Zootaxa 3467: 1–97 (2012)
www.mapress.com/zootaxa/

Monograph

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

urn:lsid:zoobank.org:pub:99A97630-B63E-4237-AED8-30472108033F

ZOOTAXA

3467

The Middle Ordovician bathyurid trilobite *Pseudoolenoides*, with a revised trilobite biostratigraphy of the Dapingian and lower Darriwilian of western Laurentia

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Magnolia Press
Auckland, New Zealand

Accepted by J.R. Paterson: 22 May 2012; published: 7 Sept. 2012

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(*Zootaxa* 3467)

97 pp.; 30 cm.

7 Sept. 2012

ISBN 978-1-86977-975-7 (paperback)

ISBN 978-1-86977-976-4 (Online edition)

FIRST PUBLISHED IN 2012 BY

Magnolia Press

P.O. Box 41-383

Auckland 1346

New Zealand

e-mail: zootaxa@mapress.com

http://www.mapress.com/zootaxa/

ISSN 1175-5326 (Print edition)

ISSN 1175-5334 (Online edition)

Table of contents

Abstract

The Middle Ordovician bathyurid trilobite *Pseudoolenoides* Hintze has been treated in only a small handful of papers and few of its species have been adequately known. Here we revise all previously known species on the basis of new material and illustrations, and describe four new species, three of which are formally named. The genus now comprises 10 species, nine of which are formally named. Five of these are Dapingian and five are early Darriwilian in age. Cladistic parsimony analysis of the nine named species results in a generally well supported hypothesis of relationship which is fully congruent with stratigraphic order. A particularly well supported subclade (11 unreversed synapomorphies and 100% bootstrap support in 10,000 pseudoreplicates) consists of six species, including the type, which are likely a product of neotenic paedomorphosis. Three other species are resolved as successive sister taxa to this derived clade. A new trilobite zonation recently proposed for the Tulean and Blackhillsian stages (Lower Ordovician) is extended through Middle Ordovician (Dapingian and lower Darriwilian) rocks in western Laurentia. New species are *P. pogonipensis* (Dapingian; *Pseudoolenoides dilectus* Zone) and *P. fossilmountainensis* (lower Darriwilian; *P. fossilmountainensis* Zone), both from the Kanosh Formation of western Utah, and *P. oilcreekensis* (lower Darriwilian) from the Oil Creek Formation of Oklahoma.

Key words: Silicified, Utah, Oklahoma, taxonomy, biostratigraphy, cladistics, paedomorphosis

Introduction

The bathyurid genus *Pseudoolenoides* Hintze, 1953, has received detailed attention in only three publications: Hintze's (1953) original monograph of Lower and Middle Ordovician trilobite faunas of western Utah, Shaw's (1974) monograph of the Simpson Group trilobites of Oklahoma, and Fortey and Droser's (1996) paper on lower Dapingian trilobites of the Great Basin. Although the genus exhibits striking morphology, most of its species have never been illustrated to a modern standard. The goals of this study are to redescribe all of the type material of all species of *Pseudoolenoides*; to revise the species with the addition of new collections of silicified material from western Utah and of unfigured material from Oklahoma in the collections of the Oklahoma Museum of Natural History; to name and describe three new species and illustrate a fourth in open nomenclature; to present a formal hypothesis of phylogenetic relationship based on parsimony analysis; and to extend the trilobite zonation of Adrain *et al*. (2009) through the Middle Ordovician Kanosh Formation.

Localities

Ibex Area, Utah

Species of *Pseudoolenoides* described herein from the classic Ibex area of western Utah all occur in the Kanosh Formation. We have also observed sclerites belonging to an undetermined species of the genus weathering on the surface of dolomitic limestones in the lower part of the overlying Lehman Formation, but no samples suitable for description were obtained from this interval. The stratigraphy of the Kanosh Formation was documented by Hintze (1951, 1953, 1973a), who described some of the trilobites occurring in the unit (1953). The type section of the formation is Hintze's (1951, 1953) original Section K at Fossil Mountain in the southern Confusion Range. This is the only complete section of the formation known in the Ibex area, and it was remeasured by Hintze (1973a) as "K-South" (Fig. 1.2). This section has yielded all of the material of the new species *P. pogonipensis* and *P. fossilmountainensis* described herein, from horizon K 1.5T m (T=talus). Other nearby exposures of the Kanosh are at Hintze's (1973a) K-North, which is immediately to the north of K-South, and at Section J, which is a few kilometres to the south. Section J is important because it yielded the articulated holotype of *P. dilectus*, revised below, but the Kanosh Formation is incomplete and faulted here. Another important section, which has yielded all of the material of *P. acicaudus* described herein, is Hintze's (1951, 1953, 1973a) Section CP, which is located just north of Crystal Peak in the Crystal Peak Hills (Fig. 1.3). The lower part of the Kanosh Formation is not exposed here, but the upper 97.5 m of the formation are continuous, though only moderately well exposed in small gullies on a treed slope.

