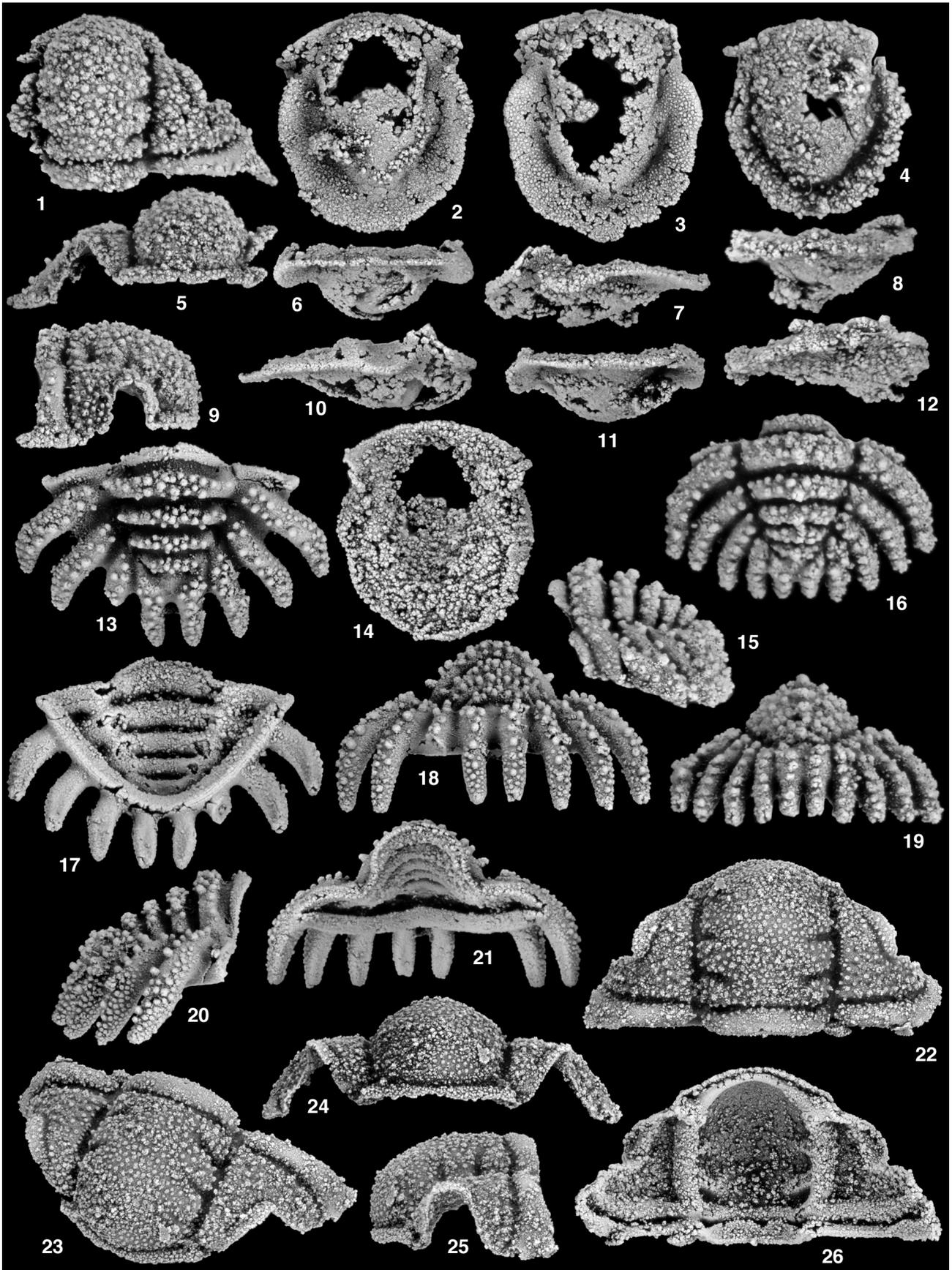


PLATE 21.



PLATE 21. 1–21. *Deltapliomera inglei* n. sp., from Section H 127.1 m, Fillmore Formation (Floian; Tulean; *Heckethornia bowiei* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

- 1, 5, 9. Cranidium, SUI 129561, dorsal, anterior, and right lateral views, x20.
2, 6, 10, 14. Hypostome, SUI 129562, ventral, posterior, right lateral, and dorsal views, x17.
3, 7, 11. Hypostome, SUI 129563, ventral, left lateral, and posterior views, x17.
4, 8, 12. Hypostome, SUI 129564, ventral, posterior, and right lateral views, x30.
13, 17, 18, 20, 21. Pygidium, **holotype**, SUI 129565, dorsal, ventral, posterior, right lateral, and anterior views, x17.
15, 16, 19. Pygidium, SUI 129566, left lateral, dorsal, and posterior views, x30.

Deltapliomera n. sp. A, from Section H 172.5T m, Fillmore Formation (Floian; Tulean; *Paniaspisp severiensis* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

- 22–26. Cranidium, SUI 115308, dorsal, oblique, anterior, left lateral, and ventral views, x12.

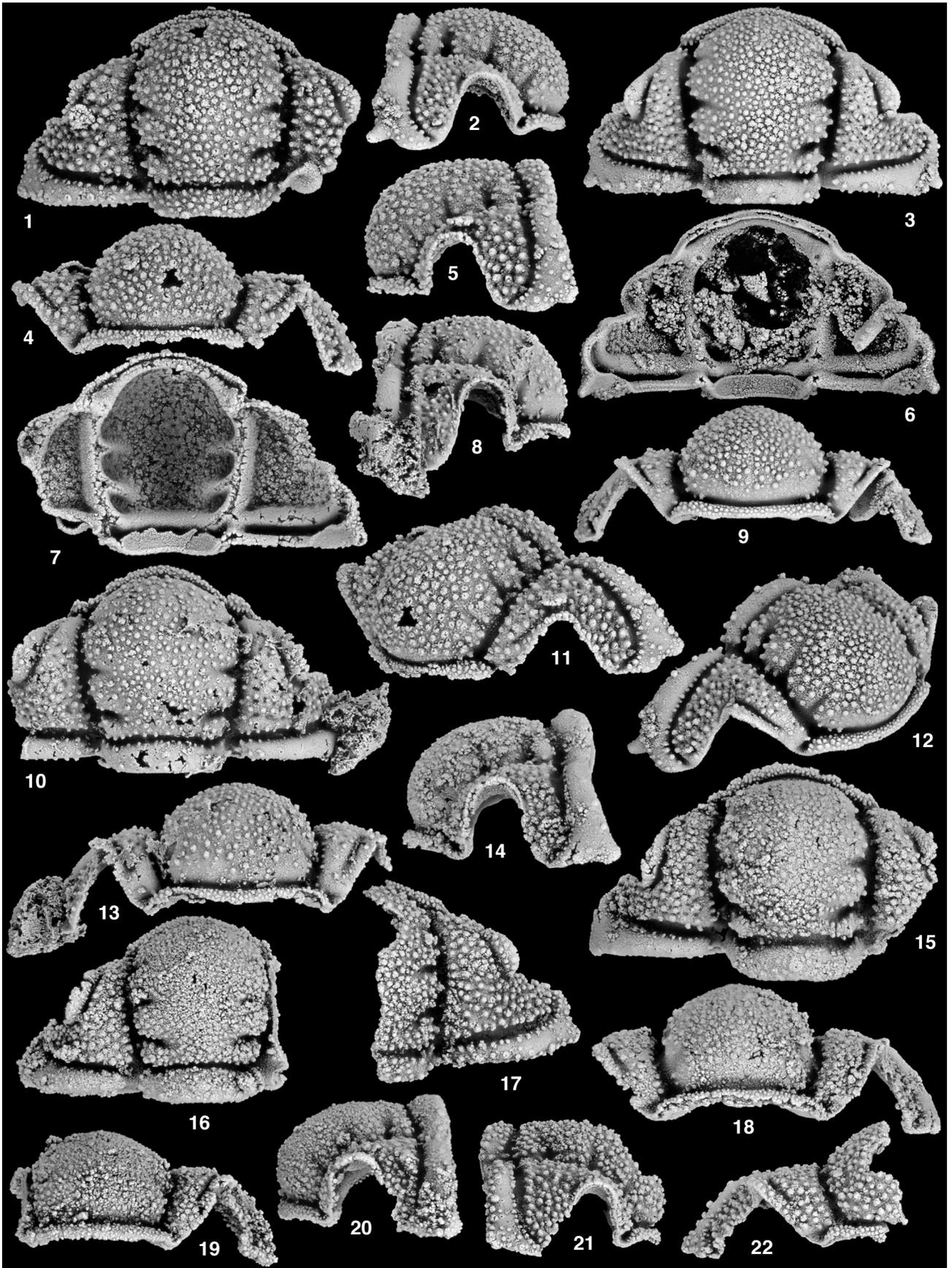


PLATE 22.



PLATE 22. *Deltapliomera heimbergi* n. sp., from Section H 166.2 m, H 173.2 m, and H 178.2 m, Fillmore Formation (Floian; Tulean; *Panisaspis sevierensis* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

1, 4, 5, 7, 11. Cranidium, SUI 129567, dorsal, anterior, left lateral, ventral, and oblique views, x14 (H 173.2 m).

2, 3, 6, 9, 12. Cranidium, **holotype**, SUI 129568, right lateral, dorsal, ventral, anterior, and oblique views, x14 (H 178.2 m).

8, 10, 13. Cranidium, SUI 129569, right lateral, dorsal, and anterior views, x14 (H 166.2 m).

14, 15, 18. Cranidium, SUI 129570, left lateral, dorsal, and anterior views, x15 (H 166.2 m).

16, 19, 20. Cranidium, SUI 129571, dorsal, anterior, and left lateral views, x15 (H 173.2 m).

17, 21, 22. Cranidium, SUI 129572, dorsal, right lateral, and anterior views, x12 (H 173.2 m).

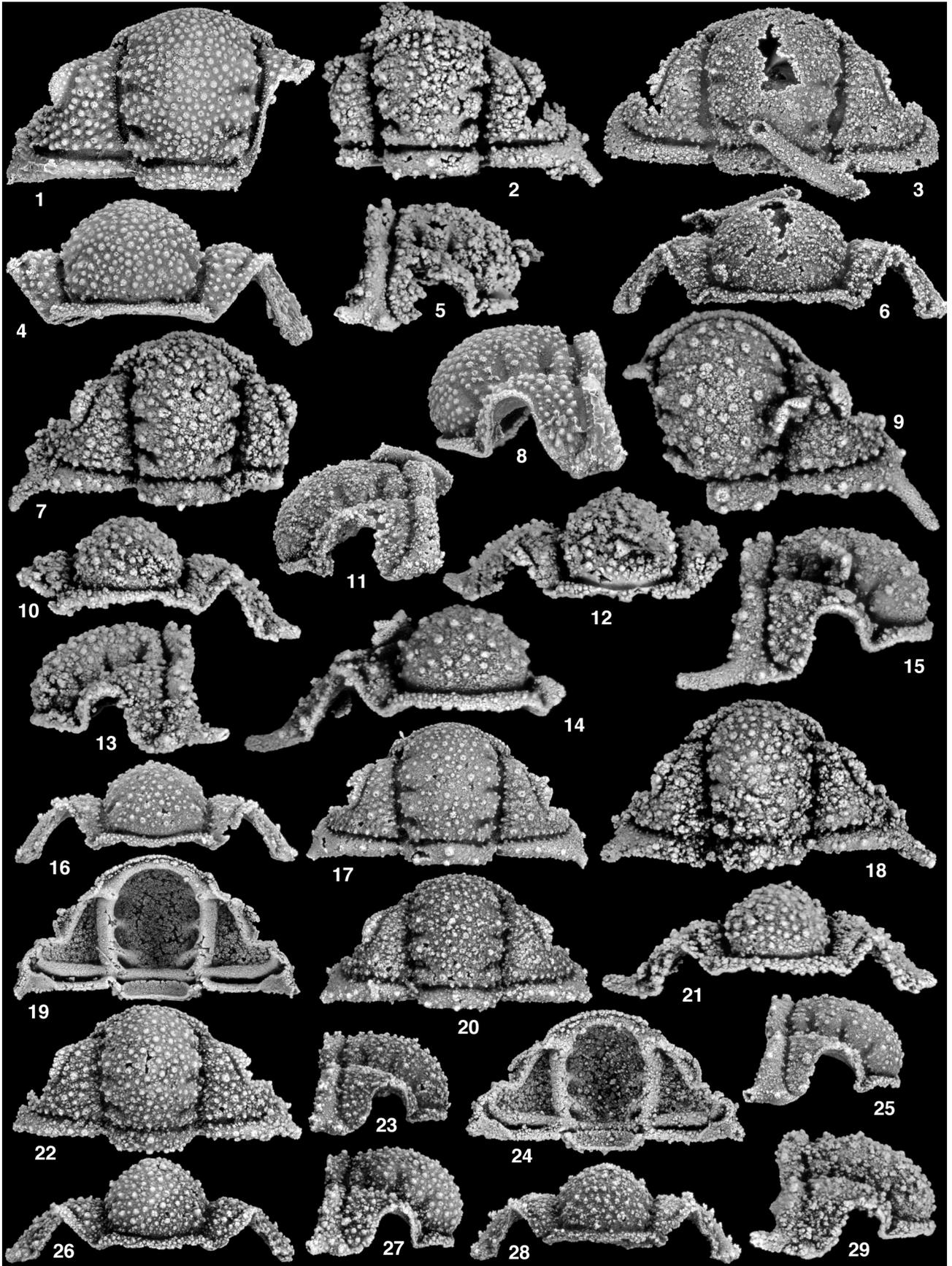


PLATE 23.



PLATE 23. *Deltapliomera heimbergi* n. sp., from Section H 172.5T m and H 173.2 m, Fillmore Formation (Floian; Tulean; *Panisaspis severiensis* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

- 1, 4, 8. Cranidium, SUI 115304, dorsal, anterior, and left lateral views, x12 (H 172.5T m).
2, 5, 12. Cranidium, SUI 129573, dorsal, right lateral, and anterior views, x20 (H 173.2 m).
3, 6, 11. Cranidium, SUI 129574, dorsal, anterior, and left lateral views, x12 (H 172.5T m).
7, 10, 13. Cranidium, SUI 129575, dorsal, anterior, and left lateral views, x20 (H 173.2 m).
9, 14, 15. Cranidium, SUI 129576, dorsal, anterior, and right lateral views, x25 (H 173.2 m).
16, 17, 19, 25. Cranidium, SUI 129577, anterior, dorsal, ventral, and right lateral views, x15 (H 172.5T m).
18, 21, 29. Cranidium, SUI 129578, dorsal, anterior, and right lateral views, x20 (H 173.2 m).
20, 23, 24, 28. Cranidium, SUI 129579, dorsal, right lateral, ventral, and anterior views, x15 (H 172.5T m).
22, 26, 27. Cranidium, SUI 129580, dorsal, anterior, and right lateral views, x15 (H 172.5T m).

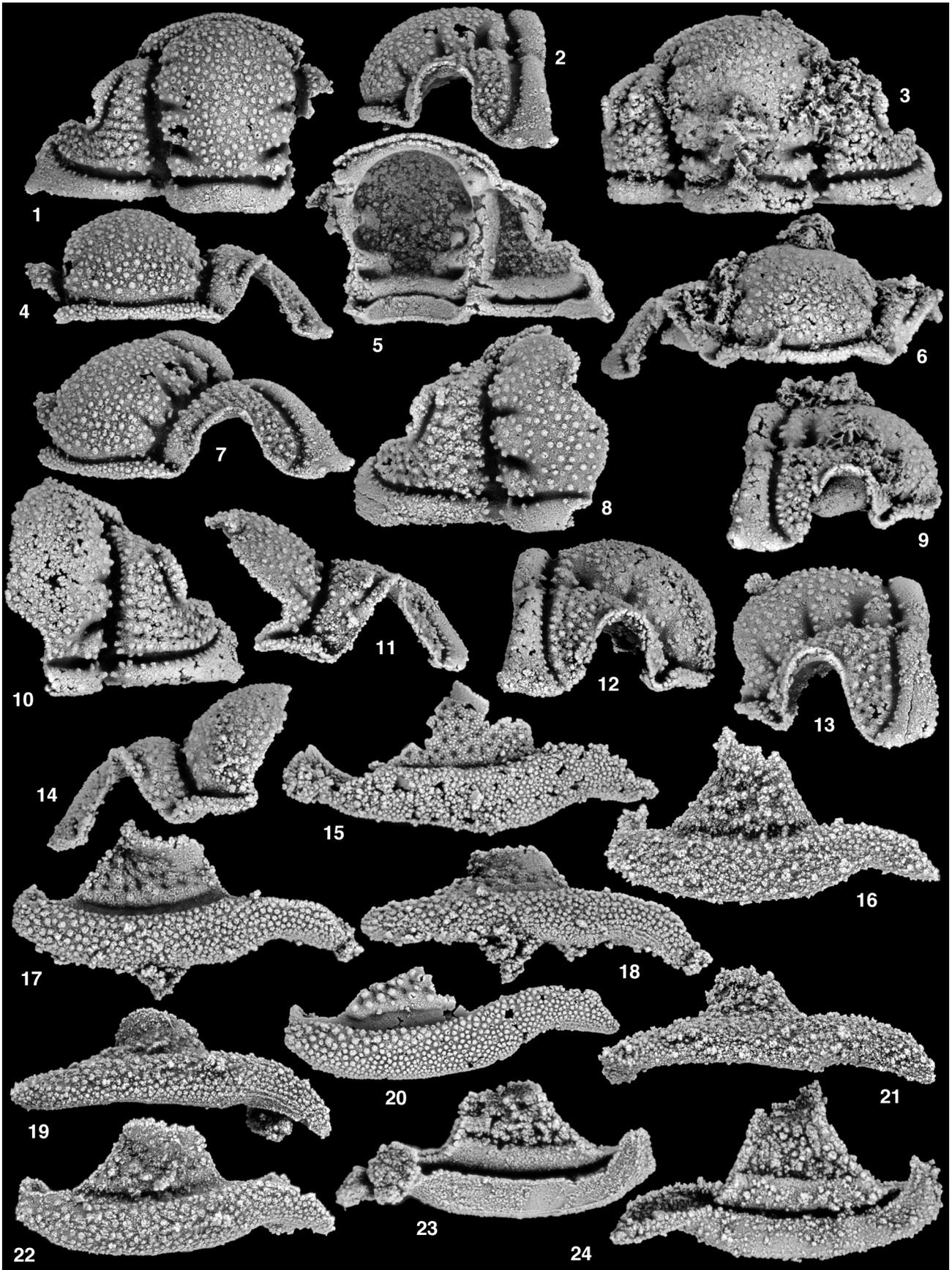


PLATE 24.



PLATE 24. *Deltapliomera heimbergi* n. sp., from Section H 166.2 m, H 172.5 m, H 172.5T m and H 173.2 m, Fillmore Formation (Floian; Tulean; *Paniaspis severiensis* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

- 1, 2, 4, 5, 7. Cranidium, SUI 129581, dorsal, left lateral, anterior, ventral, and oblique views, x17 (H 173.2 m).
- 3, 6, 9. Cranidium, SUI 129582, dorsal, anterior, and right lateral views, x17 (H 173.2 m).
- 8, 11, 13. Cranidium, SUI 129583, dorsal, anterior, and left lateral views, x15 (H 173.2 m).
- 10, 12, 14. Cranidium, SUI 129584, dorsal, right lateral, and anterior views, x15 (H 173.2 m).
15. Right librigena, SUI 129585, external view, x20 (H 172.5 m).
- 16, 21, 24. Right librigena, SUI 129586, external, ventrolateral, and internal views, x20 (H 172.5T m).
- 17, 18. Right librigena, SUI 129587, external and ventrolateral views, x20 (H 173.2 m).
- 19, 22, 23. Right librigena, SUI 129588, ventrolateral, external, and internal views, x25 (H 172.5T m).
20. Right librigena, SUI 129589, external view, x15 (H 166.2 m).

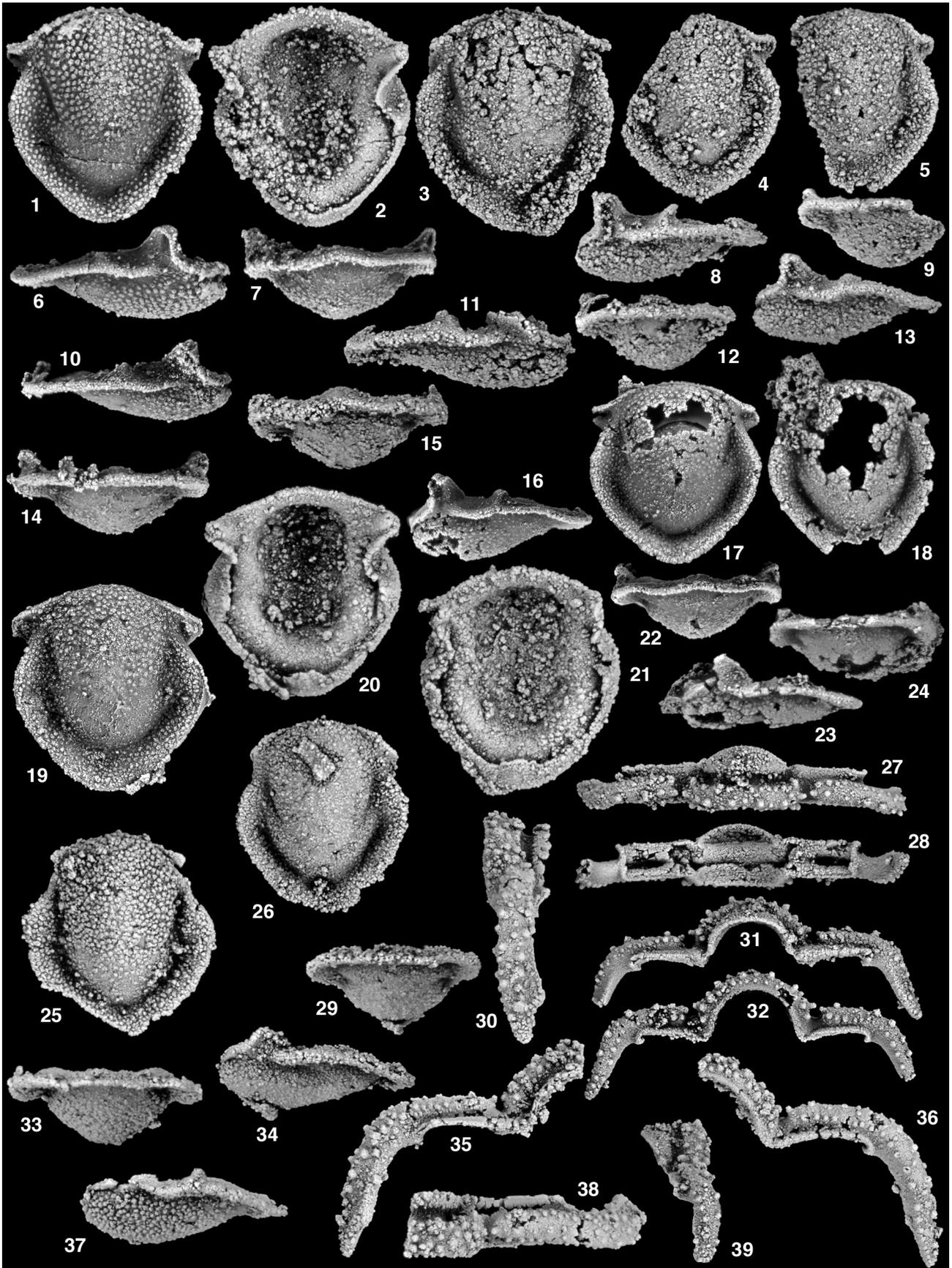


PLATE 25.



PLATE 25. *Deltapliomera heimbergi* n. sp., from Section H 166.2 m, H 172.5T m and H 173.2 m, Fillmore Formation (Floian; Tulean; *Paniaspis sevierensis* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

- 1, 2, 6, 7. Hypostome, SUI 129590, ventral, dorsal, right lateral, and posterior views, x20 (H 172.5T m).
3, 11, 15, 21. Hypostome, SUI 129591, ventral, right lateral, posterior, and dorsal views, x20 (H 173.2 m).
4, 8, 12. Hypostome, SUI 129592, ventral, left lateral, and posterior views, x20 (H 173.2 m).
5, 9, 13. Hypostome, SUI 129593, ventral, posterior, and left lateral views, x20 (H 173.2 m).
10, 14, 19, 20. Hypostome, SUI 129594, right lateral, posterior, ventral, and dorsal views, x25 (H 172.5T m).
16, 17, 22. Hypostome, SUI 129595, left lateral, ventral, and posterior views, x20 (H 172.5T m).
18, 23, 24. Hypostome, SUI 129596, ventral, left lateral, and posterior views, x25 (H 173.2 m).
25, 33, 37. Hypostome, SUI 129597, ventral, posterior, and left lateral views, x20 (H 173.2 m).
26, 29, 34. Hypostome, SUI 129598, ventral, posterior, and left lateral views, x20 (H 173.2 m).
27, 28, 31, 32, 39. Thoracic segment, SUI 129599, dorsal, ventral, anterior, posterior, and left lateral views, x15 (H 173.2 m).
30, 35, 36, 38. Thoracic segment, SUI 129600, right lateral, anterior, posterior, and dorsal views, x15 (H 166.2 m).

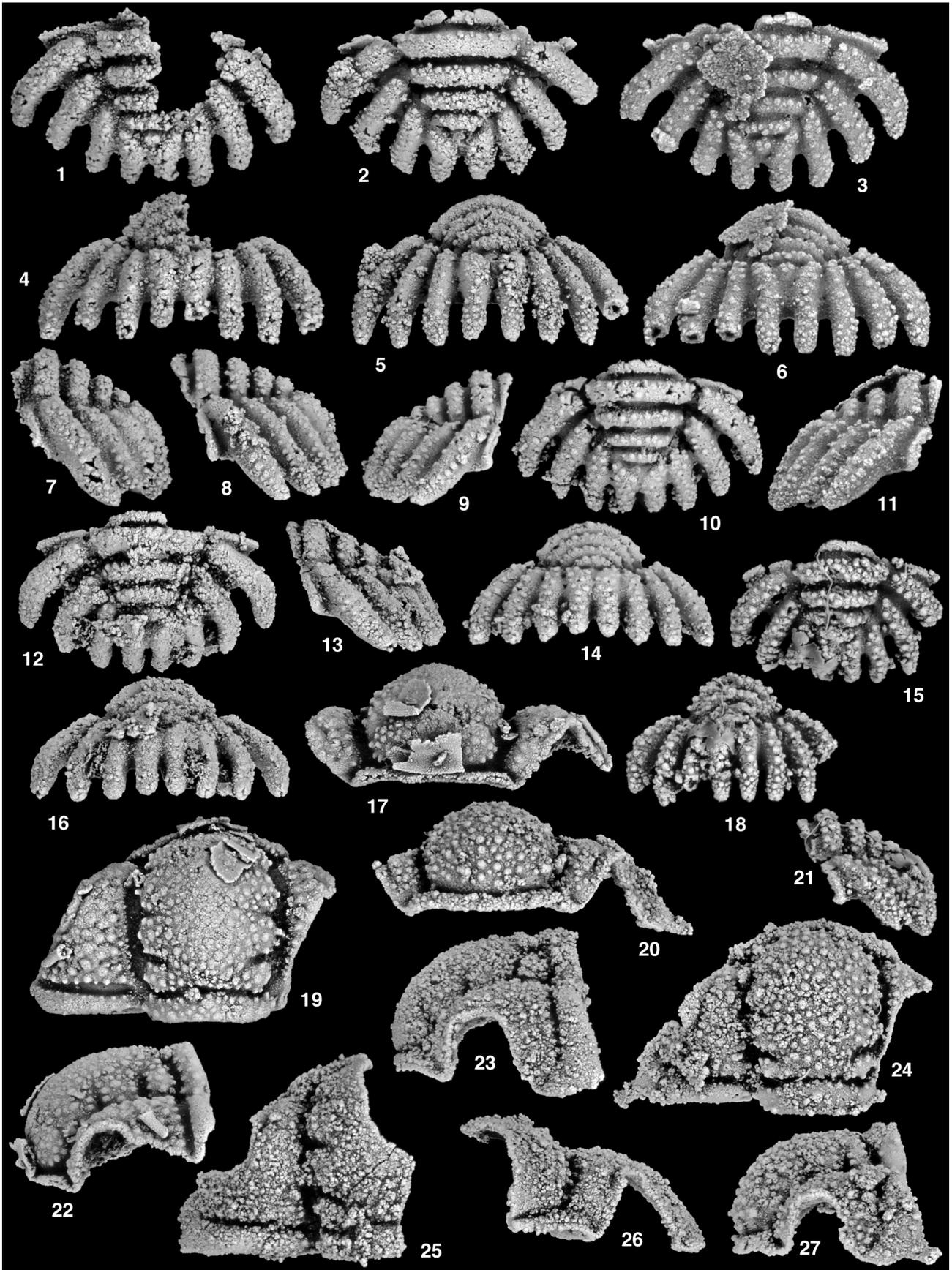


PLATE 26.



PLATE 26. *Deltaplomera heimbergi* n. sp., from Section H 166.2 m, H 172.5 m, H 172.5T m and H 173.2 m, Fillmore Formation (Floian; Tulean; *Panispis sevierensis* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

- 1, 4, 7. Pygidium, SUI 129601, dorsal, posterior, and left lateral views, x20 (H 166.2 m).
- 2, 5, 8. Pygidium, SUI 129602, dorsal, posterior, and left lateral views, x17 (H 166.2 m).
- 3, 6, 11. Pygidium, SUI 115308, dorsal, posterior, and right lateral views, x20 (H 172.5T m).
- 9, 10, 14. Pygidium, SUI 129603, right lateral, dorsal, and posterior views, x20 (H 172.5 m).
- 12, 13, 16. Pygidium, SUI 129604, dorsal, left lateral, and posterior views, x15 (H 172.5 m).
- 15, 18, 21. Pygidium, SUI 129605, dorsal, posterior, and left lateral views, x20 (H 173.2 m).
- 17, 19, 22. Cranidium, SUI 129606, anterior, dorsal, and left lateral views, x15 (H 173.2 m).
- 20, 24, 27. Cranidium, SUI 129607, anterior, dorsal, and left lateral views, x17 (H 173.2 m).
- 23, 25, 26. Cranidium, SUI 129608, left lateral, dorsal, and anterior views, x17 (H 173.2 m).

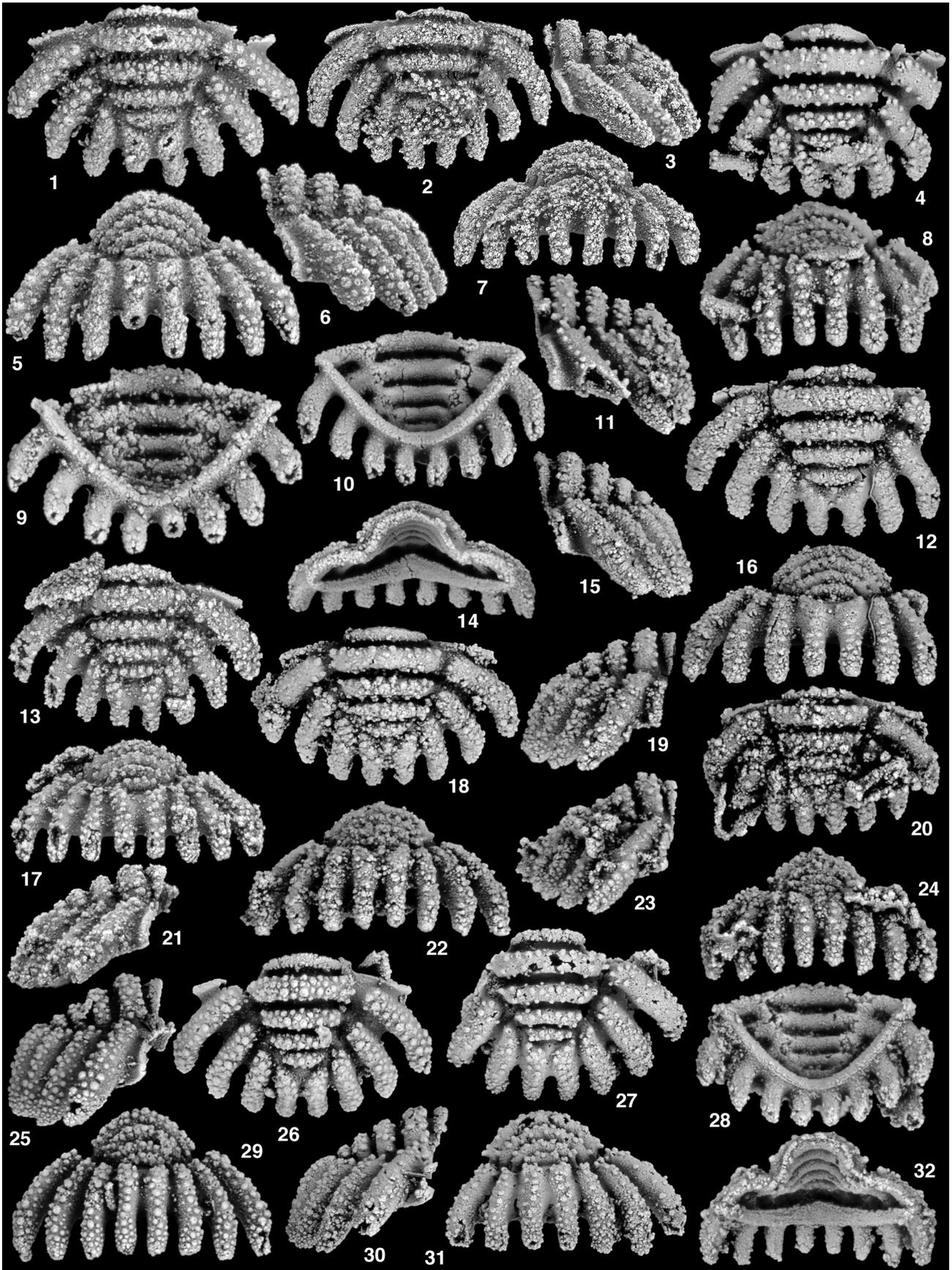


PLATE 27.



PLATE 27. *Deltapliomera heimbergi* n. sp., from Section H 166.2 m, H 172.5T m and H 173.2 m, Fillmore Formation (Floian; Tulean; *Panispaspis severiensis* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

- 1, 5, 6, 9. Pygidium, SUI 115305, dorsal, posterior, left lateral, and ventral views, x20 (H 172.5T m).
2, 3, 7, 10, 14. Pygidium, SUI 129609, dorsal, left lateral, posterior, ventral, and anterior views, x20 (H 172.5T m).
4, 8, 11. Pygidium, SUI 129610, dorsal, posterior, and left lateral views, x20 (H 173.2 m).
12, 15, 16. Pygidium, SUI 129611, dorsal, left lateral, and posterior views, x20 (H 173.2 m).
13, 17, 21. Pygidium, SUI 129612, dorsal, posterior, and right lateral views, x17 (H 172.5T m).
18, 19, 22. Pygidium, SUI 129613, dorsal, right lateral, and posterior views, x20 (H 173.2 m).
20, 23, 24, 28, 32. Pygidium, SUI 129614, dorsal, right lateral, posterior, ventral, and anterior views, x20 (H 173.2 m).
25, 26, 29. Pygidium, SUI 129615, right lateral, dorsal, and posterior views, x20 (H 173.2 m).
27, 30, 31. Pygidium, SUI 129616, dorsal, right lateral, and posterior views, x15 (H 166.2 m).

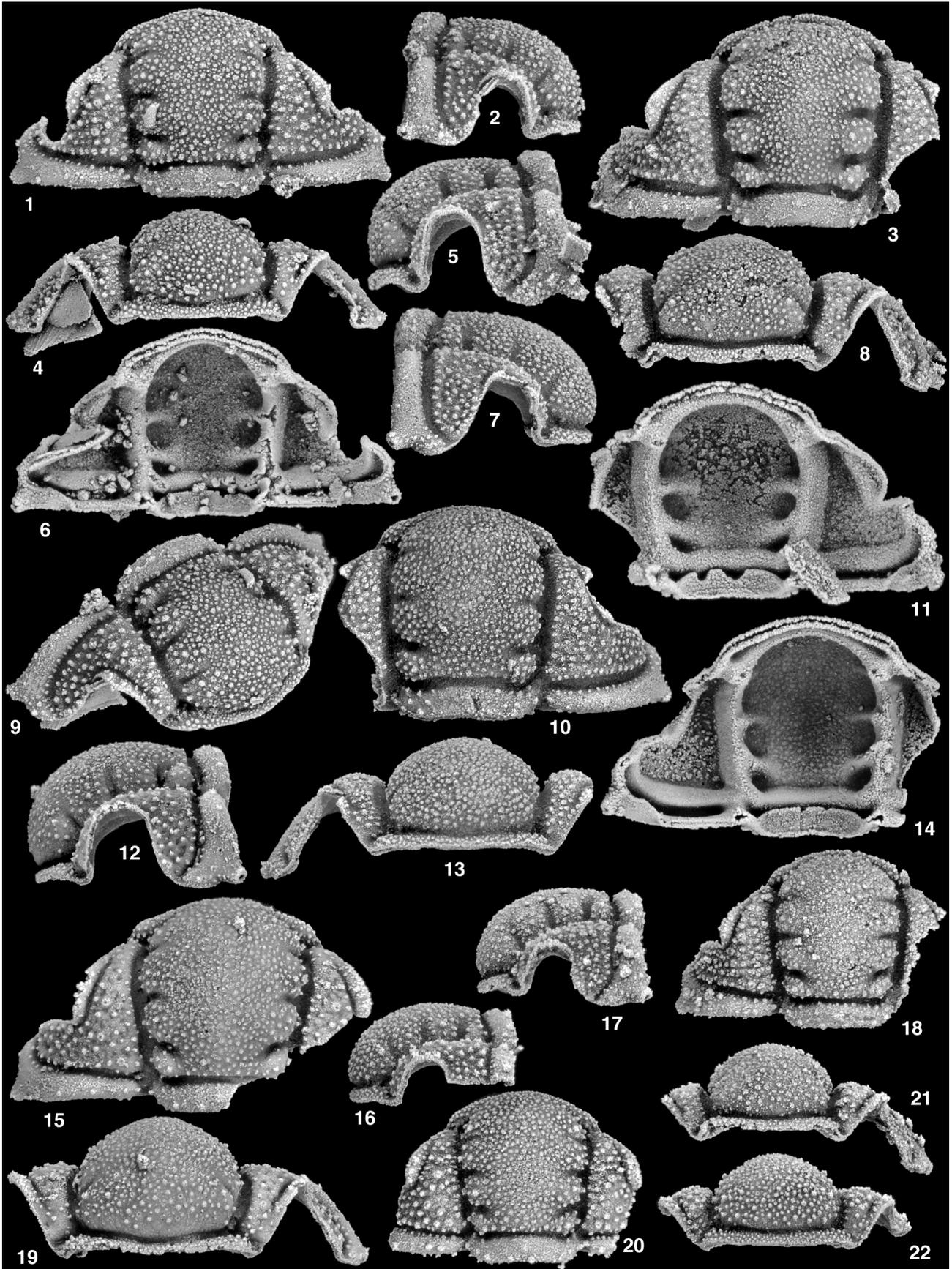


PLATE 28.



PLATE 28. *Deltapliomera eppersoni* n. sp., from Section H 191.7 m, Fillmore Formation (Floian; Blackhillsian; *Bathyrina plicolabeona* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. All magnifications are x15.

- 1, 2, 4, 6, 9. Cranidium, **holotype**, SUI 115337, dorsal, right lateral, anterior, ventral, and oblique views.
3, 5, 8, 11. Cranidium, SUI 129617, dorsal, left lateral, anterior, and ventral views.
7, 10, 13, 14. Cranidium, SUI 129618, right lateral, dorsal, anterior, and ventral views.
12, 15, 19. Cranidium, SUI 129619, left lateral, dorsal, and anterior views.
16, 20, 22. Cranidium, SUI 129620, left lateral, dorsal, and anterior views.
17, 18, 21. Cranidium, SUI 129621, left lateral, dorsal, and anterior views.

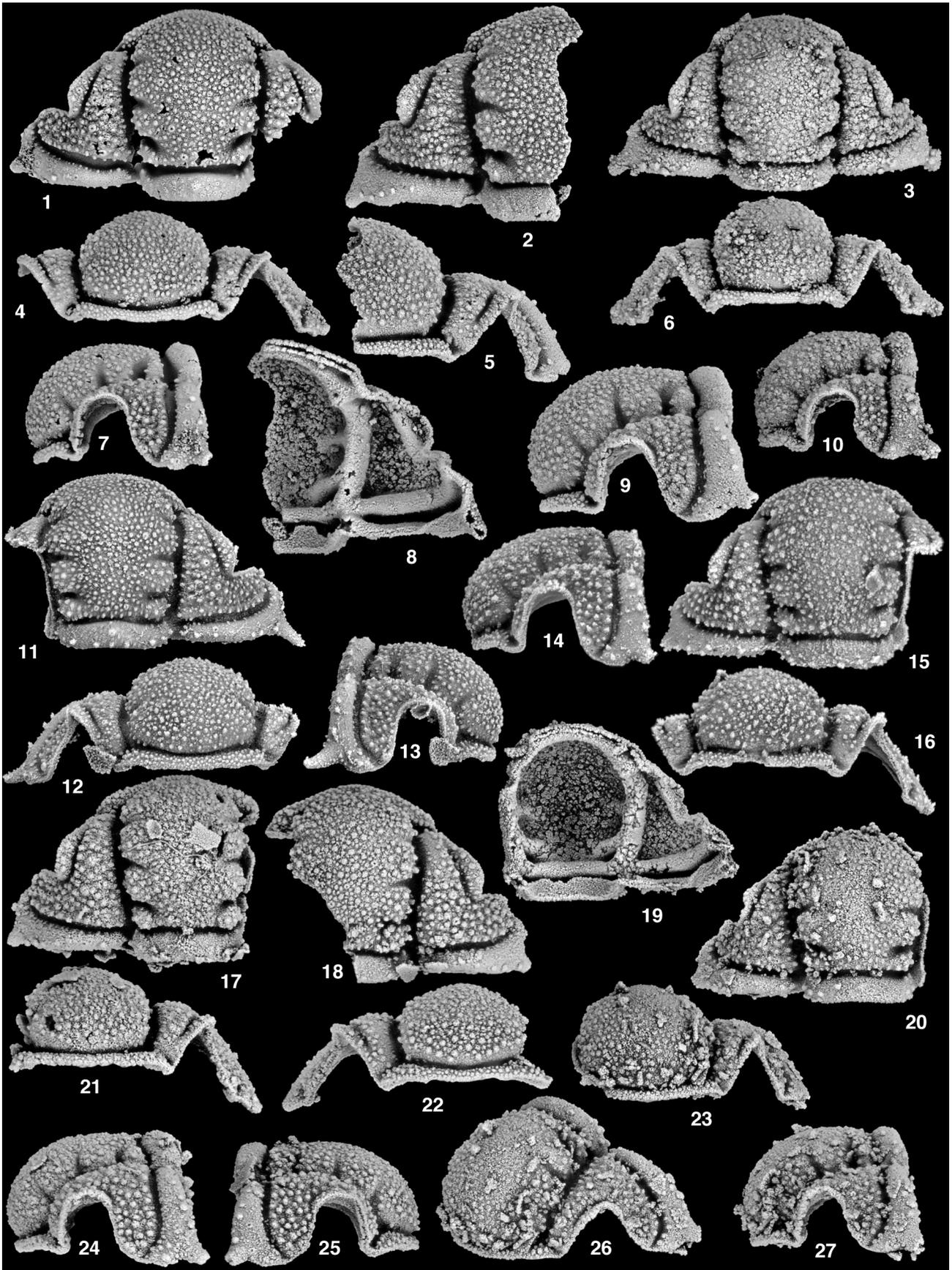


PLATE 29.