Oklahoma

The Oklahoma material of *Pseudoolenoides* illustrated herein comprises all of that from the Oil Creek Formation illustrated by Shaw (1974) along with additional specimens from the same localities in the collections of the Oklahoma Museum of Natural History. Details of the sections may be found in Shaw (1974), and the age and correlation of the intervals containing species of *Pseudoolenoides* are discussed below.

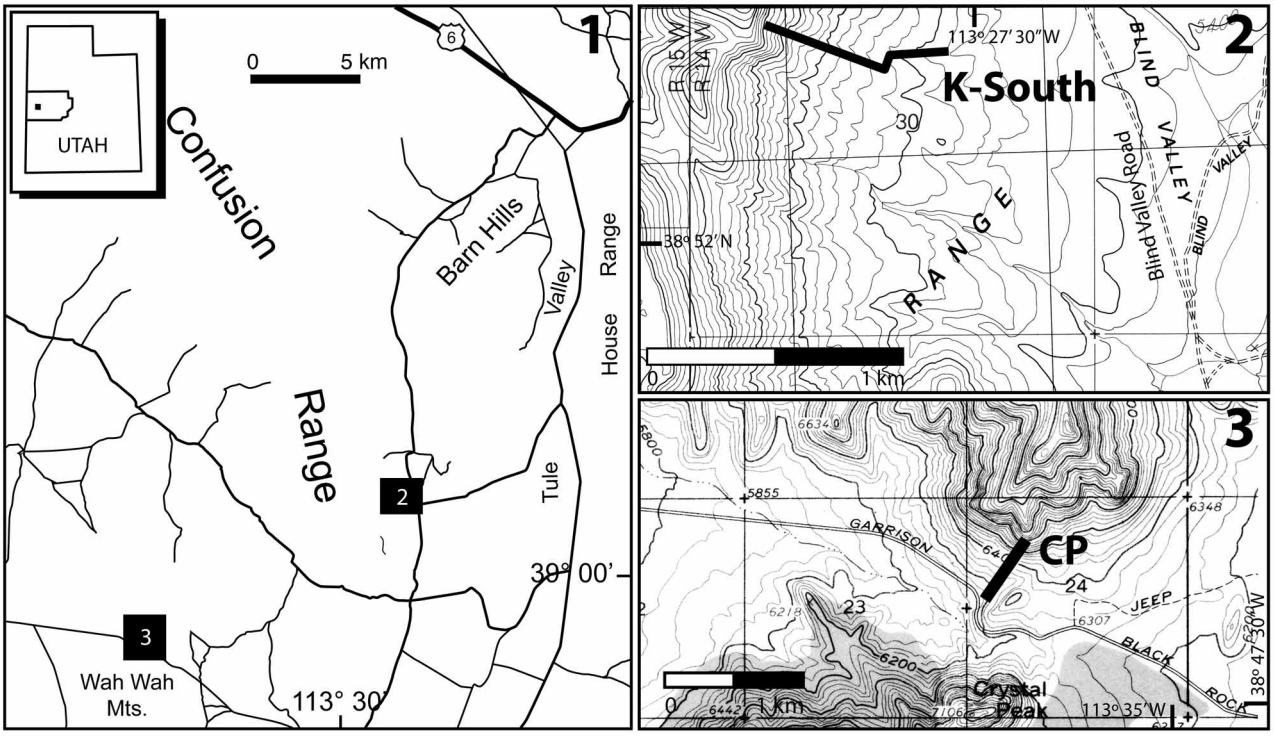

FIGURE 1. 1. Map of Tule Valley and Confusion Range in Millard County, western Utah (see inset), showing position of lines of sections. 2. Line of Section K-South (Fossil Mountain), southern Confusion Range, Ibex area, on portion of U.S. Geological Survey 1:24,000 Warm Point provisional 7.5' quadrangle topographical map (1991). 3. Line of Section CP, Crystal Peak Hills, on portion of U.S. Geological Survey 1:24,000 Crystal Peak 7.5' quadrangle topographical map (1960).

Biostratigraphy

Adrain *et al.* (2009) proposed a revised trilobite biostratigraphy for most of the Tulean and Blackhillsian stages (together, more or less corresponding to the Floian, though the position of base *Tetragraptus approximatus* is difficult to determine in the sections and the lower part of the Tulean may be upper Tremadocian in global terms). The uppermost part of the Blackhillsian, the "*Pseudocybele nasuta* Zone" (Ross, 1951; Hintze, 1953; Ross *et al.*, 1997), was not revised, pending ongoing work in progress. This interval is much more biostratigraphically complex than has been appreciated, and Adrain and McAdams (2012, fig. 1) indicated that it comprises at least six distinct faunal intervals. Here we extend the zonation through the Middle Ordovician (Dapingian and Darriwilian) strata exposed in the Ibex area, based primarily on previous zones (and subzones) proposed by Hintze (1953) and Fortey and Droser (1996). The zonal scheme is shown in Figure 2.

<table>
<tr><th>Global Series</th><th>Global Stages</th><th>Regional Series</th><th>Regional Stages</th><th colspan="2">Hintze (1953)</th><th>This Paper</th></tr>
<tr><td rowspan="7">Middle Ord.</td><td rowspan="2">Darriwilian</td><td rowspan="7">Whiterockian</td><td rowspan="7">"Rangerian"</td><td colspan="2">unzoned</td><td>Pseudoolenoides fossilmountainensis</td></tr>
<tr><td>N</td><td>Pseudoolenoides acicaudus</td><td>Pseudoolenoides acicaudus</td></tr>
<tr><td rowspan="5">Dapingian</td><td>M</td><td>Pseudoolenoides dilectus</td><td>Pseudoolenoides dilectus</td></tr>
<tr><td rowspan="3">L</td><td rowspan="3">Orthis subalata</td><td>Psephosthenaspis glabrior</td></tr>
<tr><td>Psephosthenaspis pseudobathyurus</td></tr>
<tr><td>Psephosthenaspis microspinosa</td></tr>
<tr><td>Lower Ord.</td><td>Floian (upper)</td><td>Ibexian</td><td>Black-hillsian</td><td>J</td><td>Pseudocybele nasuta</td><td>Zonation In Progress
(see Adrain and McAdams, 2012)</td></tr>
</table>

FIGURE 2. Middle Ordovician trilobite zonation proposed herein, as compared with Hintze's (1953) scheme and the regional and global stages and series. The trilobite zones are largely based on work by Hintze (1953) and Fortey and Droser (1996).

The species of *Pseudoolenoides* dealt with herein are all Middle Ordovician in age. The base of the Dapingian Stage is defined as the first appearance of the conodont *Baltoniodus triangularis* (Lindström, 1955) at the GSSP in Huanghuachang, Hubei, China. It is taken at Ibex at the approximately equivalent level of the first appearance of the zonal name-bearing conodont *Tripodus laevis* Bradshaw, 1969, in the Wah Wah Formation, 11.3 m beneath the base of the overlying Juab Formation (Ross *et al.*, 1997). The base of the Darriwilian Stage is defined as the first appearance of the zonal name-bearing graptolite *Undulograptus austrodentatus* (Harris and Keble, 1932) at the GSSP in the Huangnitang Section, Zhejiang, China. This level is difficult to locate in shallow water sections in western Laurentia, where graptolites are rare to absent. It lies within the upper part of the *Histiodella altifrons* conodont Zone in terms of the shallow water "midcontinent" biofacies and zonation applied at Ibex (Mitchell *et al.*, 1997).