PLATE 29. *Deltapliomera eppersoni* n. sp., from Section H 185.6 m, H 186.2 m, and H 191.7 m, Fillmore Formation (Floian; Blackhillsian; *Bathyrina plicolabeona* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

- 1, 4, 7. Cranidium, SUI 129622, dorsal, anterior, and left lateral views, x15 (H 186.2 m).
2, 5, 8, 9. Cranidium, SUI 129623, dorsal, anterior, ventral, and left lateral views, x15 (H 185.6 m).
3, 6, 10. Cranidium, SUI 129624, dorsal, anterior, and left lateral views, x15 (H 186.2 m).
11–13. Cranidium, SUI 129625, dorsal, anterior, and right lateral views, x15 (H 191.7 m).
14–16. Cranidium, SUI 129626, left lateral, dorsal, and anterior views, x15 (H 191.7 m).
17, 21, 24. Cranidium, SUI 129627, dorsal, anterior, and left lateral views, x15 (H 191.7 m).
18, 22, 25. Cranidium, SUI 129628, dorsal, anterior, and right lateral views, x15 (H 191.7 m).
19, 20, 23, 26, 27. Cranidium, SUI 129629, ventral, dorsal, anterior, oblique, and left lateral views, x14 (H 185.6 m).

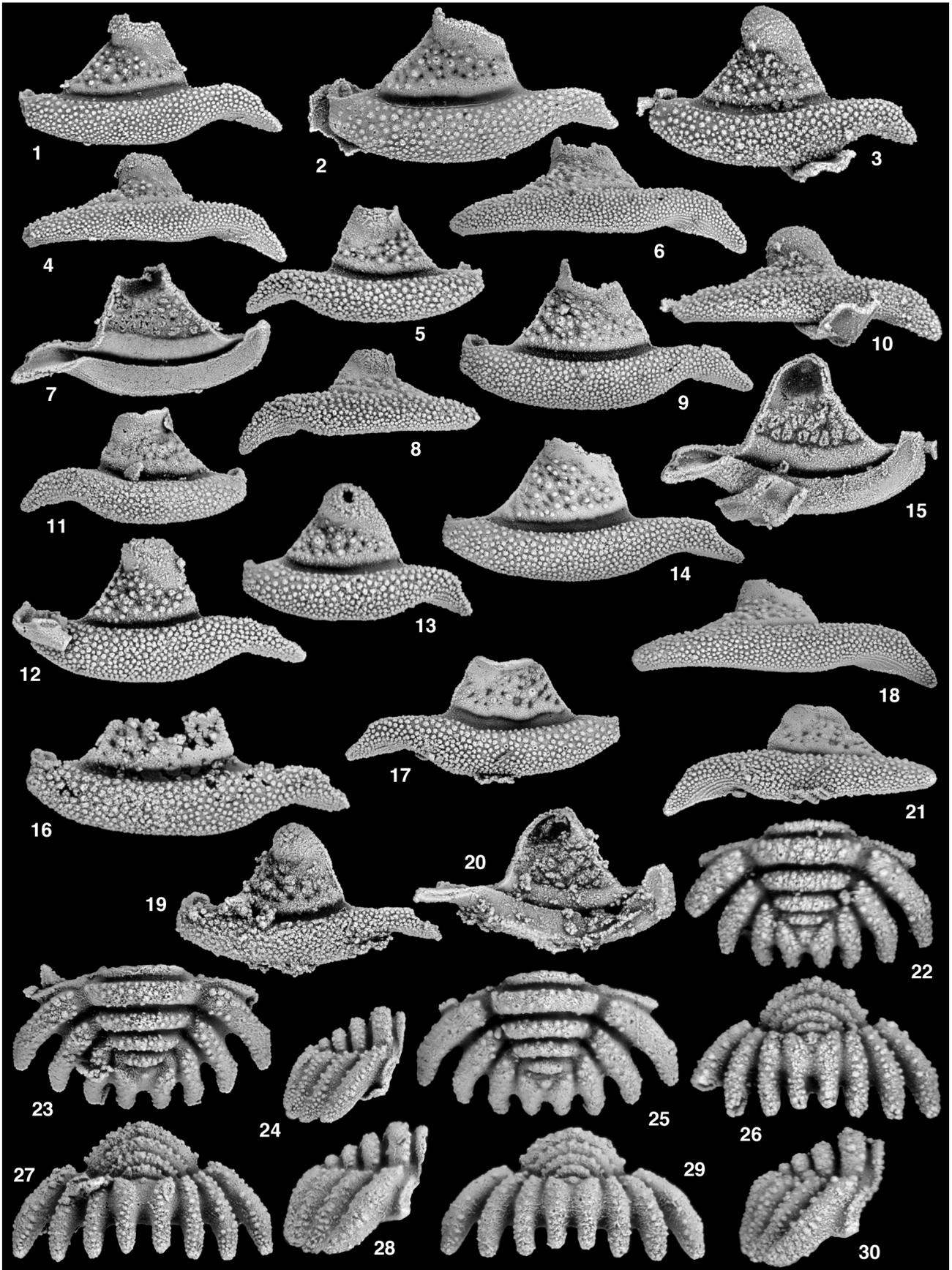


PLATE 30.



PLATE 30. *Deltapliomera eppersoni* n. sp., from Section H 186.2 m, H 187.4 m, and H 191.7 m, Fillmore Formation (Floian; Blackhillsian; *Bathyrina plicolabeona* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

- 1, 4, 7. Right librigena, SUI 129630, external, ventrolateral, and internal views, x15 (H 191.7 m).
2. Right librigena, SUI 129631, external view, x20 (H 191.7 m).
- 3, 10, 15. Right librigena, SUI 129632, external, ventrolateral, and internal views, x15 (H 191.7 m).
- 5, 8. Left librigena, SUI 129633, external and ventrolateral views, x15 (H 191.7 m).
- 6, 9. Right librigena, SUI 129634, ventrolateral and external views, x15 (H 191.7 m).
11. Left librigena, SUI 129635, external view, x15 (H 191.7 m).
12. Right librigena, SUI 129636, external view, x17 (H 191.7 m).
13. Right librigena, SUI 129637, external view, x20 (H 191.7 m).
- 14, 18. Right librigena, SUI 129638, external and ventrolateral views, x15 (H 191.7 m).
16. Right librigena, SUI 129639, external view, x20 (H 187.4 m).
- 17, 21. Left librigena, SUI 129640, external and ventrolateral views, x15 (H 191.7 m).
- 19, 20. Right librigena, SUI 129641, external and internal views, x15 (H 186.2 m).
- 22, 26, 30. Pygidium, SUI 129642, dorsal, posterior, and right lateral views, x30 (H 191.7 m).
- 23, 24, 27. Pygidium, SUI 129643, dorsal, right lateral, and posterior views, x20 (H 191.7 m).
- 25, 28, 29. Pygidium, SUI 129644, dorsal, right lateral, and posterior views, x25 (H 191.7 m).

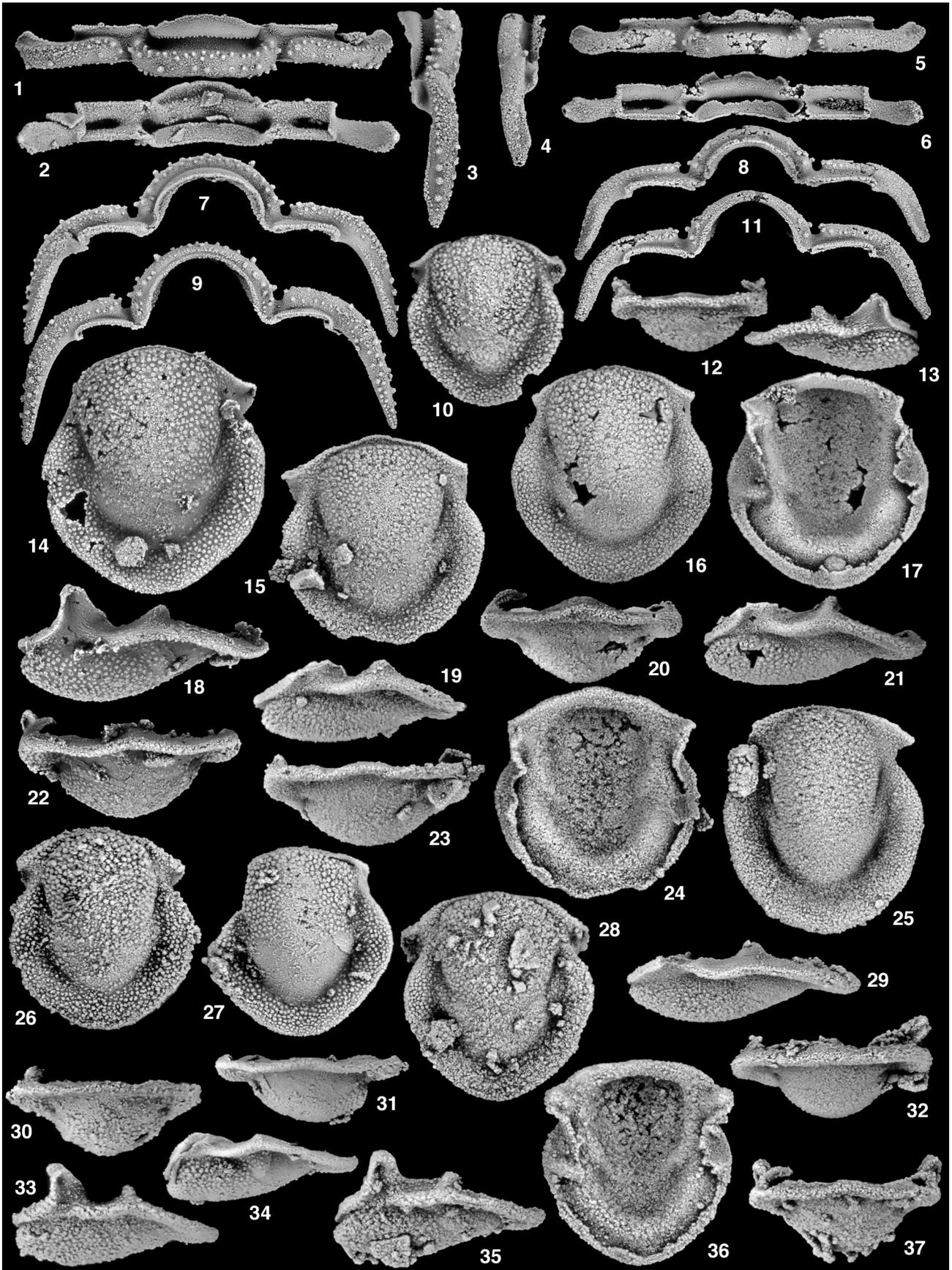


PLATE 31.



PLATE 31. *Deltaplomera eppersoni* n. sp., from Section H 185.6 m, H 186.2 m, H 187.4 m, and H 191.7 m, Fillmore Formation (Floian; Blackhillsian; *Bathyrina plicolabeona* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

1–3, 7, 9. Thoracic segment, SUI 129645, dorsal, ventral, left lateral, anterior, and posterior views, x12 (H 191.7 m).

4–6, 8, 11. Thoracic segment, SUI 129646, right lateral, dorsal, ventral, anterior, and posterior views, x12 (H 191.7 m).

10, 12, 13. Hypostome, SUI 129647, ventral, posterior, and right lateral views, x25 (H 191.7 m).

14, 18, 22. Hypostome, SUI 129648, ventral, left lateral, and posterior views, x20 (H 185.6 m).

15, 19, 23, 24. Hypostome, SUI 129649, ventral, left lateral, posterior, and dorsal views, x20 (H 185.6 m).

16, 17, 20, 21. Hypostome, SUI 129650, ventral, dorsal, posterior, and left lateral views, x20 (H 186.2 m).

25, 29, 32. Hypostome, SUI 129651, ventral, left lateral, and posterior views, x17 (H 187.4 m).

26, 30, 33. Hypostome, SUI 129652, ventral, posterior, and left lateral views, x25 (H 191.7 m).

27, 31, 34. Hypostome, SUI 129653, ventral, posterior, and left lateral views, x20 (H 191.7 m).

28, 35–37. Hypostome, SUI 129654, ventral, left lateral, dorsal, and posterior views, x20 (H 186.2 m).

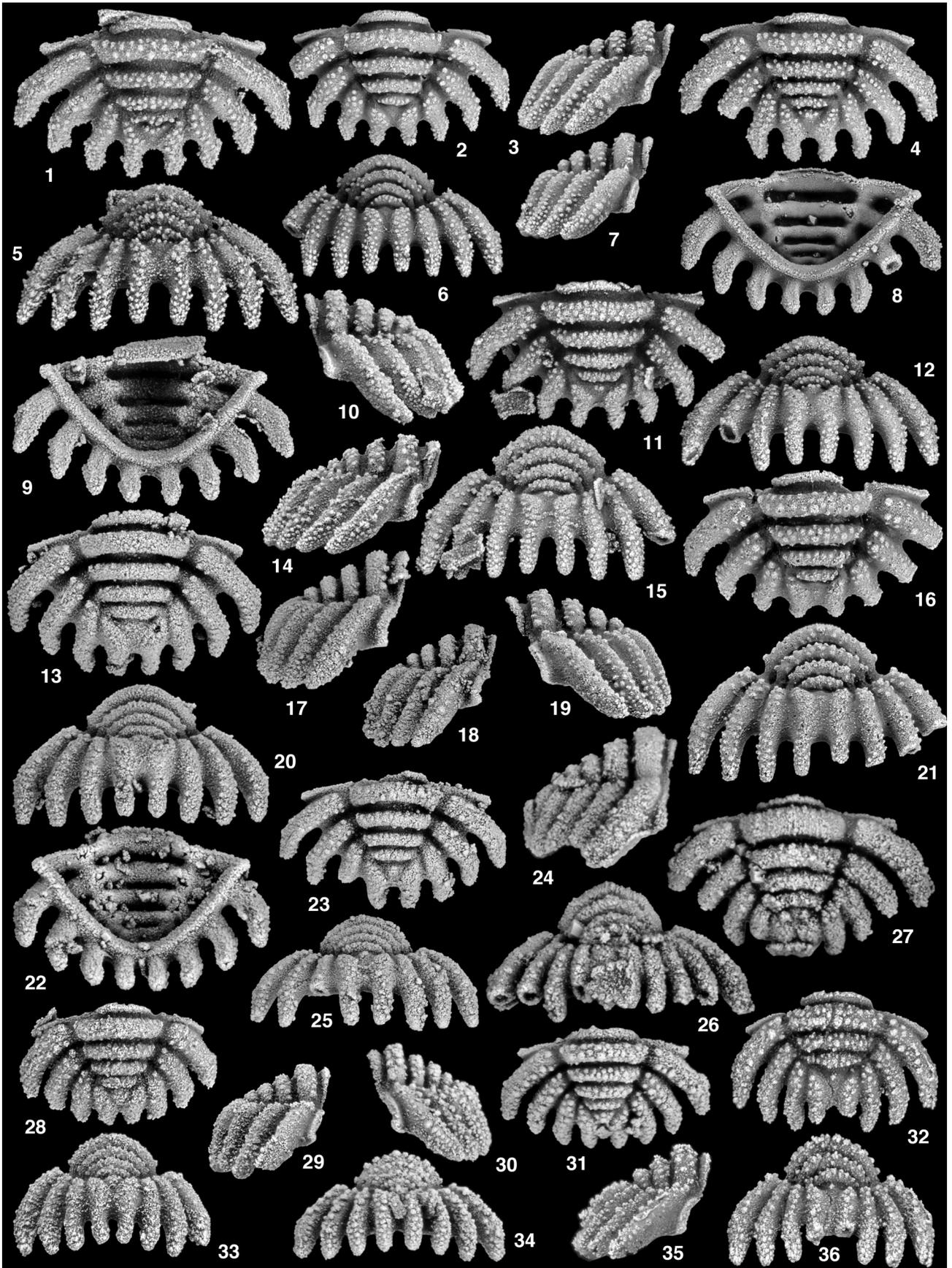


PLATE 32.



PLATE 32. *Deltaplomera eppersoni* n. sp., from Section H 185.6 m and H 191.7 m, Fillmore Formation (Floian; Blackhillsian; *Bathyrina plicolabeona* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

- 1, 5, 9, 14. Pygidium, SUI 115338, dorsal, posterior, ventral, and right lateral views, x15 (H 191.7 m).
- 2, 6, 7. Pygidium, SUI 129655, dorsal, posterior, and right lateral views, x15 (H 191.7 m).
- 3, 4, 8, 12. Pygidium, SUI 129656, right lateral, dorsal, ventral, and posterior views, x15 (H 191.7 m).
- 10, 11, 15. Pygidium, SUI 129657, left lateral, dorsal, and posterior views, x15 (H 191.7 m).
- 13, 17, 20, 22. Pygidium, SUI 129658, dorsal, right lateral, posterior, and ventral views, x17 (H 185.6 m).
- 16, 19, 21. Pygidium, SUI 129659, dorsal, left lateral, and posterior views, x20 (H 191.7 m).
- 18, 23, 25. Pygidium, SUI 129660, right lateral, dorsal, and posterior views, x12 (H 187.4 m).
- 24, 26, 27. Pygidium, SUI 129661, right lateral, posterior, and dorsal views, x30 (H 185.6 m).
- 28, 29, 33. Pygidium, SUI 129662, dorsal, right lateral, and posterior views, x20 (H 191.7 m).
- 30, 31, 34. Pygidium, SUI 129663, left lateral, dorsal, and posterior views, x20 (H 191.7 m).
- 32, 35, 36. Pygidium, SUI 129664, dorsal, right lateral, and posterior views, x25 (H 191.7 m).

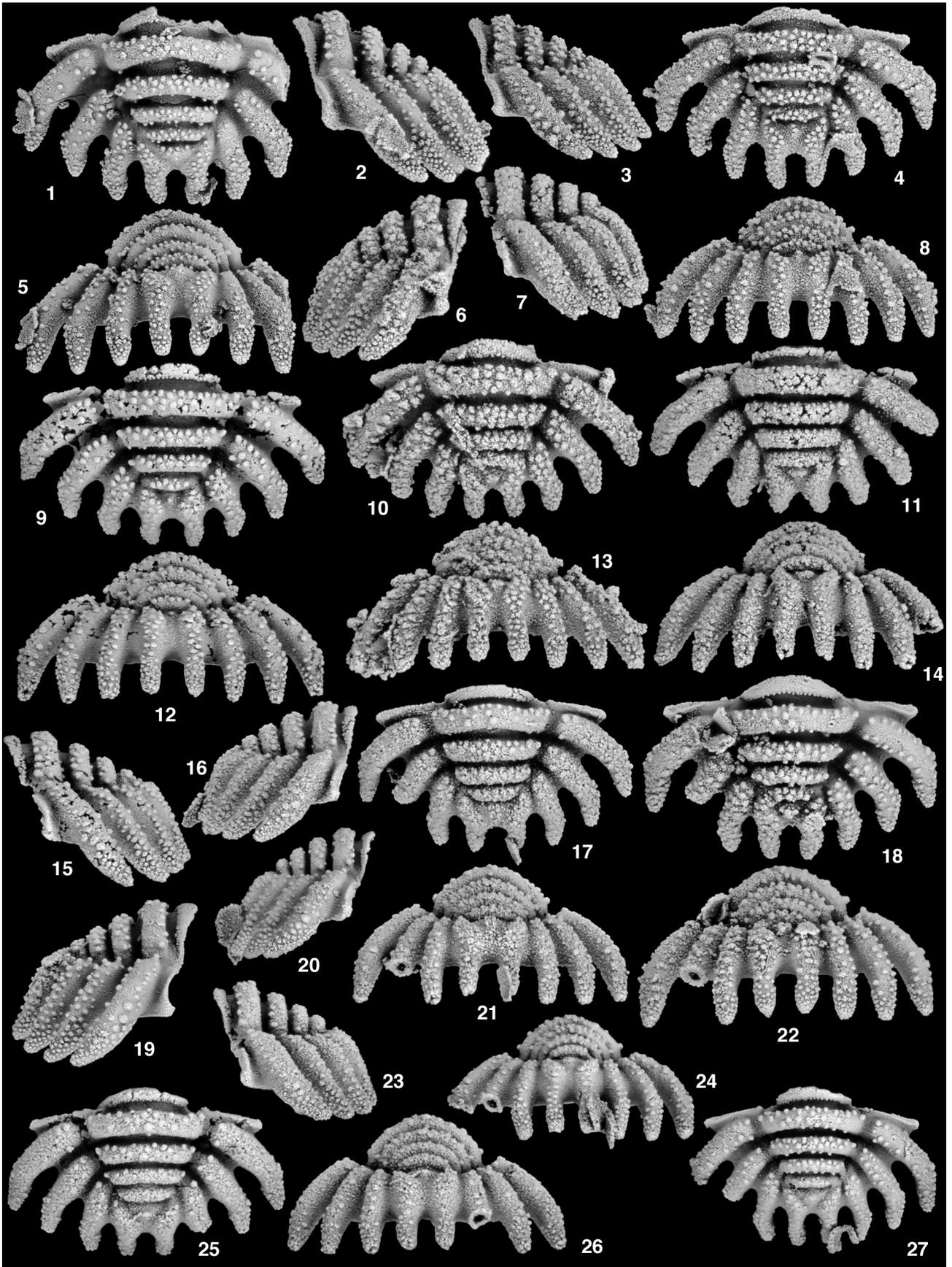


PLATE 33.



PLATE 33. *Deltapliomera eppersoni* n. sp., from Section H 191.7 m, Fillmore Formation (Floian; Blackhillsian; *Bathyrina plicolabeona* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

- 1, 2, 5. Pygidium, SUI 129665, dorsal, left lateral, and posterior views, x15.
3, 4, 8. Pygidium, SUI 129666, left lateral, dorsal, and posterior views, x15.
6, 10, 13. Pygidium, SUI 129667, right lateral, dorsal, and posterior views, x17.
7, 11, 14. Pygidium, SUI 129668, left lateral, dorsal, and posterior views, x17.
9, 12, 15. Pygidium, SUI 129669, dorsal, posterior, and left lateral views, x17.
16, 17, 21. Pygidium, SUI 129670, right lateral, dorsal, and posterior views, x17.
18, 19, 22. Pygidium, SUI 129671, dorsal, right lateral, and posterior views, x17.
20, 24, 27. Pygidium, SUI 129672, right lateral, posterior, and dorsal views, x17.
23, 25, 26. Pygidium, SUI 129673, left lateral, dorsal, and posterior views, x20.

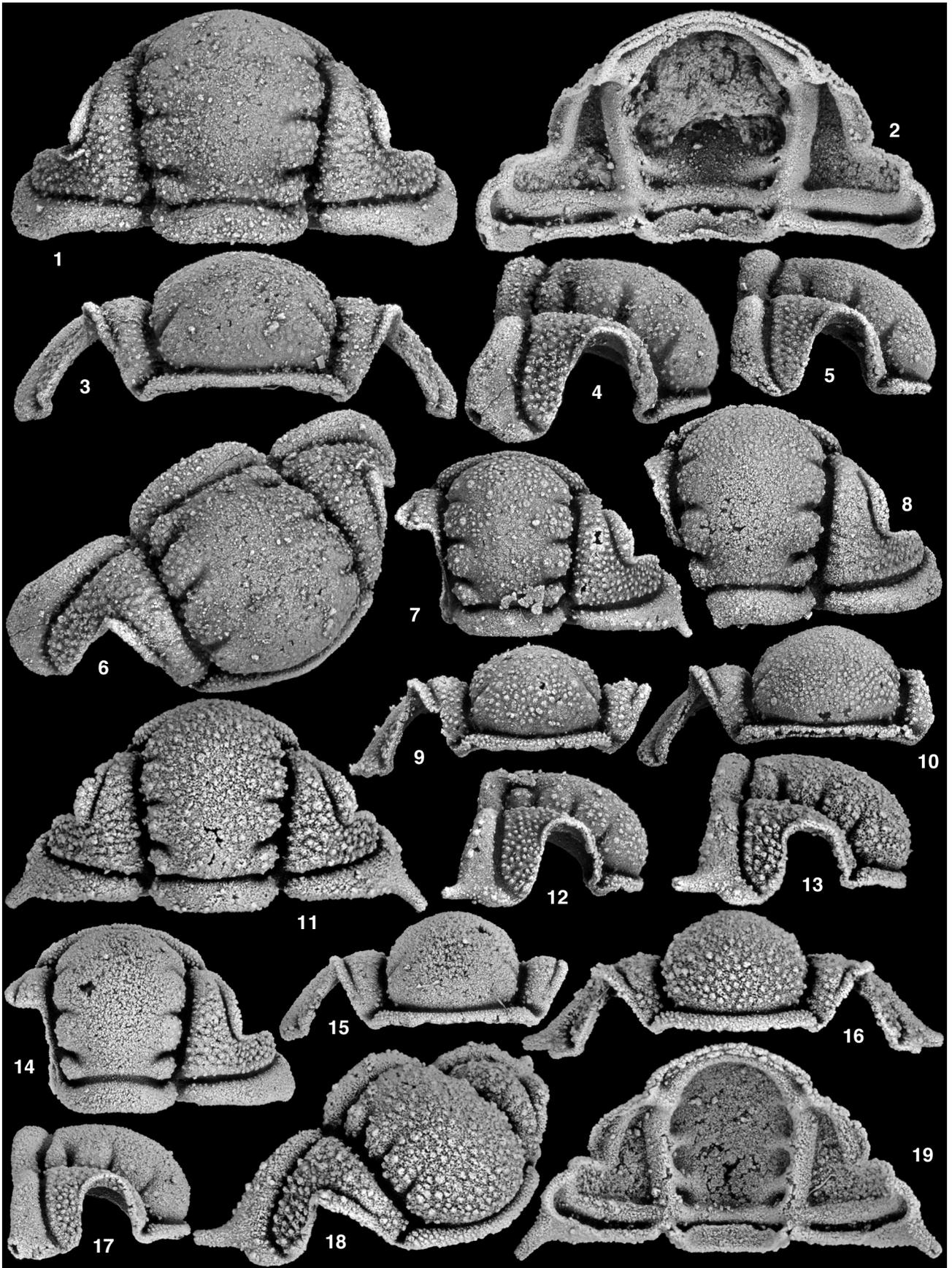


PLATE 34.



PLATE 34. *Deltapliomera humphriesi* n. sp., from Section H 208.2 m, Fillmore Formation (Floian; Blackhillsian; *Carolinites nevadensis* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

1–4, 6. Cranidium, SUI 115358, dorsal, ventral, anterior, right lateral, and oblique views, x15.

5, 8, 10. Cranidium, SUI 129674, right lateral, dorsal, and anterior views, x15.

7, 9, 12. Cranidium, SUI 129675, dorsal, anterior, and right lateral views, x15.

11, 13, 16, 18, 19. Cranidium, SUI 129676, dorsal, right lateral, anterior, oblique, and ventral views, x20.

14, 15, 17. Cranidium, SUI 129677, dorsal, anterior, and right lateral views, x15.

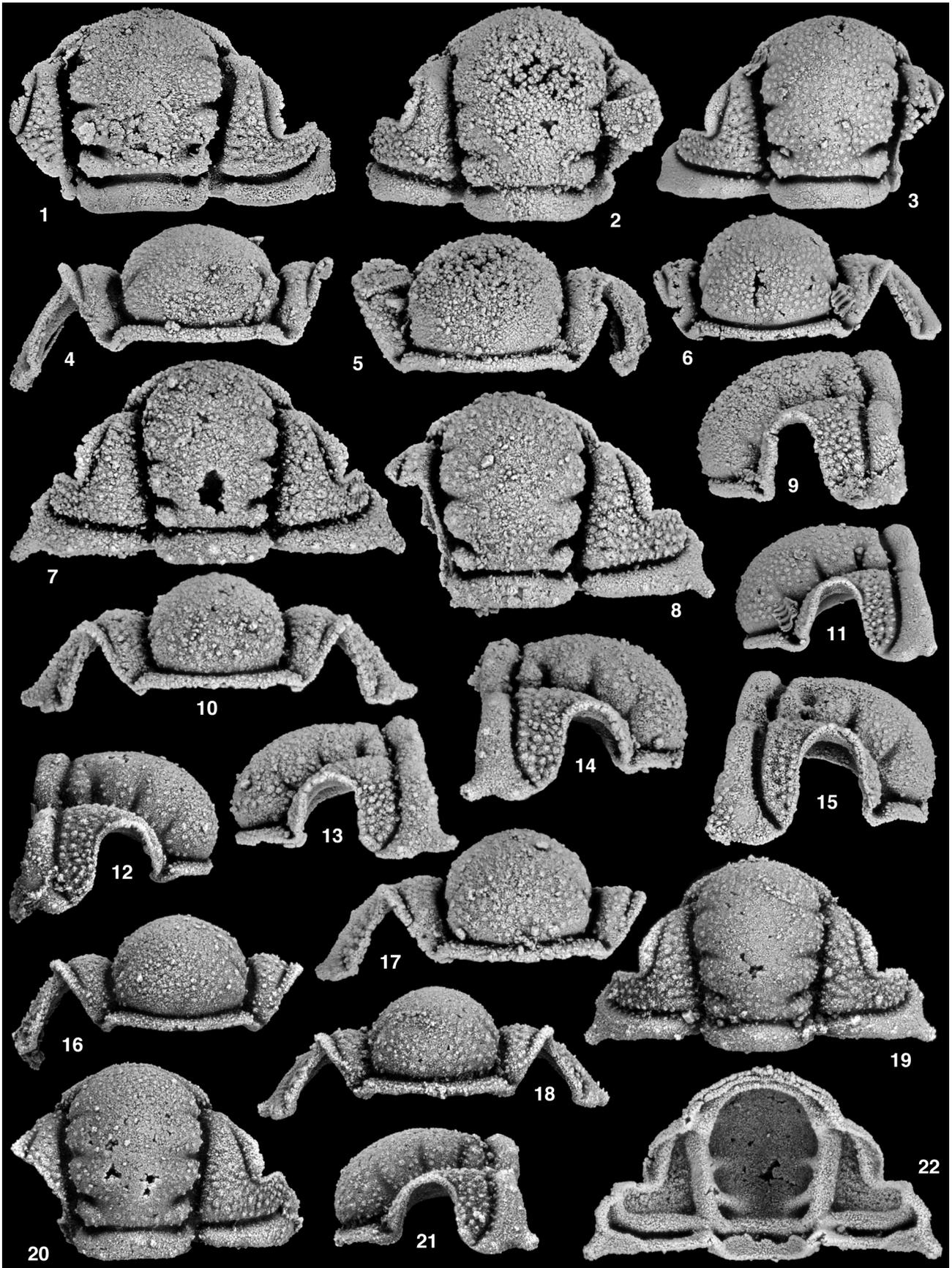


PLATE 35.



PLATE 35. *Deltapliomera humphriesi* n. sp., from Section H 208.2 m, Fillmore Formation (Floian; Blackhillsian; *Carolinites nevadensis* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

- 1, 4, 15. Cranidium, SUI 129678, dorsal, anterior, and right lateral views, x14.
- 2, 5, 9. Cranidium, SUI 129679, dorsal, anterior, and left lateral views, x14.
- 3, 6, 11. Cranidium, SUI 129680, dorsal, anterior, and left lateral views, x14.
- 7, 10, 13. Cranidium, SUI 129681, dorsal, anterior, and left lateral views, x20.
- 8, 14, 17. Cranidium, SUI 129682, dorsal, right lateral, and anterior views, x20.
- 12, 16, 20. Cranidium, SUI 129683, right lateral, anterior, and dorsal views, x17.
- 18, 19, 21, 22. Cranidium, SUI 129684, anterior, dorsal, left lateral, and ventral views, x17.

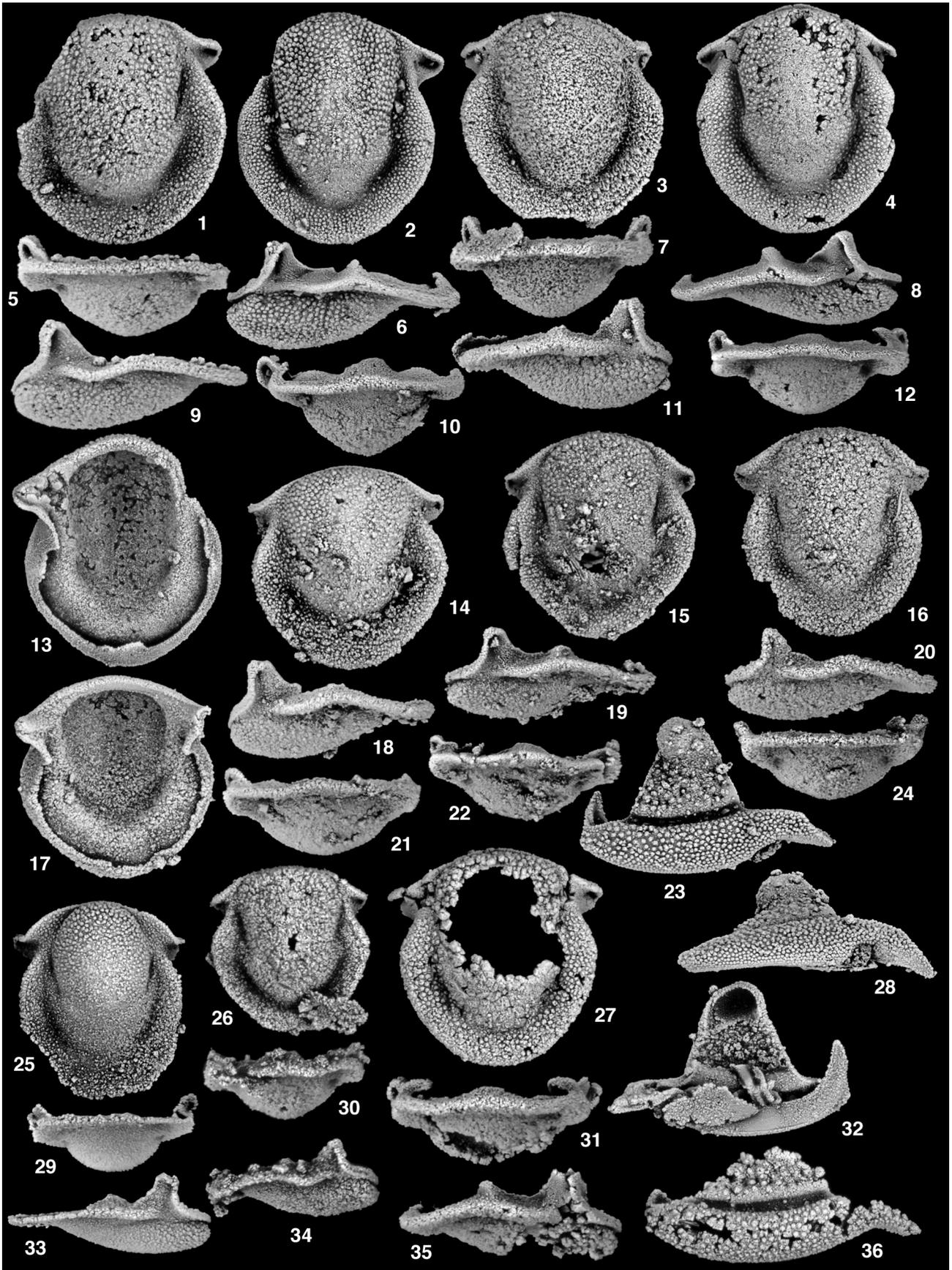


PLATE 36.

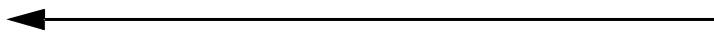


PLATE 36. *Deltapliomera humphriesi* n. sp., from Section H 208.2 m, Fillmore Formation (Floian; Blackhillsian; *Carolinites nevadensis* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

- 1, 5, 9, 13. Hypostome, SUI 129685, ventral, posterior, left lateral, and dorsal views, x20.
- 2, 6, 10. Hypostome, SUI 129686, ventral, left lateral, and posterior views, x17.
- 3, 7, 11. Hypostome, SUI 129687, ventral, posterior, and right lateral views, x17.
- 4, 8, 12. Hypostome, SUI 129688, ventral, right lateral, and posterior views, x17.
- 14, 17, 18, 21. Hypostome, SUI 129689, ventral, left lateral, dorsal, and posterior views, x20.
- 15, 19, 22. Hypostome, SUI 129690, ventral, left lateral, and posterior views, x20.
- 16, 20, 24. Hypostome, SUI 129691, ventral, left lateral, and posterior views, x17.
- 23, 28, 32. Right librigena, SUI 129692, external, ventrolateral, and internal views, x15.
- 25, 29, 33. Hypostome, SUI 129693, ventral, posterior, and right lateral views, x20.
- 26, 30, 34. Hypostome, SUI 129694, ventral, posterior, and right lateral views, x25.
- 27, 31, 35. Hypostome, SUI 129695, ventral, posterior, and right lateral views, x20.
36. Right librigena, SUI 129696, external view, x20.

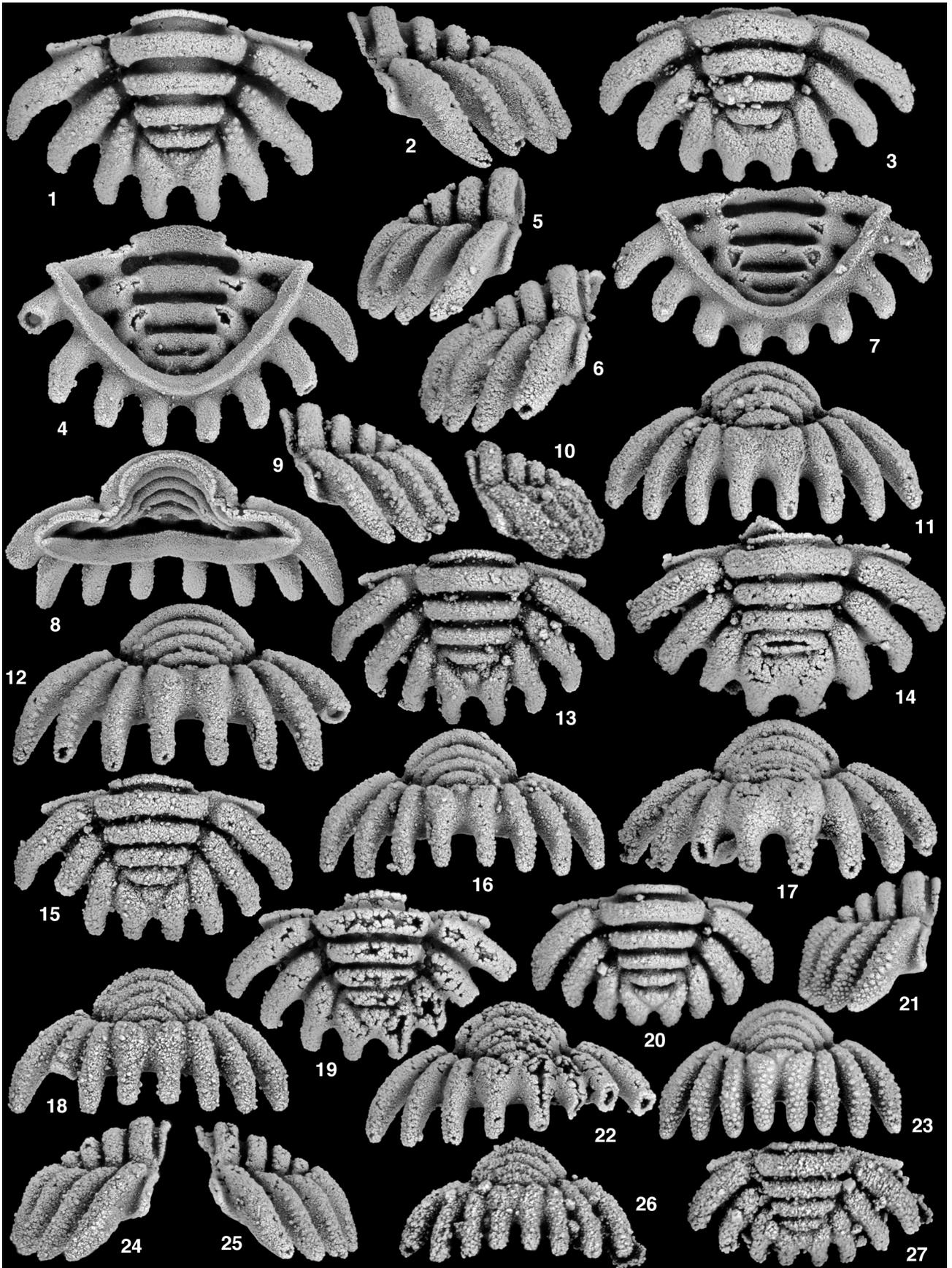


PLATE 37.



PLATE 37. *Deltapliomera humphriesi* n. sp., from Section H 208.2 m, Fillmore Formation (Floian; Blackhillsian; *Carolinites nevadensis* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

- 1, 2, 4, 8, 12. Pygidium, SUI 129697, dorsal, left lateral, ventral, anterior, and posterior views, x15.
3, 5, 7, 11. Pygidium, SUI 129698, dorsal, right lateral, ventral, and posterior views, x17.
6, 14, 17. Pygidium, SUI 129699, right lateral, dorsal, and posterior views, x15.
9, 13, 16. Pygidium, SUI 129700, left lateral, dorsal, and posterior views, x17.
10, 26, 27. Pygidium, SUI 129701, left lateral, posterior, and dorsal views, x25.
15, 18, 24. Pygidium, SUI 129702, dorsal, posterior, and right lateral views, x17.
19, 22, 25. Pygidium, SUI 129703, dorsal, posterior, and left lateral views, x17.
20, 21, 23. Pygidium, SUI 129704, dorsal, right lateral, and posterior views, x20.