Given that the trilobite faunas are very stratigraphically restricted in occurrence (though rich where found) in the Kanosh Formation, it is possible to assign the zones used herein to the Dapingian or Darriwilian with confidence. According to Ethington and Clark (1981, p. 12), the beginning of their "*Pteracontiodus cryptodens—Histiodella altifrons—Multioistodus auritus* Interval" is at 6 feet (1.8 m) above the base of the Kanosh Formation. This dates the *Pseudoolenoides dilectus* Zone (described below), which occurs at 1.5 m above the base of the Kanosh at K-South, as securely upper Dapingian. The base of their "*Histiodella sinuosa* Interval" (Ethington and Clark, 1981, p. 13), which is definitely Darriwilian, lies 217 feet (66.1 m) above the base of the Kanosh Formation. *Pseudoolenoides acicaudus* has not been collected from K-South and is known only from Section CP. However it occurs there in association with a moderately diverse fauna including *Thaleops utahensis* (Hintze, 1953). *Thaleops* Conrad, 1843, was reported (as *Illaenus* Dalman, 1827) by Hintze (1973a, p. 30) at 315 feet (96.0 m) in Section K-South. This agrees well with the equivalent position extrapolated from the base of the high calcisiltite unit of the Kanosh Formation. At Section CP, the rich *P. acicaudus* fauna is found about 145 feet (44.2 m) beneath the base of the calcisiltite. The approximately equivalent position at K-South is 278 feet (84.7 m). This is well above the base of the *H. sinuosa* Zone (217 feet/66.1 m) and hence the *P. acicaudus* Zone is lower Darriwilian. We recovered *P. fossilmountainensis* from 500 feet (152.4 m) and 524 feet (159.7 m) at K-South. According to Ethington and Clark (1981), all of the upper Kanosh Formation lies within the *H. sinuosa* Zone and hence the *P. fossilmountainensis* Zone is also lower Darriwilian.

Species of *Pseudoolenoides* occurring in the Simpson Group of Oklahoma (Shaw, 1974) are comparable to those found in the Kanosh Formation, and in fact Shaw (1974) identified one in common, though this is clearly erroneous (see below). Conodont data from Oklahoma are broadly in agreement with those from Ibex. *Pseudoolenoides oilcreekensis* n. sp. occurs at 104.5 m and 126.8 m above the base of the US Highway 77/ Interstate 35 Section (Carter County, Oklahoma) according to Shaw (1974). Bauer (2010) assigned these horizons to the lower part of his *Histiodella labiosa* Zone (he listed [2010, table 1] the first appearance of *H. labiosa* as 101 m in this section). The *H. labiosa* Zone was described (Bauer, 2010, fig. 2) as a "local zone established on conodont occurrences in the Simpson Group" and is a subdivision of the standard *H. sinuosa* Zone. *Pseudoolenoides carterensis* occurs in this section at 175.6 m (576'; Shaw, 1974) and is from the same conodont zone. *Pseudoolenoides derbyi* does not occur in this section, but at the West Spring Creek Section (Murray County, Oklahoma) it occurs about 60 m beneath *P. carterensis* which, based on thicknesses at the Highway 77 Section, would also place it within the same zone, approximately similar in age to *P. oilcreekensis*. Hence, the Oklahoma species are all from the lower Darriwilian *H. sinuosa* Zone (or its local subdivision), as are the most comparable species, *P. acicaudus* and *P. fossilmountainensis*, at Ibex.

TABLE 1. Taxon-character matrix for cladistic analysis of *Pseudoolenoides*. A new species of *Acidiphorus* Raymond, 1925, was used as the outgroup. See text for discussion and Figure 3 for results of analysis.

Taxa	Characters																										
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
***Acidiphorus* n. sp.**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
P. aspinosus	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0
P. pogonipensis	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	1	1	0	0	0	1	0	0	0	0	0	0
P. ludificatus	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	1	1	0	0	0	1	1	0	0	0	0	0
P. dilectus	1	0	0	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	0	0	1	1	1	1	0	0	0
P. derbyi	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	?	?	3	1	0	1	1
P. acicaudus	1	1	1	1	1	1	1	2	1	1	1	0	1	1	1	1	1	1	1	1	1	?	?	2	1	0	1	1
P. oilcreekensis	1	1	1	1	1	1	1	2	1	1	1	0	1	1	1	1	1	1	1	1	1	?	?	3	1	1	1	2
P. fossilmountainensis	1	1	1	1	1	1	1	2	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	3	1	1	1	2
P. carterensis	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	1	1	1	0	1	?	?	3	1	1	1	2