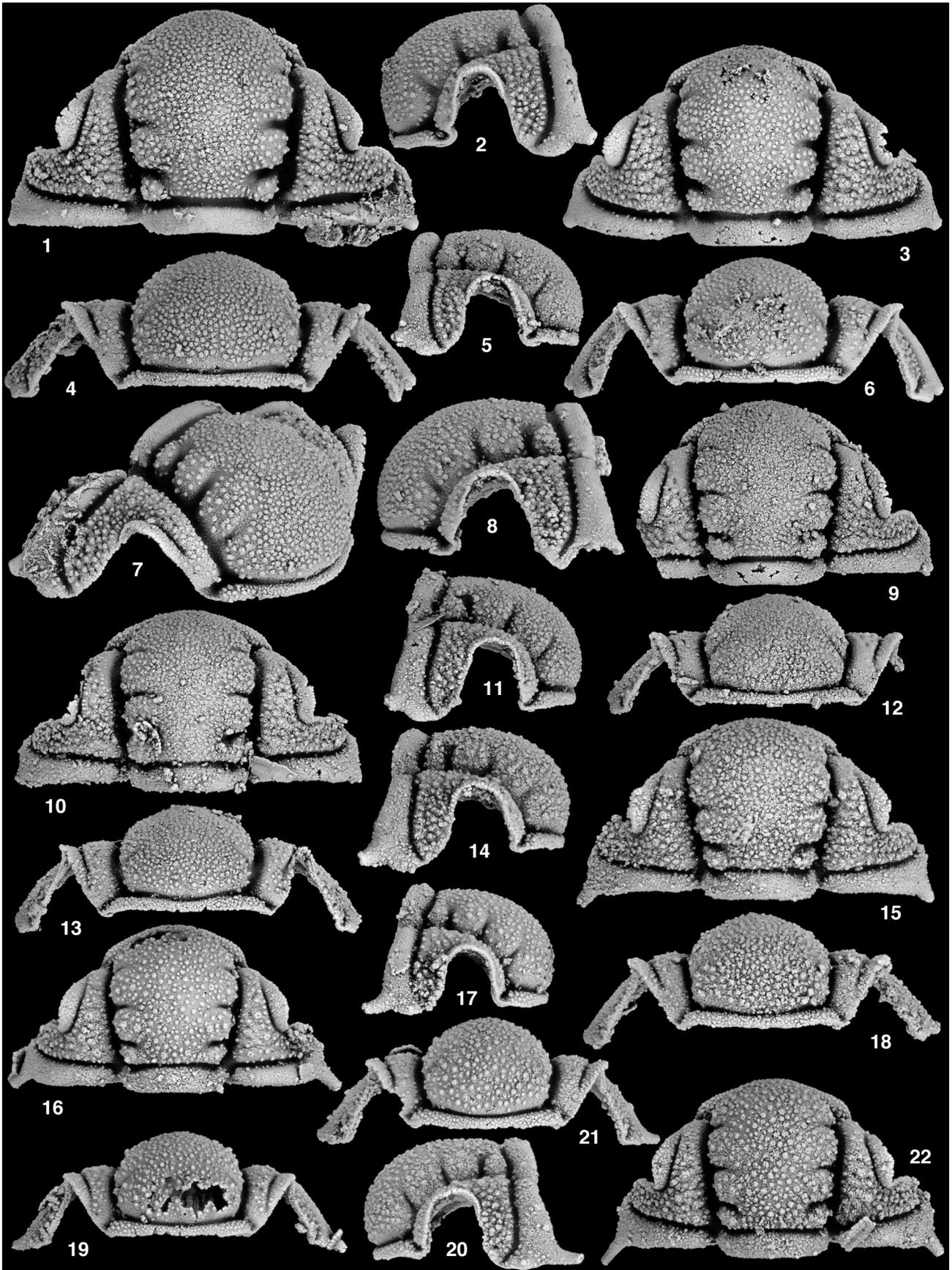


PLATE 38.



PLATE 38. *Deltapliomera humphriesi* n. sp., from Section H 222.1 m, Fillmore Formation (Floian; Blackhillsian; *Carolinites nevadensis* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

- 1, 4, 7, 8. Cranidium, SUI 129705, dorsal, anterior, oblique, and left lateral views, x12.
2, 3, 6. Cranidium, SUI 129706, left lateral, dorsal, and anterior views, x12.
5, 9, 12. Cranidium, SUI 129707, right lateral, dorsal, and anterior views, x12.
10, 11, 13. Cranidium, SUI 129708, dorsal, right lateral, and anterior views, x12.
14, 15, 18. Cranidium, SUI 129709, right lateral, dorsal, and anterior views, x15.
16, 17, 19. Cranidium, SUI 129710, dorsal, right lateral, and anterior views, x15.
20–22. Cranidium, SUI 129711, left lateral, anterior, and dorsal views, x15.

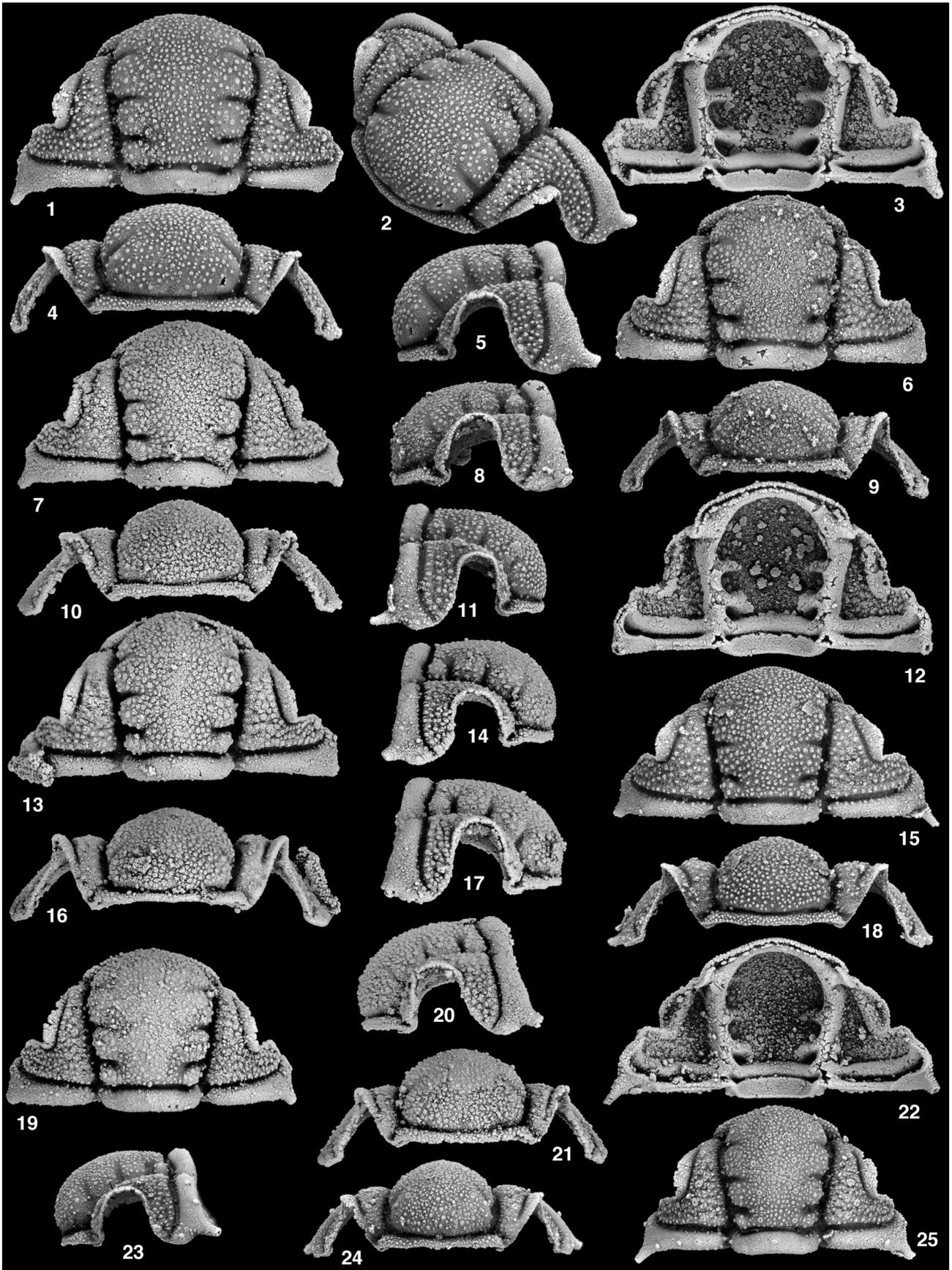


PLATE 39.



PLATE 39. *Deltapliomera humphriesi* n. sp., from Section H 222.1 m, Fillmore Formation (Floian; Blackhillsian; *Carolinites nevadensis* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. All magnifications are x12.

- 1–5. Cranidium, SUI 129712, dorsal, oblique, ventral, anterior, and left lateral views.
6, 8, 9, 12. Cranidium, SUI 129713, dorsal, left lateral, anterior, and ventral views.
7, 10, 14. Cranidium, SUI 129714, dorsal, anterior, and right lateral views.
11, 15, 18, 22. Cranidium, SUI 129715, left lateral, dorsal, anterior, and ventral views.
13, 16, 17. Cranidium, SUI 129716, dorsal, anterior, and right lateral views.
19–21. Cranidium, SUI 129717, dorsal, left lateral, and anterior views.
23–25. Cranidium, SUI 129718, left lateral, anterior, and dorsal views.

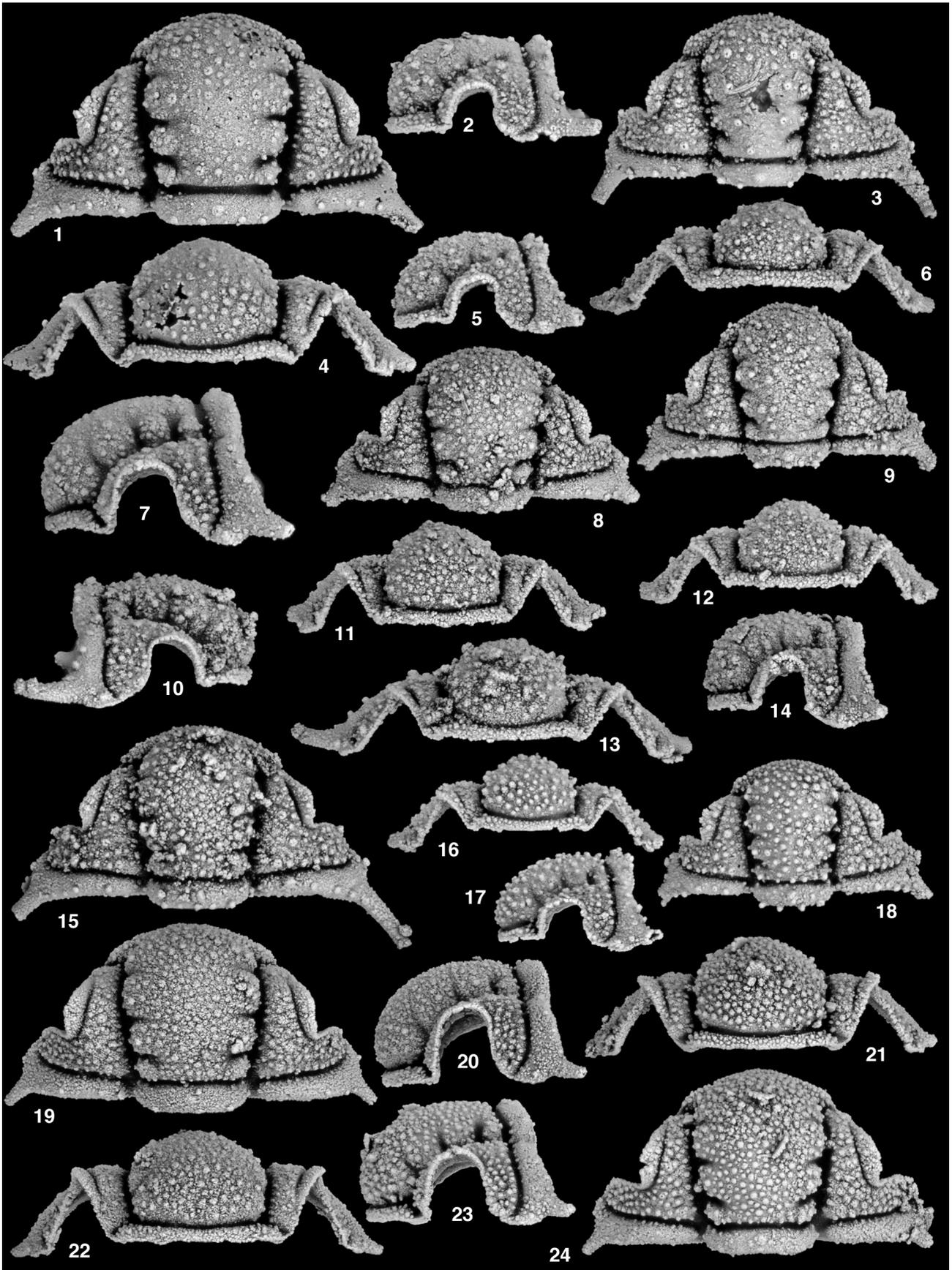


PLATE 40.

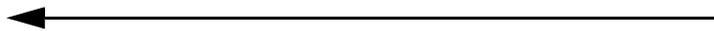


PLATE 40. *Deltapliomera humphriesi* n. sp., from Section H 222.1 m, Fillmore Formation (Floian; Blackhillsian; *Carolinites nevadensis* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

- 1, 4, 7. Cranidium, SUI 129719, dorsal, anterior, and left lateral views, x20.
- 2, 3, 6. Cranidium, SUI 129720, left lateral, dorsal, and anterior views, x20.
- 5, 9, 12. Cranidium, SUI 129721, left lateral, dorsal, and anterior views, x20.
- 8, 11, 14. Cranidium, SUI 129722, dorsal, anterior, and left lateral views, x17.
- 10, 13, 15. Cranidium, SUI 129723, right lateral, anterior, and dorsal views, x20.
- 16–18. Cranidium, SUI 129724, anterior, left lateral, and dorsal views, x20.
- 19, 20, 22. Cranidium, SUI 129725, dorsal, left lateral, and anterior views, x17.
- 21, 23, 24. Cranidium, SUI 129726, anterior, left lateral, and dorsal views, x17.

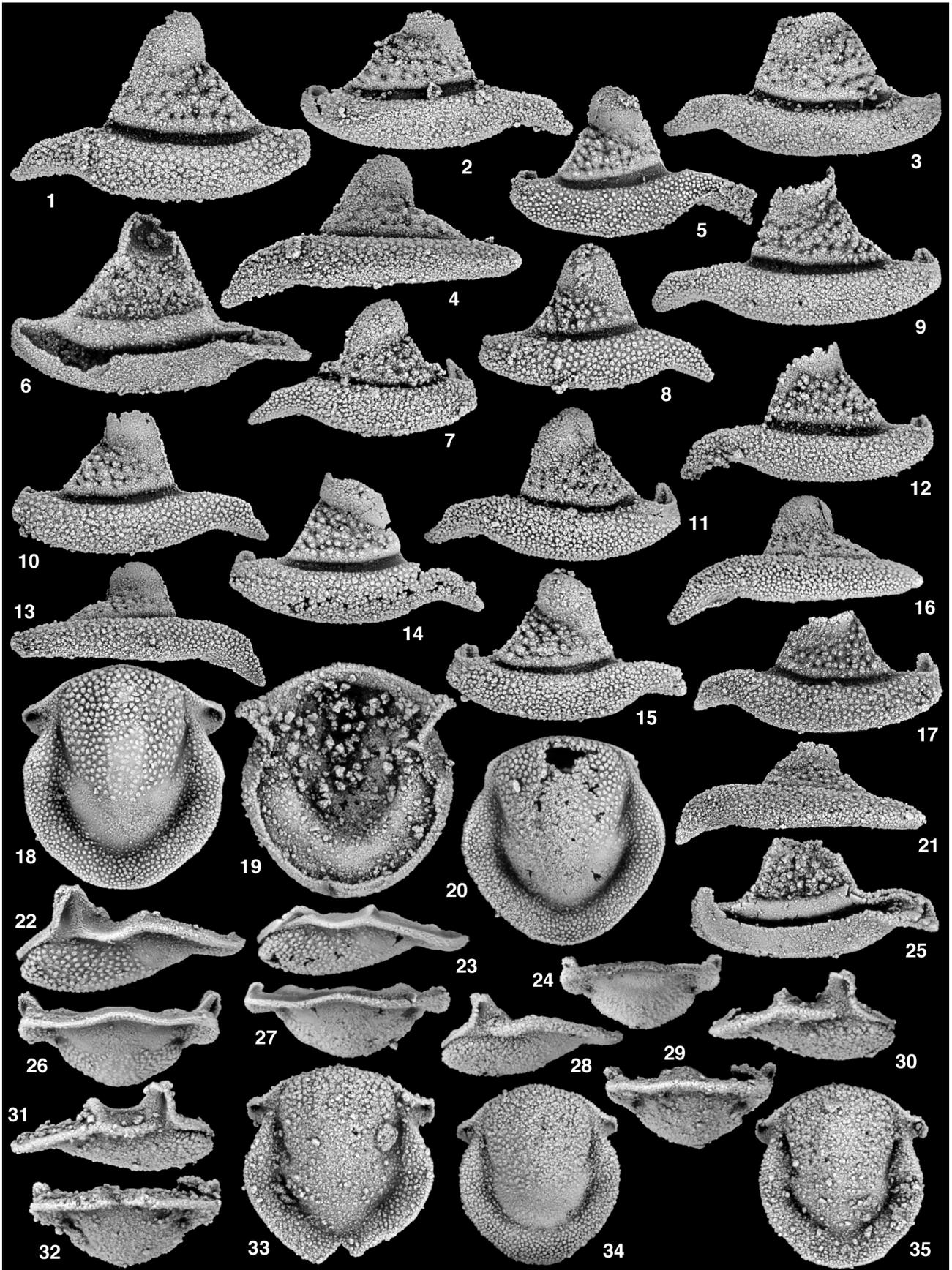


PLATE 41.



PLATE 41. *Deltapliomera humphriesi* n. sp., from Section H 222.1 m, Fillmore Formation (Floian; Blackhillsian; *Carolinites nevadensis* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

- 1, 4, 6. Left librigena, SUI 129727, external, ventrolateral, and internal views, x15.
2. Right librigena, SUI 129728, external view, x15.
3. Left librigena, SUI 129729, external view, x15.
5. Right librigena, SUI 129730, external view, x15.
7. Left librigena, SUI 129731, external view, x15.
8. Right librigena, SUI 129732, external view, x17.
9. Left librigena, SUI 129733, external view, x15.
- 10, 13. Right librigena, SUI 129734, external and ventrolateral views, x15.
- 11, 16. Left librigena, SUI 129735, external and ventrolateral views, x15.
12. Left librigena, SUI 129736, external view, x15.
14. Right librigena, SUI 129737, external view, x17.
15. Right librigena, SUI 129738, external view, x17.
- 17, 21, 25. Left librigena, SUI 129739, external, ventrolateral, and internal views, x17.
- 18, 19, 22, 26. Hypostome, SUI 129740, ventral, dorsal, left lateral, and posterior views, x20.
- 20, 23, 27. Hypostome, SUI 129741, ventral, left lateral, and posterior views, x20.
- 24, 28, 34. Hypostome, SUI 129742, posterior, left lateral, and ventral views, x20.
- 29, 30, 35. Hypostome, SUI 129743, posterior, right lateral, and ventral views, x20.
- 31–33. Hypostome, SUI 129744, right lateral, posterior, and ventral views, x20.

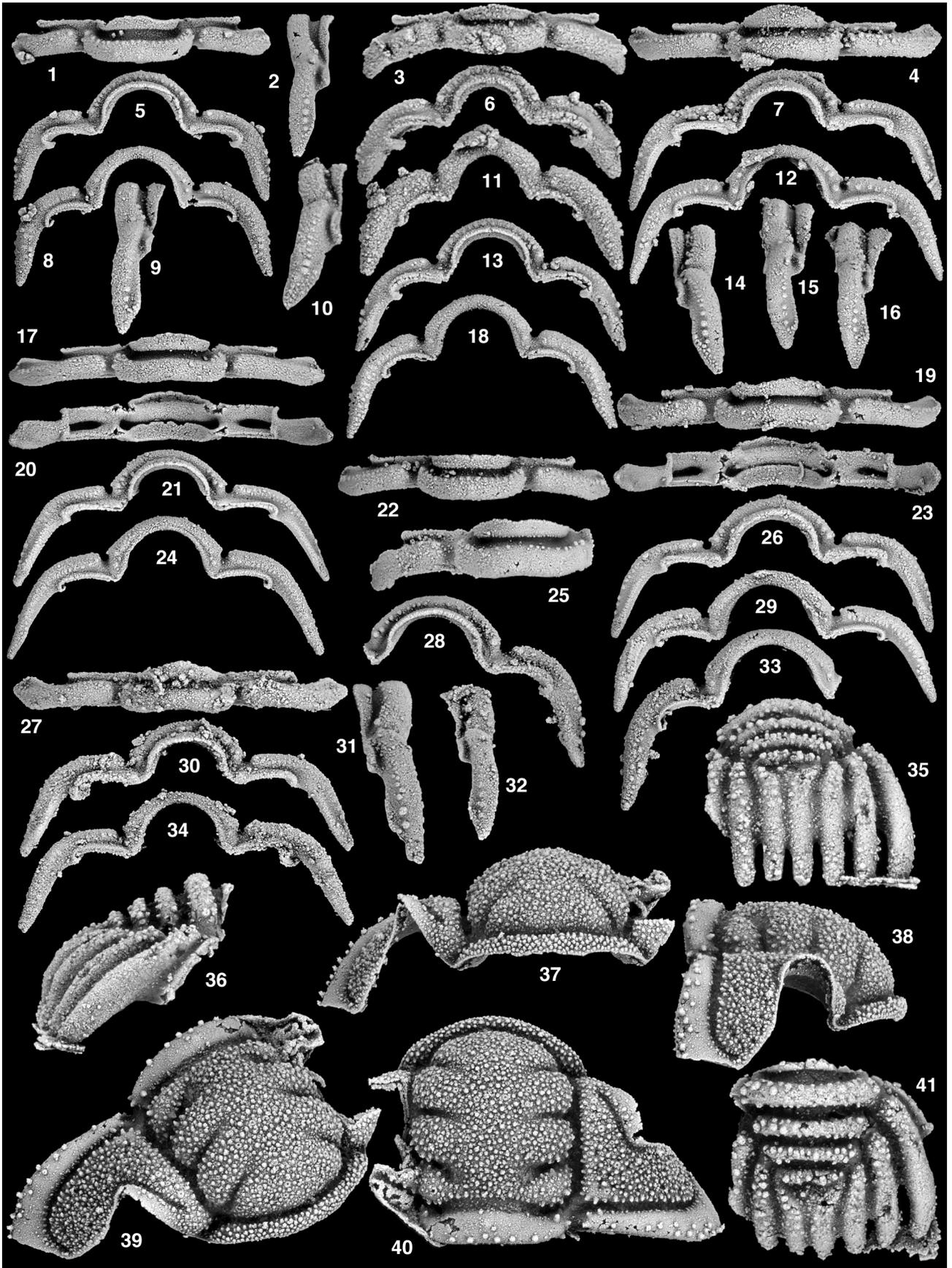


PLATE 42.



PLATE 42. *Deltapliomera humphriesi* n. sp., from Section H 222.1 m, Fillmore Formation (Floian; Blackhillsian; *Carolinites nevadensis* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

- 1, 2, 5, 8. Thoracic segment, SUI 129745, dorsal, right lateral, anterior, and posterior views, x12.
3, 6, 10, 11. Thoracic segment, SUI 129746, dorsal, anterior, right lateral, and posterior views, x20.
4, 7, 12, 16. Thoracic segment, SUI 129747, dorsal, anterior, posterior, and right lateral views, x12.
9, 17, 20, 21, 24. Thoracic segment, SUI 129748, right lateral, dorsal, ventral, anterior, and posterior views, x12.
13, 14, 18, 22. Thoracic segment, SUI 129749, anterior, left lateral, posterior, and dorsal views, x15.
15, 19, 23, 26, 29. Thoracic segment, SUI 129750, right lateral, dorsal, ventral, anterior, and posterior views, x12.
25, 28, 31, 33. Thoracic segment, SUI 129751, dorsal, anterior, left lateral, and posterior views, x15.
27, 30, 32, 34. Thoracic segment, SUI 129752, dorsal, anterior, left lateral, and posterior views, x12.

Tuleaspis n. sp. A, from Section HC5 203.7-204.2T m, Garden City Formation, east side of Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho, USA, and Section G 155.6 m, Fillmore Formation, southern Confusion Range, Ibex area, Millard County, western Utah, USA. Both are from the lower Floian (Tulean; *Psalikilopsis cuspidicauda* Zone).

- 35, 36, 41. Pygidium, SUI 129753, posterior, right lateral, and dorsal views, x20 (G 155.6 m).
37–40. Cranidium, SUI 129754, anterior, right lateral, oblique, and dorsal views, x15 (HC5 203.7-204.2T m).

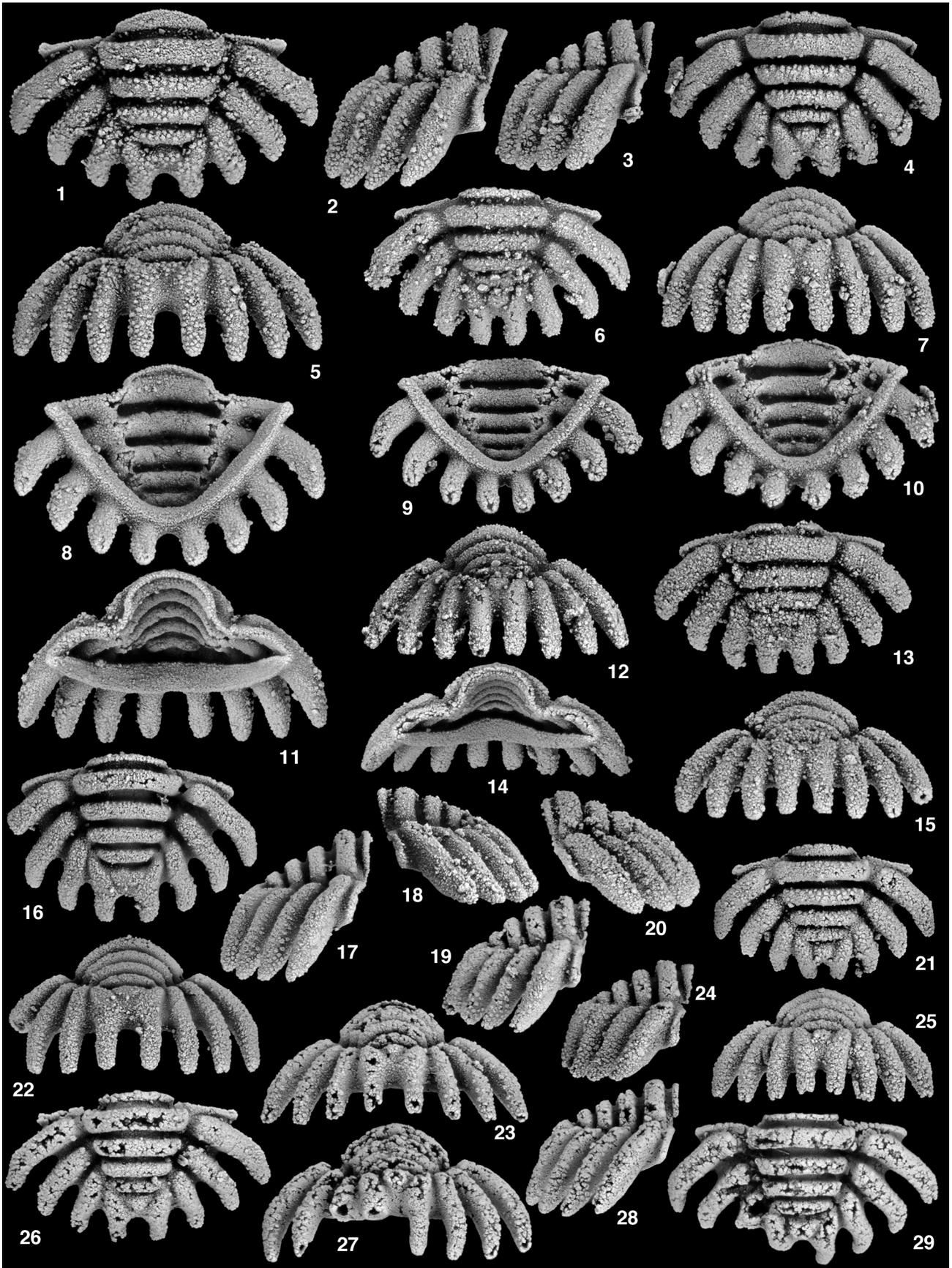


PLATE 43.



PLATE 43. *Deltapliomera humphriesi* n. sp., from Section H 222.1 m, Fillmore Formation (Floian; Blackhillsian; *Carolinites nevadensis* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. All magnifications are x15.

1, 2, 5, 8, 11. Pygidium, **holotype**, SUI 129755, dorsal, right lateral, posterior, ventral, and anterior views.

3, 4, 7, 10. Pygidium, SUI 129756, right lateral, dorsal, posterior, and ventral views.

6, 9, 12, 14, 18 Pygidium, SUI 115357, dorsal, ventral, posterior, anterior, and left lateral views.

13, 15, 20. Pygidium, SUI 129757, dorsal, posterior, and left lateral views.

16, 17, 22. Pygidium, SUI 129758, dorsal, right lateral, and posterior views.

19, 23, 26. Pygidium, SUI 129759, right lateral, posterior, and dorsal views.

21, 24, 25. Pygidium, SUI 129760, dorsal, right lateral, and posterior views.

27–29. Pygidium, SUI 129761, posterior, right lateral, and dorsal views.

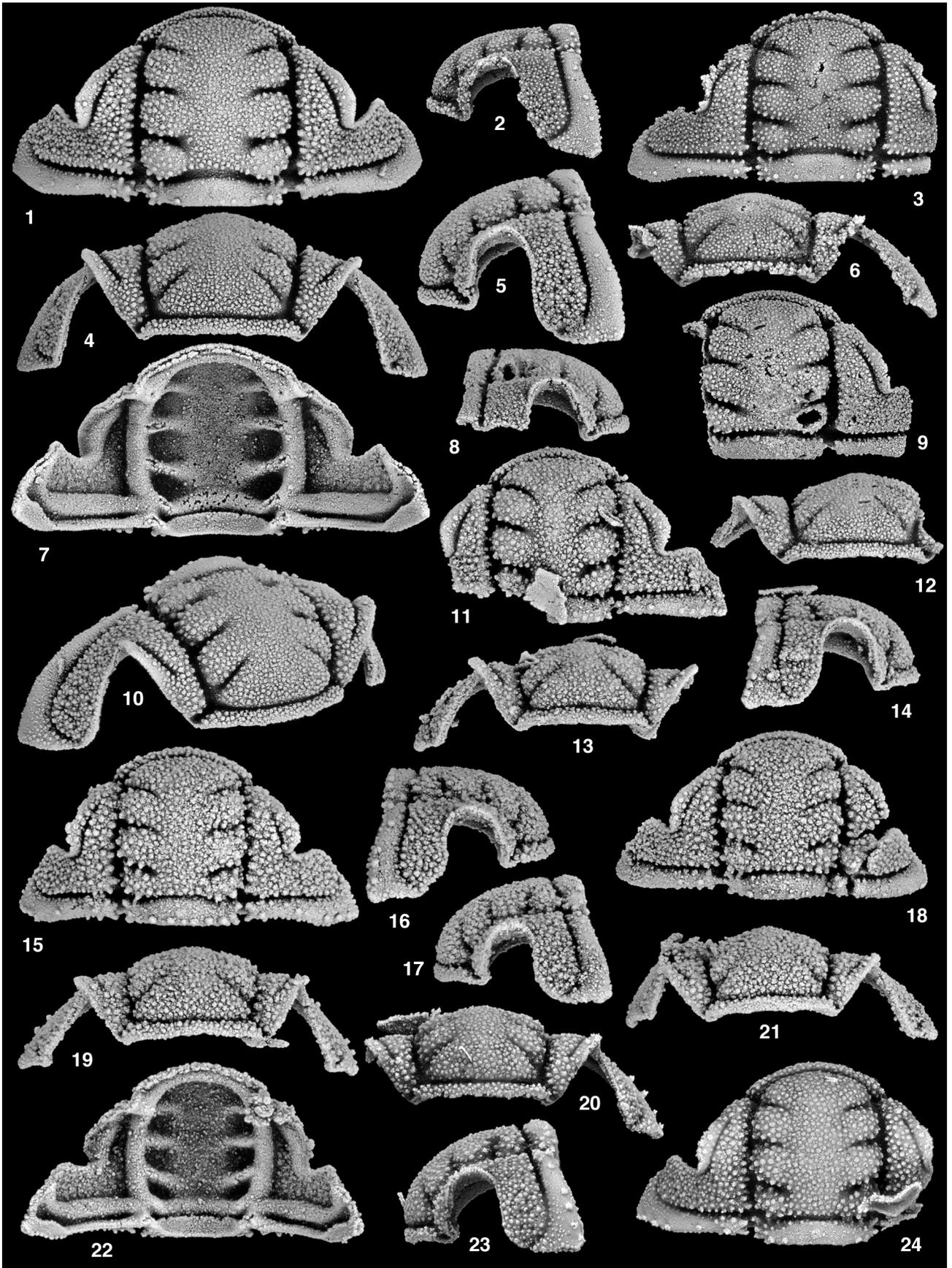


PLATE 44.



PLATE 44. *Tuleaspis jeneki* n. sp., from Section G 210.2 m, Fillmore Formation (Floian; Tulean; *Protopliomerella contracta* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

- 1, 4, 5, 7, 10. Cranidium, **holotype**, SUI 129505, dorsal, anterior, left lateral, ventral, and oblique views, x12.
2, 3, 6. Cranidium, SUI 115250, left lateral, dorsal, and anterior views, x12.
8, 9, 12. Cranidium, SUI 129506, right lateral, dorsal, and anterior views, x12.
11, 13, 14. Cranidium, SUI 129507, dorsal, anterior, and right lateral views, x15.
15, 16, 19, 22. Cranidium, SUI 129508, dorsal, right lateral, anterior, and ventral views, x15.
17, 18, 21. Cranidium, SUI 129509, left lateral, dorsal, and anterior views, x15.
20, 23, 24. Cranidium, SUI 129510, anterior, left lateral, and dorsal views.

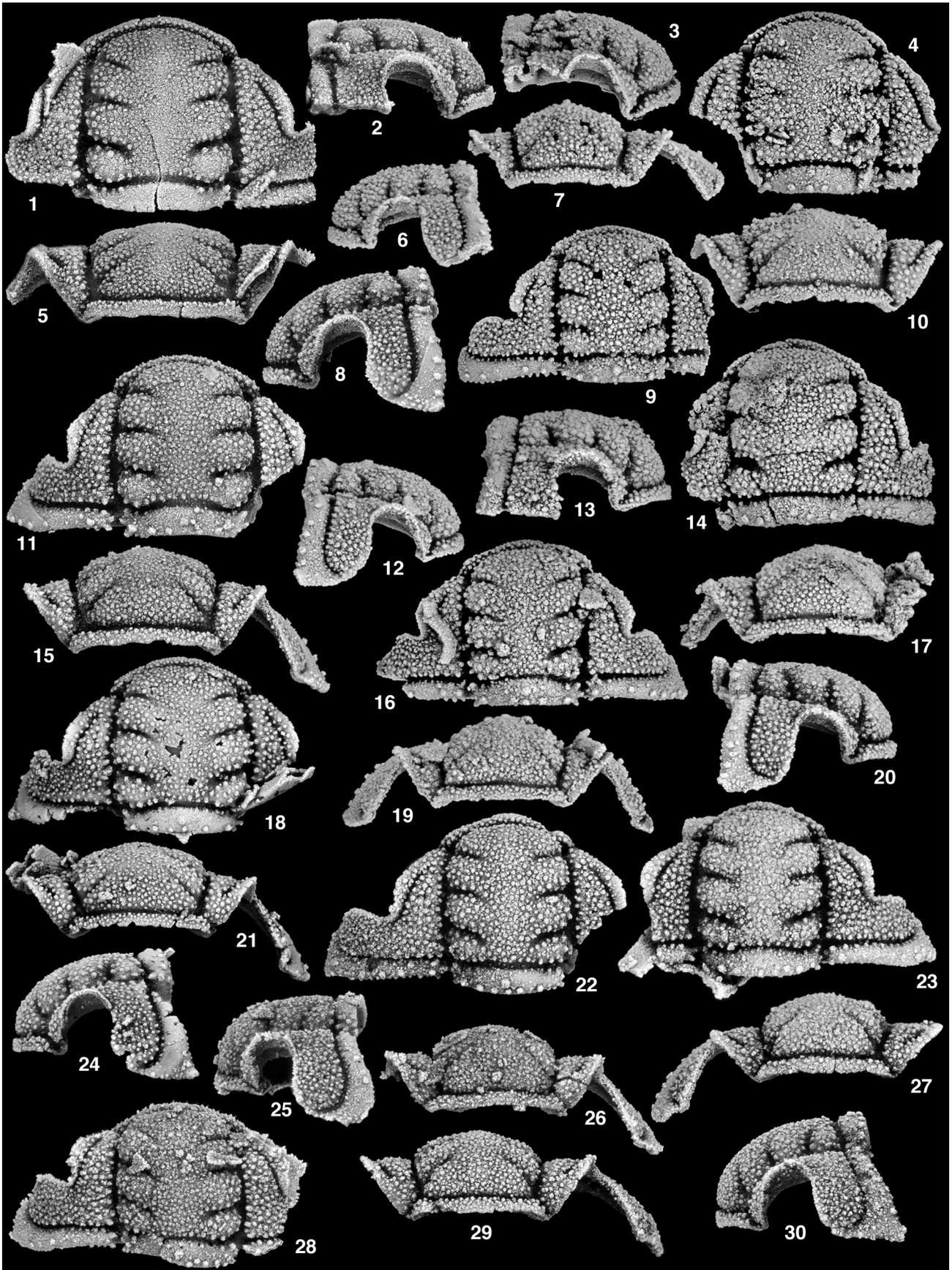


PLATE 45.



PLATE 45. *Tuleaspis jeneki* n. sp., from Section G 210.2 m, Fillmore Formation (Floian; Tulean; *Protopliomerella contracta* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

- 1, 2, 5. Cranidium, SUI 129511, dorsal, right lateral, and anterior views, x15.
- 3, 4, 10. Cranidium, SUI 129512, right lateral, dorsal, and anterior views, x15.
- 6, 7, 9. Cranidium, SUI 129513, left lateral, anterior, and dorsal views, x17.
- 8, 11, 15. Cranidium, SUI 129514, left lateral, dorsal, and anterior views, x15.
- 12, 16, 19. Cranidium, SUI 129515, right lateral, dorsal, and anterior views, x17.
- 13, 14, 17. Cranidium, SUI 129516, right lateral, dorsal, and anterior views, x17.
- 18, 21, 24. Cranidium, SUI 129517, dorsal, anterior, and left lateral views, x15.
- 20, 23, 27. Cranidium, SUI 129518, right lateral, dorsal, and anterior views, x20.
- 22, 29, 30. Cranidium, SUI 129519, dorsal, anterior, and left lateral views, x17.
- 25, 26, 28. Cranidium, SUI 129520, left lateral, dorsal, and anterior views, x15.

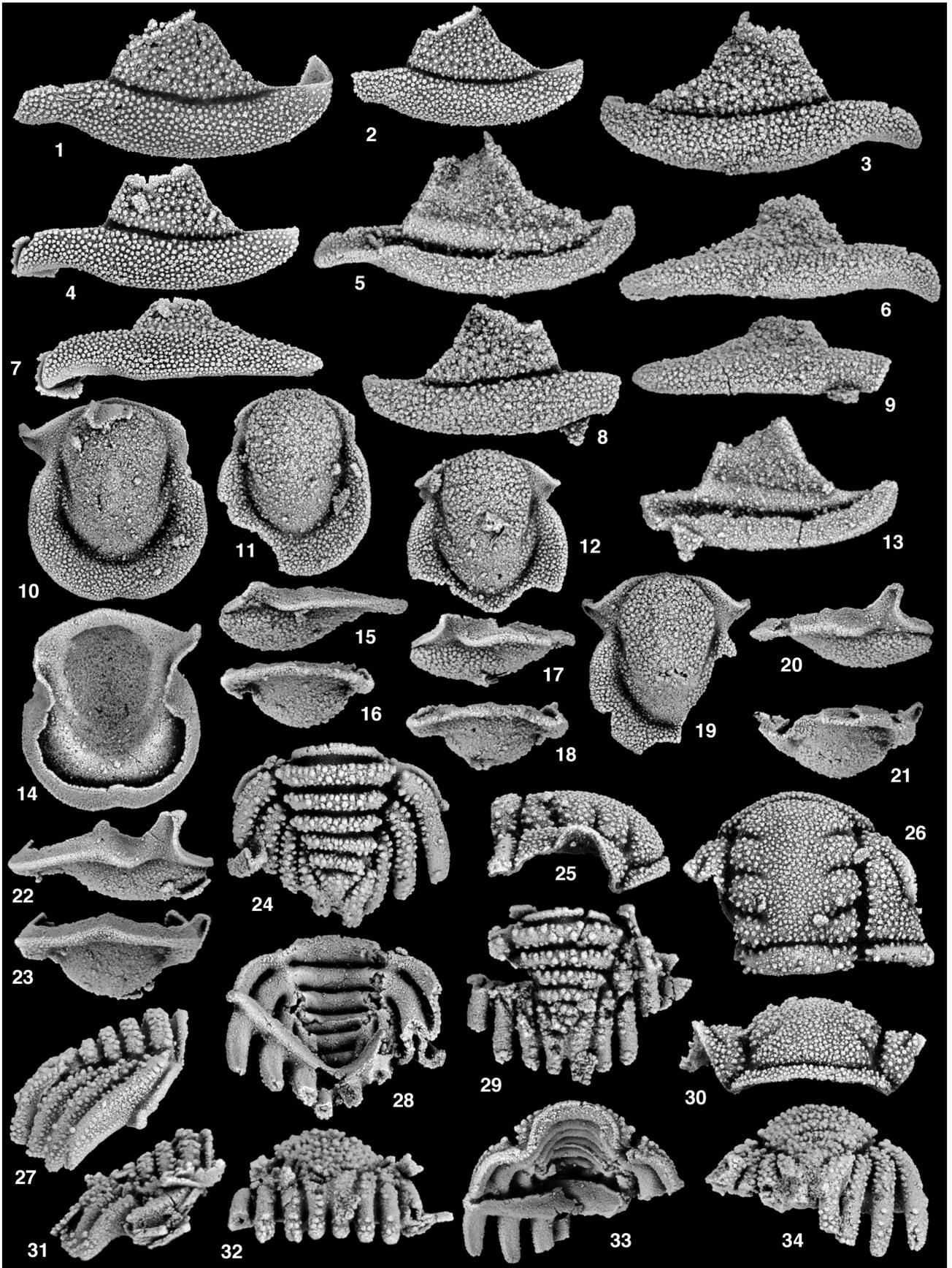


PLATE 46.



PLATE 46. *Tuleaspis jeneki* n. sp., from Section G 210.2 m, Fillmore Formation (lower Floain; Tulean; *Protopliomerella contracta* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

1. Left librigena, SUI 129521, external view, x15.
2. Left librigena, SUI 129522, external view, x15.
- 3, 5, 6. Right librigena, SUI 129523, external, internal, and ventrolateral views, x20.
- 4, 7. Left librigena, SUI 129524, external and ventrolateral views, x15.
- 8, 9, 13. Right librigena, SUI 129525, external, ventrolateral, and internal views, x20.
- 10, 14, 22, 23. Hypostome, SUI 129526, ventral, dorsal, right lateral, and posterior views, x15.
- 11, 15, 16. Hypostome, SUI 129527, ventral, left lateral, and posterior views, x15.
- 12, 17, 18. Hypostome, SUI 129528, ventral, left lateral, and posterior views, x17.
- 19–21. Hypostome, SUI 129529, ventral, right lateral, and posterior views, x15.
- 24, 27, 28, 33, 34. Pygidium, SUI 129530, dorsal, right lateral, ventral, anterior, and posterior views, x15.
- 25, 26, 30. Cranidium, SUI 129531, right lateral, dorsal, and anterior views, x17.
- 29, 31, 32. Pygidium, SUI 129532, dorsal, right lateral, and posterior views, x20.

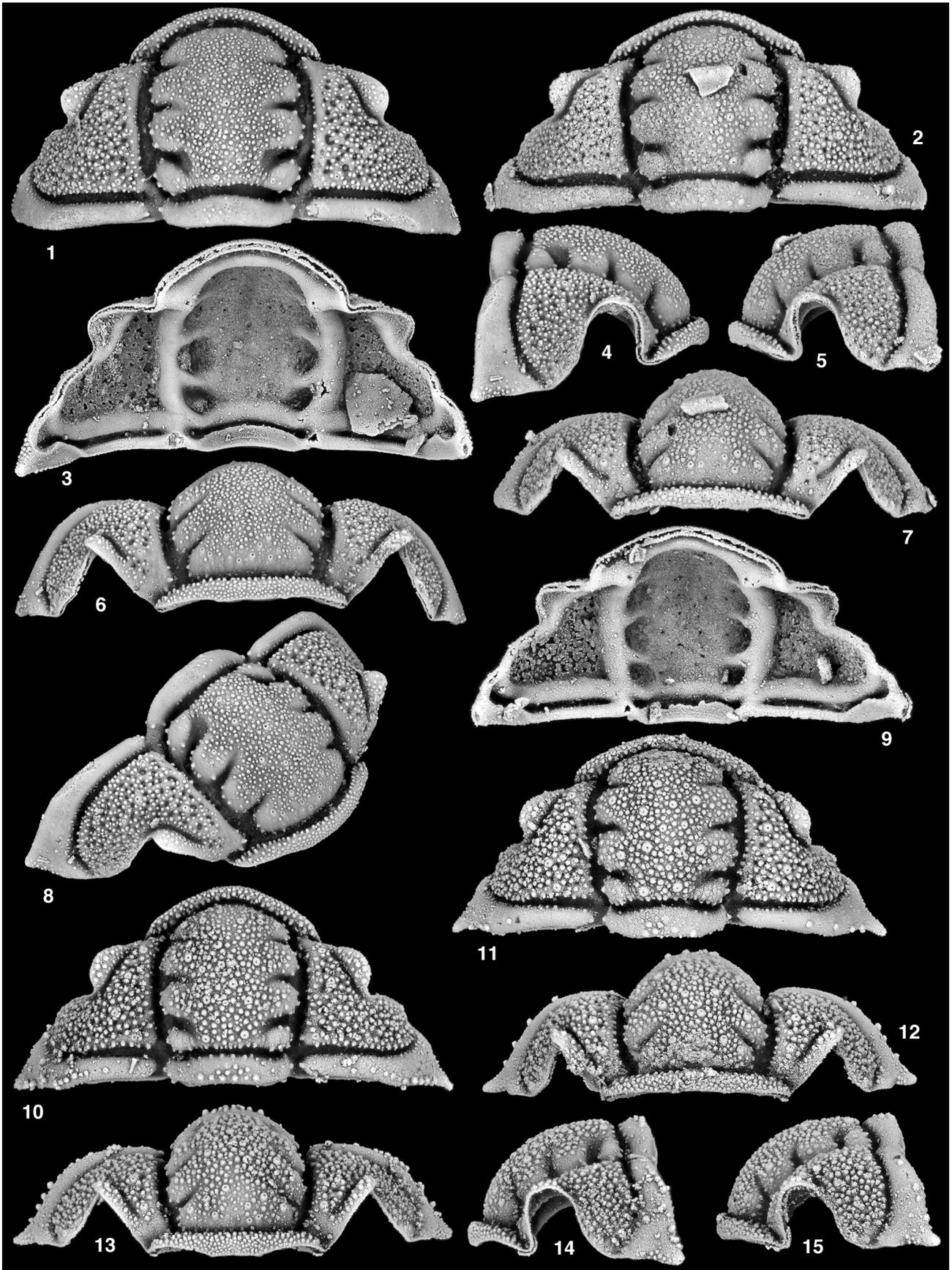


PLATE 47.



PLATE 47. *Millardaspis milsteadii* n. sp., from Section HC6 226.5 m, Garden City Formation (Floian; Tulean; *Heckethornia hyndeae* Zone), west side of Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho, USA.

1, 3, 4, 6, 8. Cranidium, **holotype**, SUI 135528, dorsal, ventral, right lateral, anterior, and oblique views, x12.

2, 5, 7, 9. Cranidium, SUI 135529, dorsal, left lateral, anterior, and ventral views, x15.

10, 13, 14. Cranidium, SUI 135530, dorsal, anterior, and left lateral views, x15.

11, 12, 15. Cranidium, SUI 135531, dorsal, anterior, and left lateral views, x15.

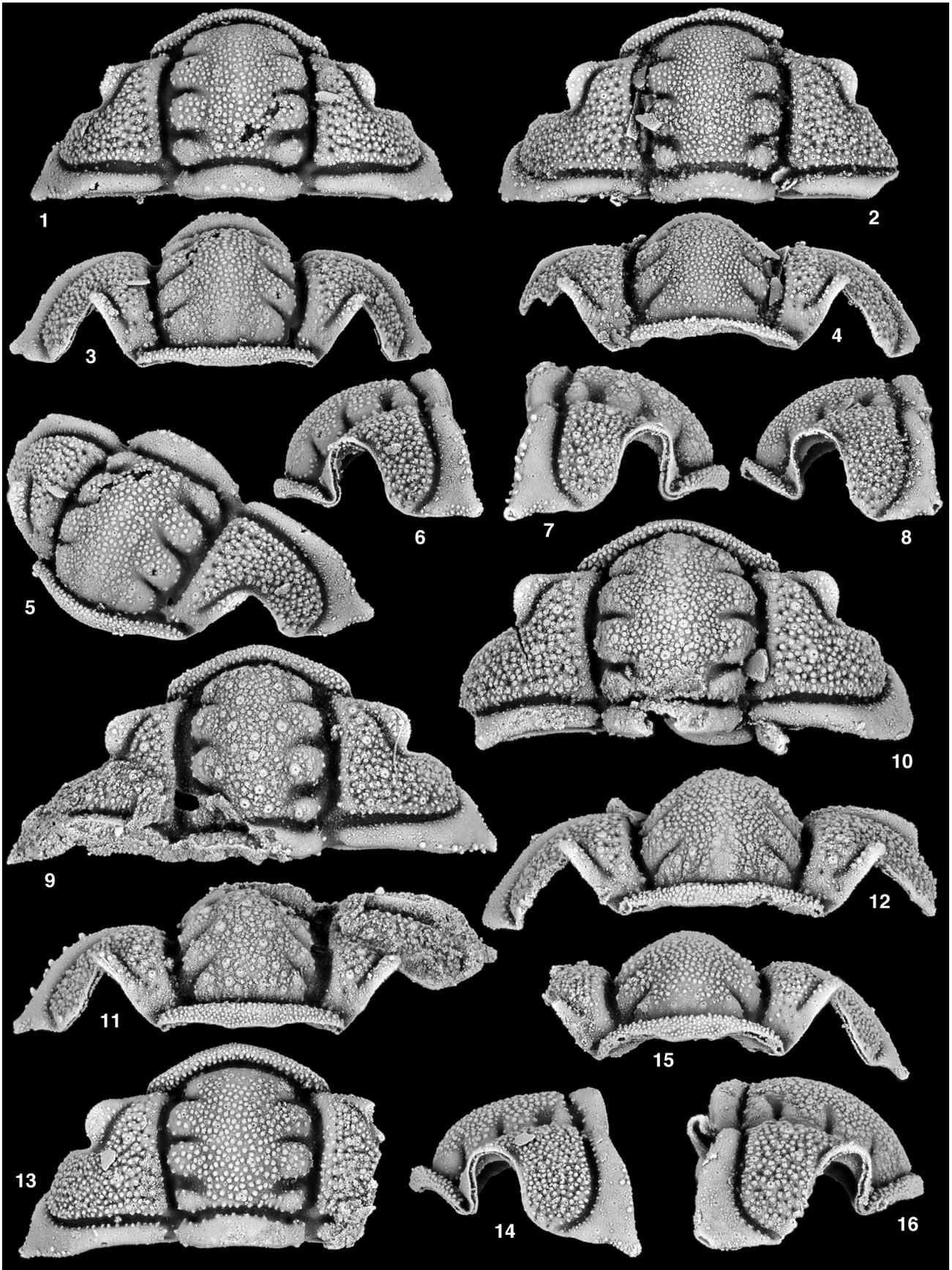


PLATE 48.



PLATE 48. *Millardaspis milsteadii* n. sp., from Section HC6 226.5 m, Garden City Formation (Floian; Tulean; *Heckethornia hyndeae* Zone), west side of Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho, USA.

1, 3, 5, 6. Cranidium, SUI 135532, dorsal, anterior, oblique, and left lateral views, x12.

2, 4, 8. Cranidium, SUI 135533, dorsal, anterior, and left lateral views, x12.

7, 9, 11. Cranidium, SUI 135534, right lateral, dorsal, and anterior views, x15.

10, 12, 16. Cranidium, SUI 135535, dorsal, anterior, and right lateral views, x15.

13–15. Cranidium, SUI 135536, dorsal, left lateral, and anterior views, x12.

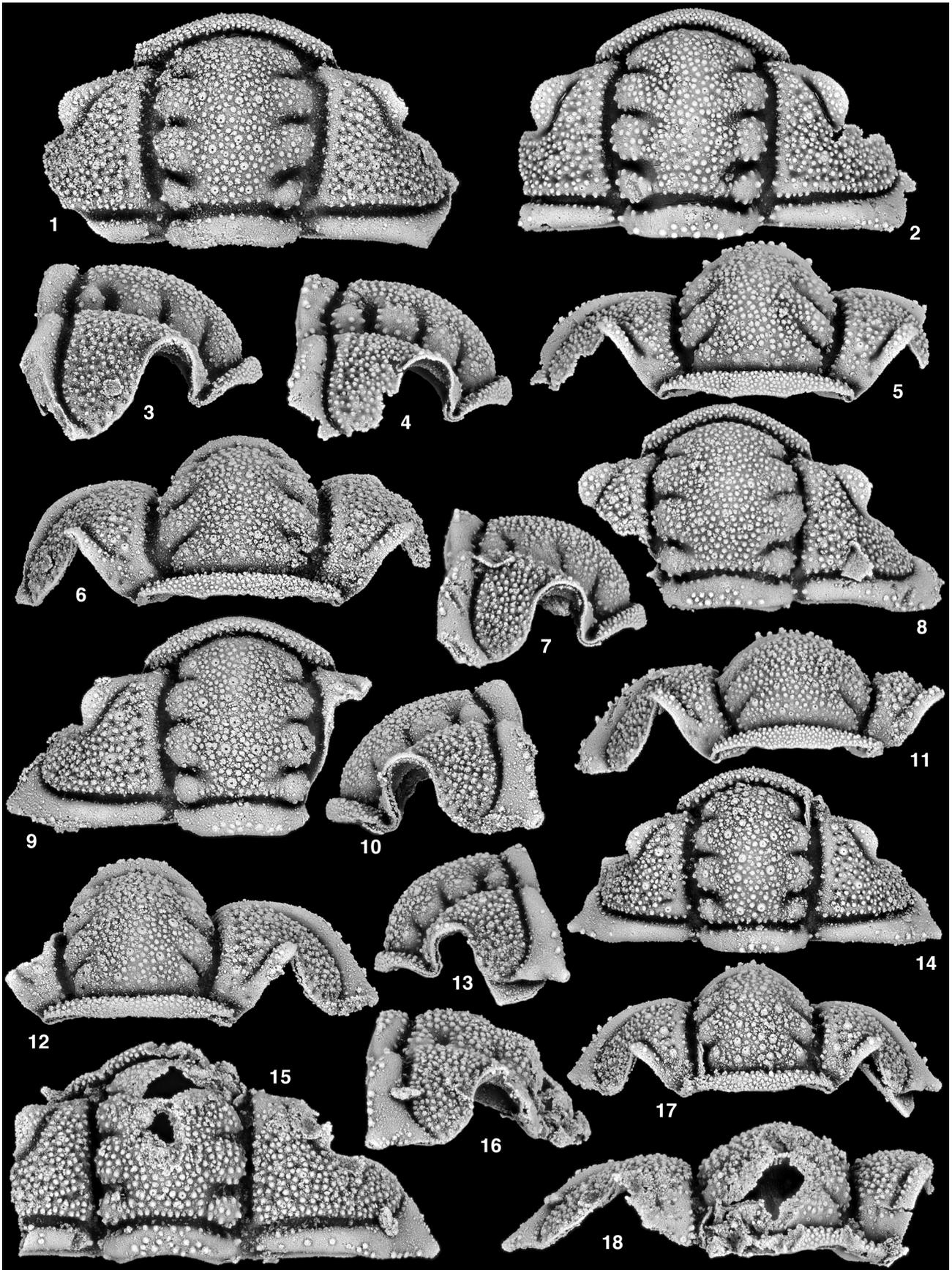


PLATE 49.



PLATE 49. *Millardaspis milsteadii* n. sp., from Section HC6 226.5 m, Garden City Formation (Floian; Tulean; *Heckethornia hyndeeae* Zone), west side of Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho, USA.

- 1, 3, 6. Cranidium, SUI 135537, dorsal, right lateral, and anterior views, x14.
- 2, 4, 5. Cranidium, SUI 135538, dorsal, right lateral, and anterior views, x15.
- 7, 8, 11. Cranidium, SUI 135539, right lateral, dorsal, and anterior views, x15.
- 9, 10, 12. Cranidium, SUI 135540, dorsal, left lateral, and anterior views, x15.
- 13, 14, 17. Cranidium, SUI 135541, left lateral, dorsal, and anterior views, x15.
- 15, 16, 18. Cranidium, SUI 135542, dorsal, right lateral, and anterior views, x15.

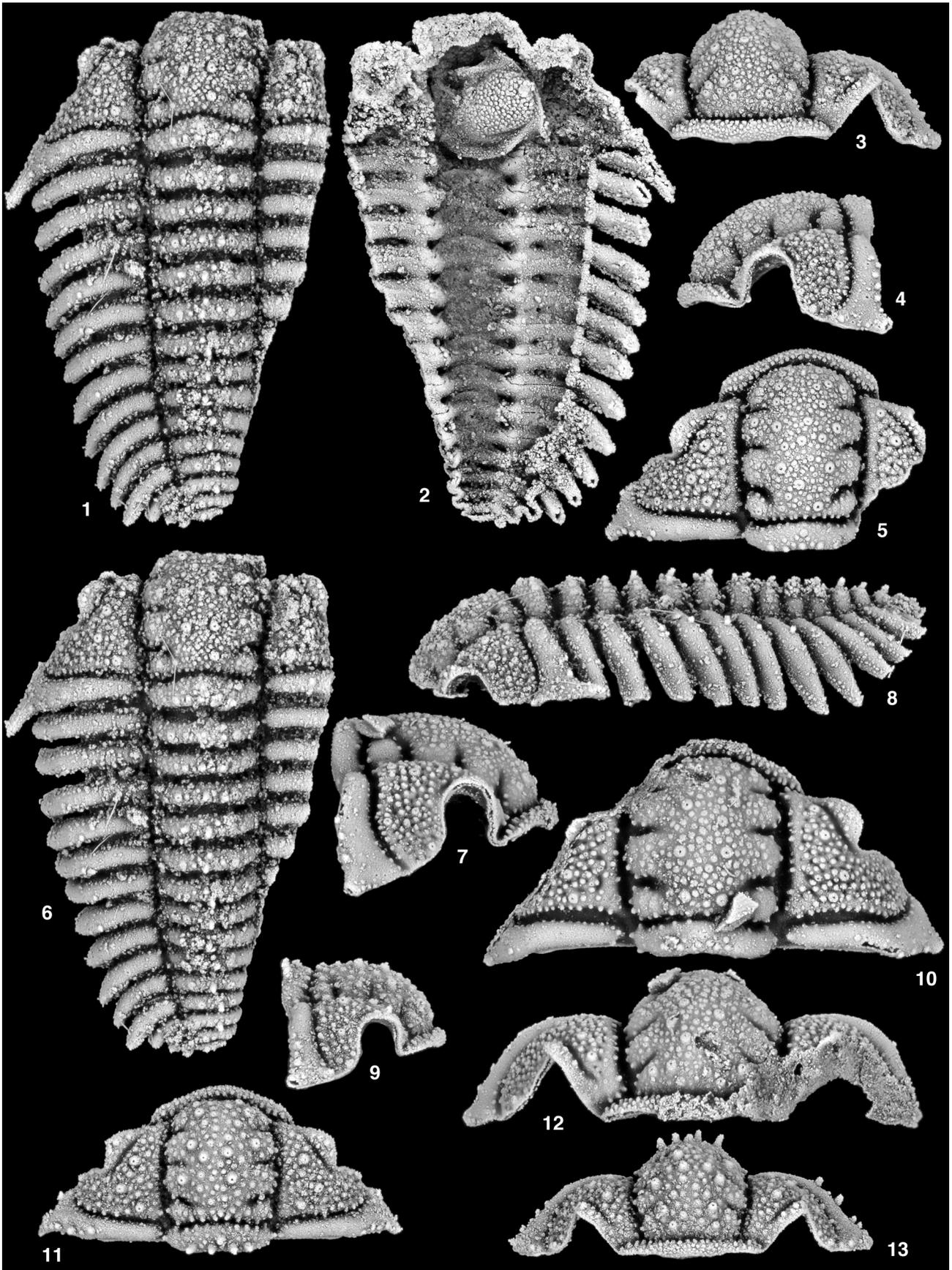


PLATE 50.



PLATE 50. *Millardaspis milsteadi* n. sp., from Section HC6 226.5 m, Garden City Formation (Floian; Tulean; *Heckethornia hyndeae* Zone), west side of Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho, USA. All magnifications are x20.

1, 2, 6, 8. Dorsal exoskeleton, SUI 135543, dorsal thoracic, ventral, dorsal cranidial, and left lateral views.

3–5. Cranidium, SUI 135544, anterior, left lateral, and dorsal views.

7, 10, 12. Cranidium, SUI 135545, right lateral, dorsal, and anterior views.

9, 11, 13. Cranidium, SUI 135546, right lateral, dorsal, and anterior views.

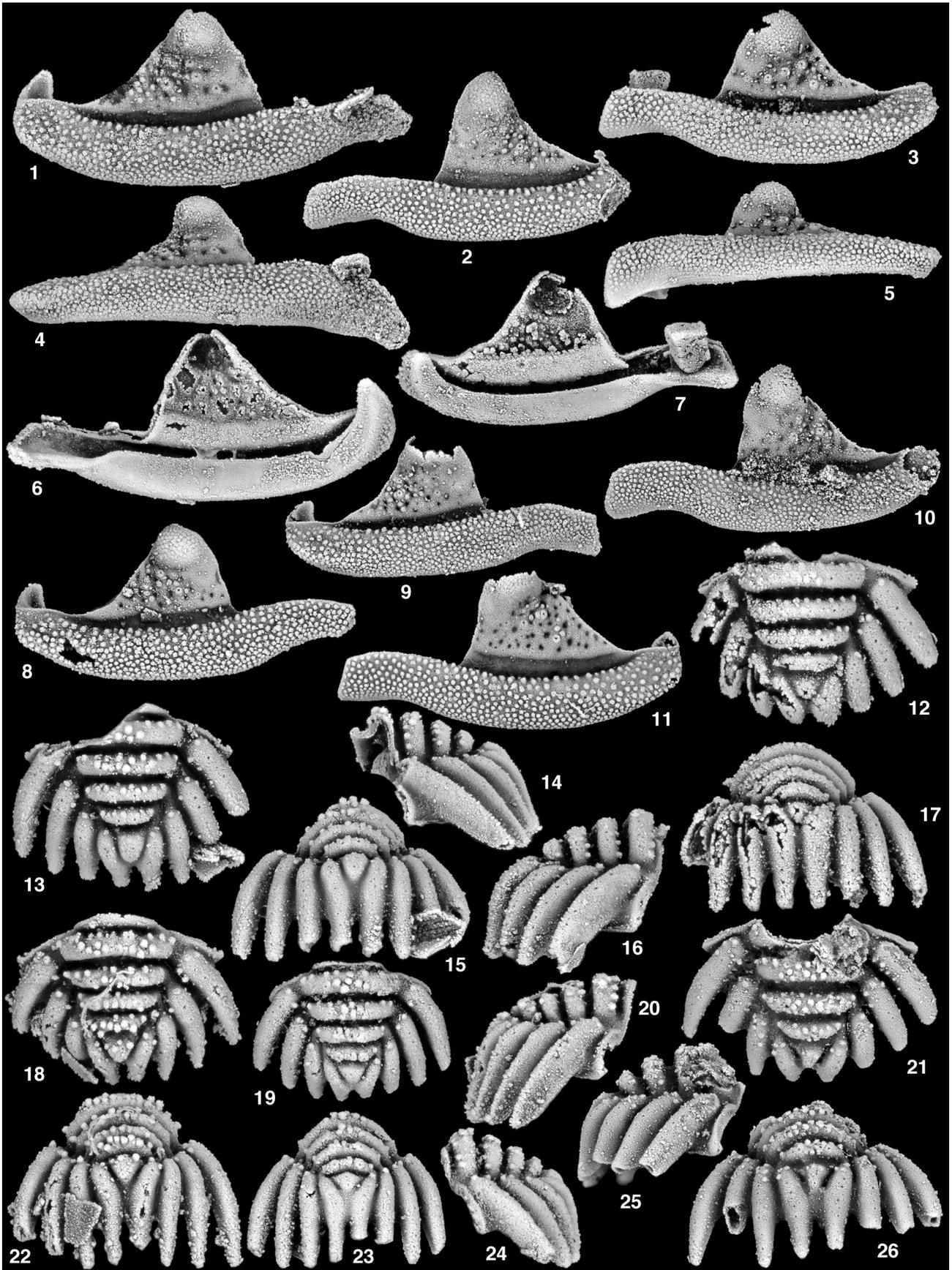


PLATE 51.

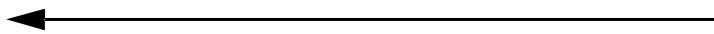


PLATE 51. *Millardaspis milsteadi* n. sp., from Section HC6 226.5 m, Garden City Formation (Floian; Tulean; *Heckethornia hyndeae* Zone), west side of Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho, USA.

- 1, 4, 6. Right librigena, SUI 135547, external, ventrolateral, and internal views, x17.
2. Left librigena, SUI 135548, external view, x17.
- 3, 5, 7. Left librigena, SUI 135549, external, ventrolateral, and internal views, x17.
8. Right librigena, SUI 135550, external view, x17.
9. Right librigena, SUI 135551, external view, x17.
10. Left librigena, SUI 135552, external view, x15.
11. Left librigena, SUI 135553, external view, x17.
- 12, 16, 17. Pygidium, SUI 135554, dorsal, right lateral, and posterior views, x20.
- 13–15. Pygidium, SUI 135555, dorsal, left lateral, and posterior views, x20.
- 18, 20, 22. Pygidium, SUI 135556, dorsal, right lateral, and posterior views, x20.
- 19, 23, 24. Pygidium, SUI 135557, dorsal, posterior, and left lateral views, x20.
- 21, 25, 26. Pygidium, SUI 135558, dorsal, right lateral, and posterior views, x17.

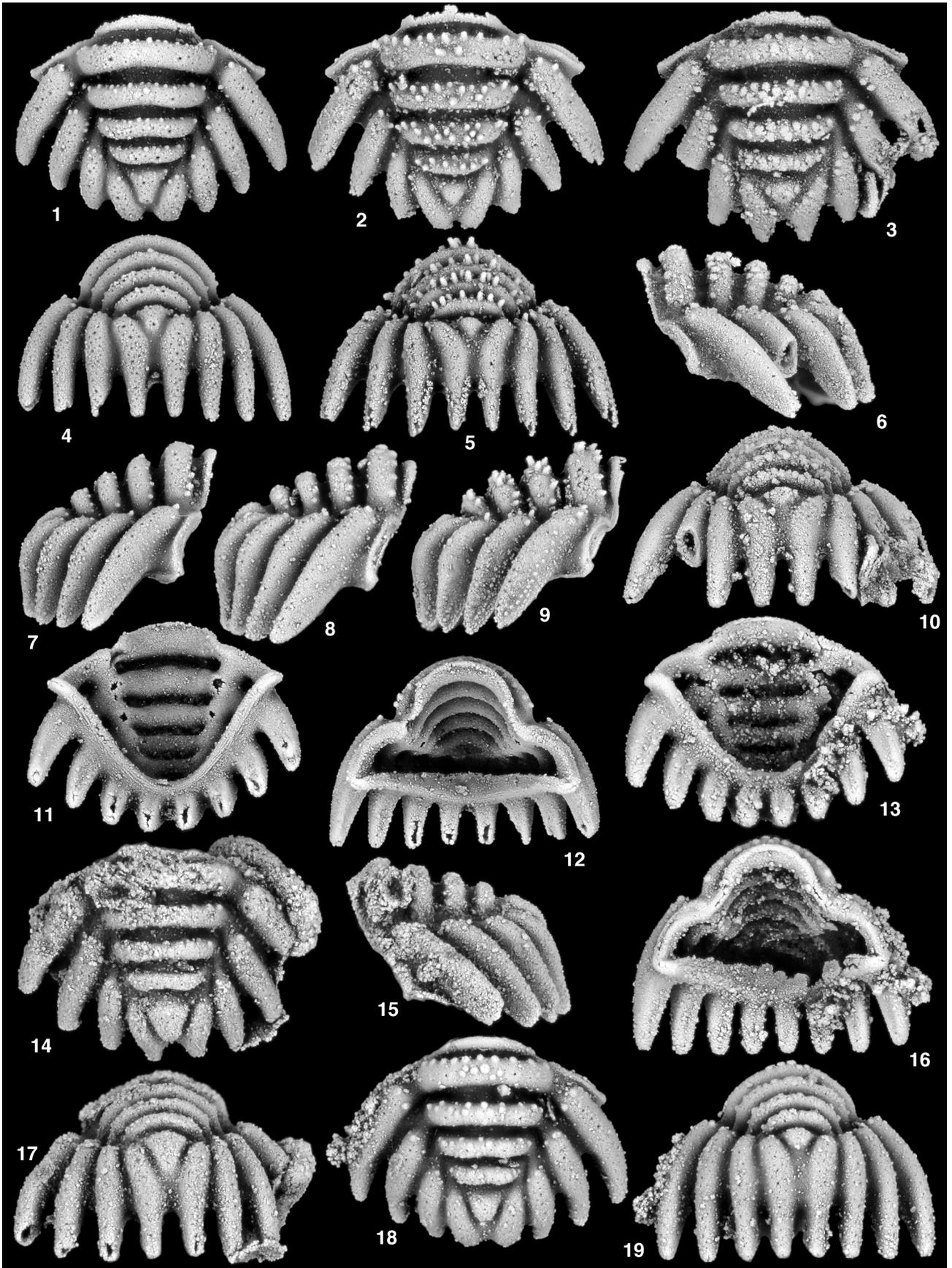


PLATE 52.



PLATE 52. *Millardaspis milsteadii* n. sp., from Section HC6 226.5 m, Garden City Formation (Floian; Tulean; *Heckethornia hyndeae* Zone), west side of Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho, USA.

1, 4, 7, 11, 12. Pygidium, SUI 135559, dorsal, posterior, right lateral, ventral, and anterior views, x20.

2, 5, 9. Pygidium, SUI 135560, dorsal, posterior, and right lateral views, x20.

3, 6, 10. Pygidium, SUI 135561, dorsal, left lateral, and posterior views, x20.

8, 13, 16, 18, 19. Pygidium, SUI 135562, right lateral, ventral, anterior, dorsal, and posterior views, x25.

14, 15, 17. Pygidium, SUI 135563, dorsal, left lateral, and posterior views, x25.

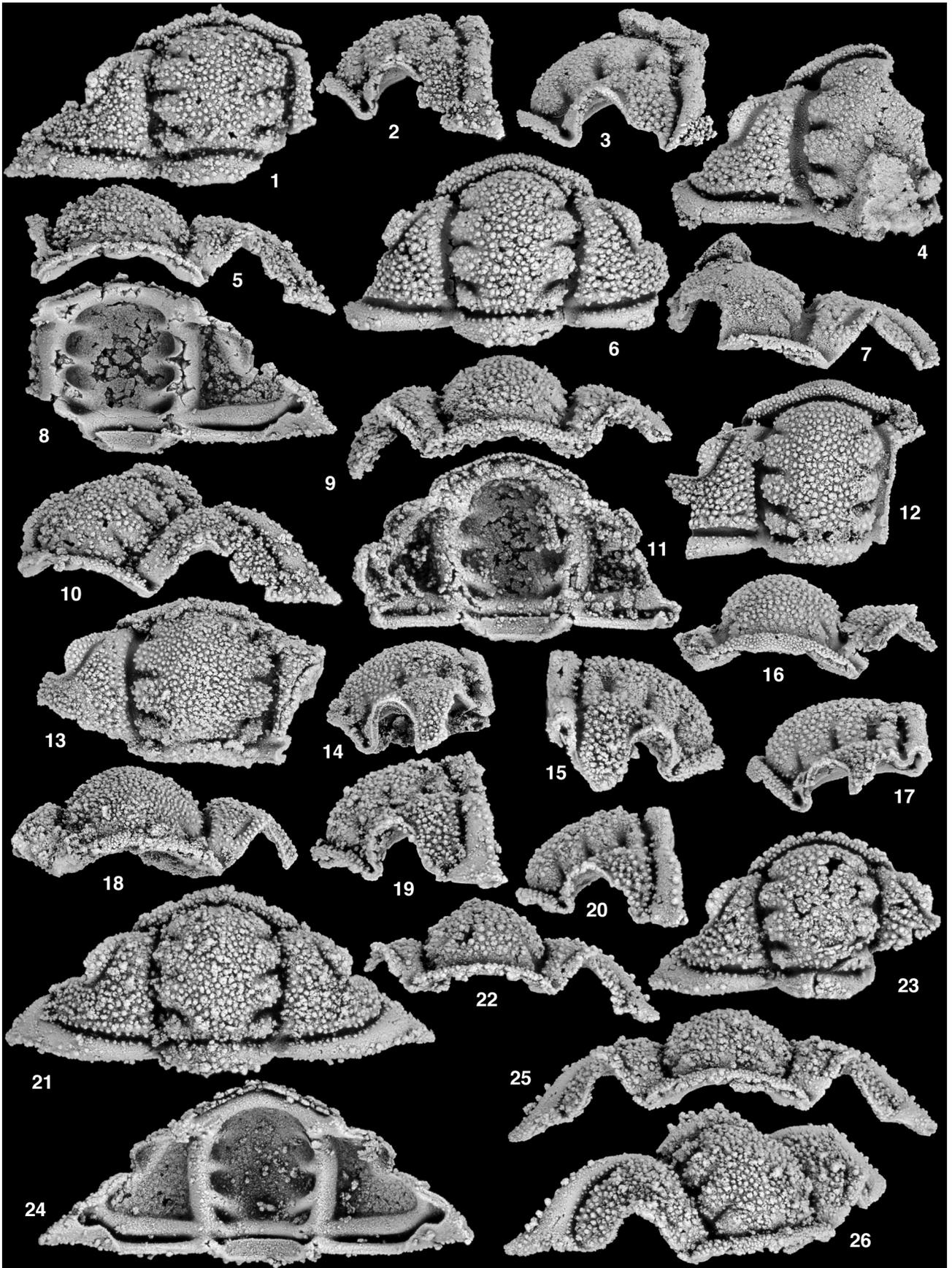


PLATE 53.



PLATE 53. *Millardaspis milsteadi* n. sp., from Section YH 128.9 m, Yellow Hill Limestone (Floian; Tulean; *Heckethornia hyndeeae* Zone), Yellow Hill, near Pioche, Lincoln County, Nevada, USA.

- 1, 2, 5, 8, 10. Cranidium, SUI 129533, dorsal, left lateral, anterior, ventral, and oblique views, x12.
3, 4, 7. Cranidium, SUI 129534, left lateral, dorsal, and anterior views, x12.
6, 9, 11, 15. Cranidium, SUI 129535, dorsal, anterior, ventral, and right lateral views, x15.
12, 16, 17. Cranidium, SUI 129536, dorsal, anterior, and left lateral views, x12.
13, 14, 18. Cranidium, SUI 129537, dorsal, left lateral, and anterior views, x10.
19, 21, 24–26. Cranidium, SUI 115262, left lateral, dorsal, ventral, anterior, and oblique views, x15.
20, 22, 23. Cranidium, SUI 129538, left lateral, anterior, and dorsal views, x17.

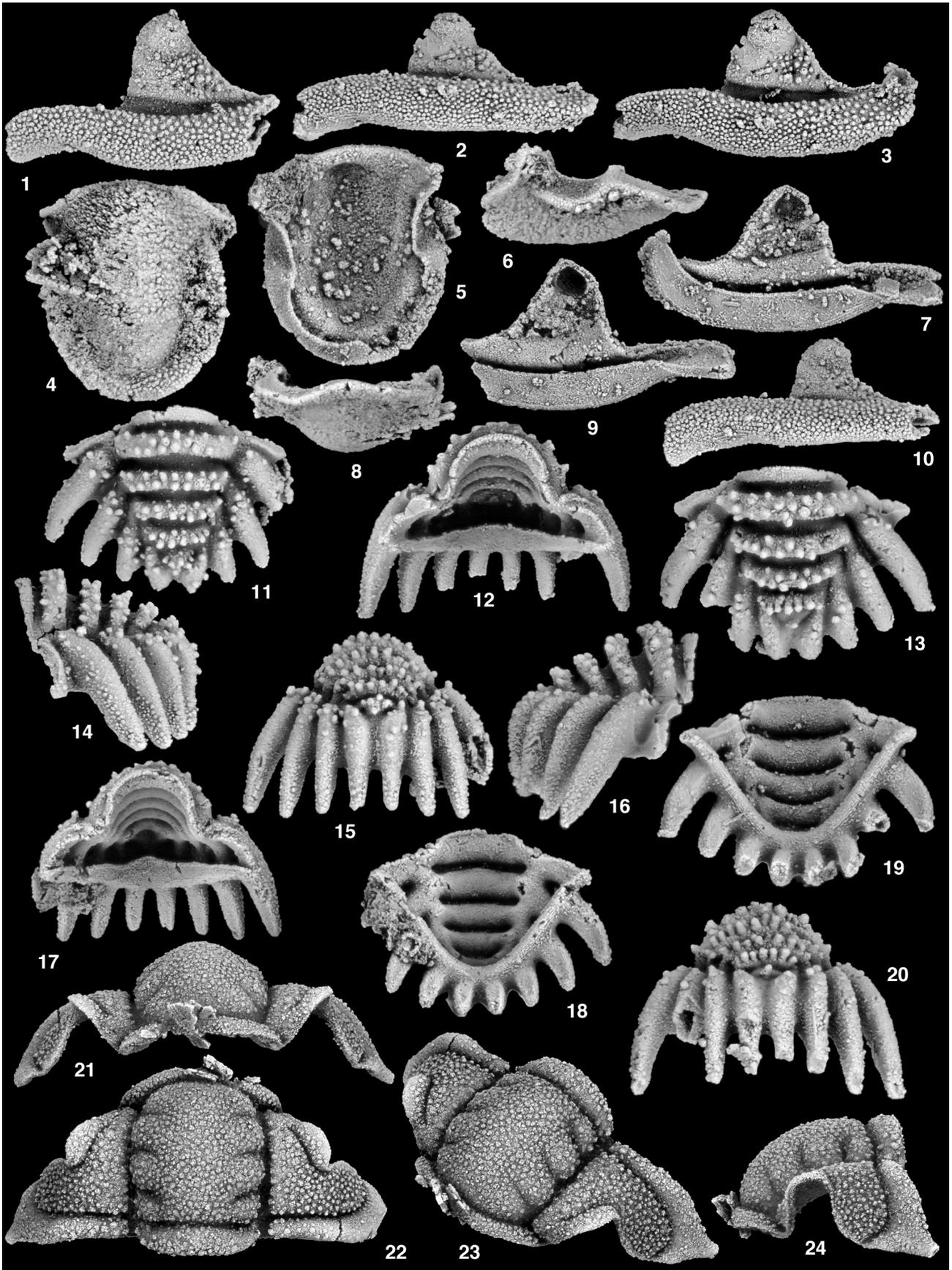


PLATE 54.



PLATE 54. 1–20. *Millardaspis milsteadi* n. sp., from Section YH 128.9 m, Yellow Hill Limestone (Floian; Tulean; *Heckethornia hyndeeae* Zone), Yellow Hill, near Pioche, Lincoln County, Nevada, USA.

1, 2, 9. Left librigena, SUI 129539, external, ventrolateral, and internal views, x17.

3, 7, 10. Left librigena, SUI 129540, external, internal, and ventrolateral views, x17.

4–6, 8. Hypostome, SUI 129541, ventral, dorsal, left lateral, and posterior views, x20.

11, 14, 15, 17, 18. Pygidium, SUI 129542, dorsal, left lateral, posterior, anterior, and ventral views, x20.

12, 13, 16, 19, 20. Pygidium, SUI 129543, anterior, dorsal, right lateral, ventral, and posterior views, x20.

Tuleaspis? n. sp. B, from Section G 210.2 m, Fillmore Formation (Floian; Tulean; *Protopliomerella contracta* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

21–24. Cranidium, SUI 115251, anterior, dorsal, oblique, and left lateral views, x15.

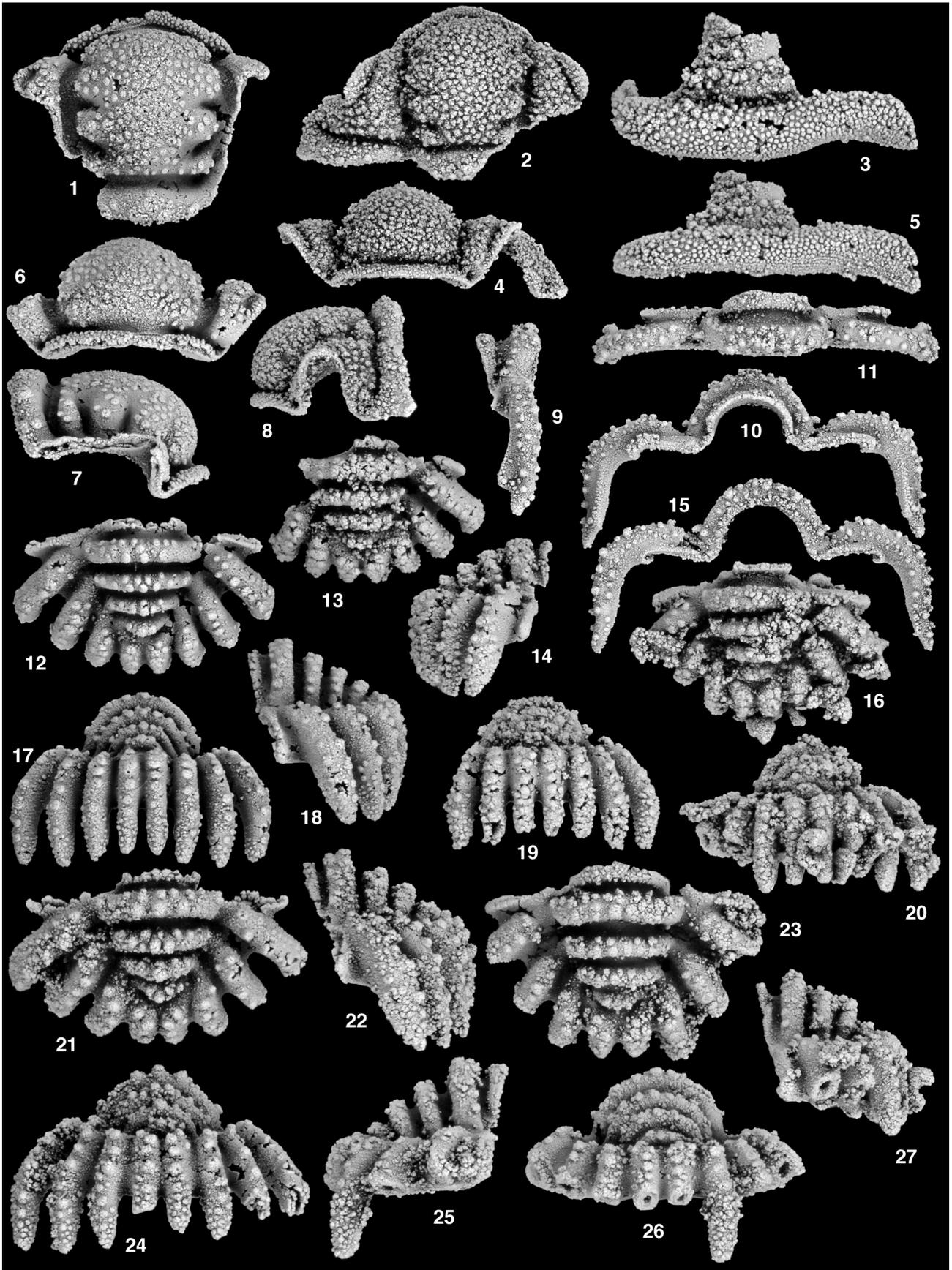


PLATE 55.



PLATE 55. *Millardaspis knoxi* n. sp., from Section H 163.3 m, Fillmore Formation (Floian; Tulean; *Paniaspis severiensis* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

- 1, 6, 7. Cranidium, SUI 129544, dorsal, anterior, and right lateral views, x15.
2, 4, 8. Cranidium, SUI 129545, dorsal, anterior, and left lateral views, x15.
3, 5. Right librigena, SUI 129546, external and ventrolateral views, x20.
9–11, 15. Thoracic segment, SUI 129547, left lateral, dorsal, anterior, and posterior views, x12.
12, 17, 18. Pygidium, **holotype**, SUI 129548, dorsal, posterior, and left lateral views, x17.
13, 14, 19. Pygidium, SUI 129549, dorsal, right lateral, and posterior views, x17.
16, 20, 27. Pygidium, SUI 129550, dorsal, posterior, and left lateral views, x15.
21, 22, 24. Pygidium, SUI 129551, dorsal, left lateral, and posterior views, x17.
23, 25, 26. Pygidium, SUI 129552, dorsal, right lateral, and posterior views, x17.