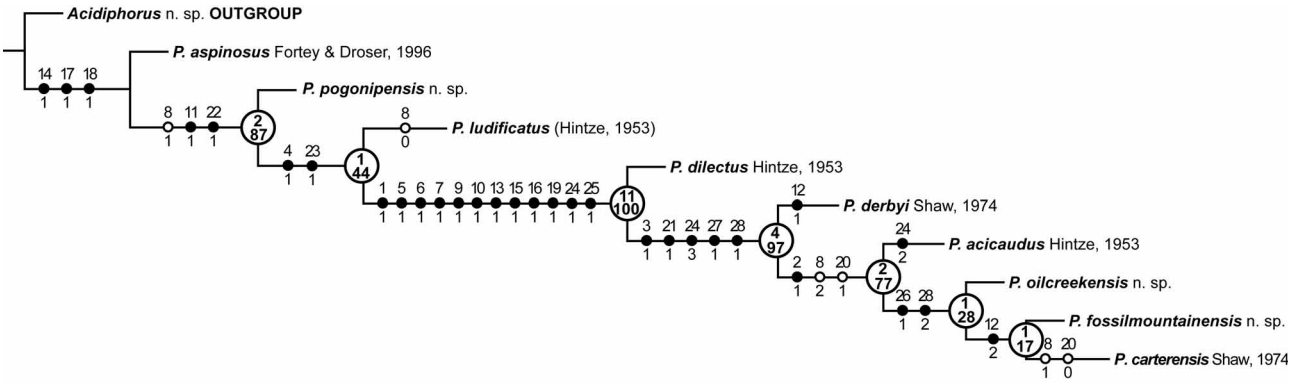

FIGURE 3. Single most parsimonious tree resulting from analysis of the matrix of Table 1. Length = 36; c.i. = 0.91; r.i. = 0.95. Open circles are characters containing homoplasy. Character optimizations are shown carried out under the ACCTRAN assumption. Upper values at nodes are Bremer support values. Lower values at nodes are bootstrapping GC scores.

Psephosthenaspis microspinosa Zone, *Psephosthenaspis pseudobathyurus* Zone, *Psephosthenaspis glabrior* Zone

These zones are as outlined by Fortey and Droser (1996), except that they were originally proposed as subzones of

a "*Psephosthenaspis* Zone". Although the use of the term "zones" based on the ranges of genera has been standard practice in Laurentian Cambrian and Lower Ordovician biostratigraphy, it reflects a pre-modern approach to systematics. Genera are human constructs. They are based on explicit hypotheses of synapomorphy, though the vast majority of trilobite genera have yet to be treated in modern systematic terms. Even when genera have been supported by modern phylogenetic analysis, their inclusivity (i.e., where to draw the basal node) remains a matter of subjective human decision. For this reason, "zones" based on the ranges of genera have essentially arbitrary bases. Further, definition of biostratigraphic units based on higher taxon ranges risks allowing the biostratigraphic scheme to drive the systematics: if everyone knows that a taxon is from a given "zone", then it should not occur outside that "zone" and when encountered there it is given a different name. This tail wagging the dog effect has plagued Laurentian Cambrian trilobite systematics, in which stratigraphic (and geographic) range has been explicitly advocated as a criterion for supraspecific taxonomy (e.g., Palmer, 1960, pp. 57–59).

The "subzones" recognized by Fortey and Droser (1996), on the other hand, are species-level units based on the first appearance of particular species and containing substantially distinct sets of species which only rarely cross zonal boundaries. They are directly equivalent in practice to the zones recognized by Adrain *et al.* (2009) and hence we elevate them here to full zonal level. All are Dapingian, and fall within the *Tripodus laevis* conodont Zone (Ross *et al.*, 1997). The species content of each zone was described in detail by Fortey and Droser (1996).

***Pseudoolenoides dilectus* Zone**

This zone is as outlined by Hintze (1953, pp. 20–21). *Pseudoolenoides dilectus* is perhaps not the best choice as name bearer, as it is very rare (we did not encounter it in our sampling), whereas the cooccurring *P. ludificatus* is one of the most common trilobites in collections from the zone. Nevertheless, the original name is retained for clarity's sake, although none of the names have been referred to often in the literature. In addition to the faunal list given by Hintze (1953, table 11), we here describe an additional species of *Pseudoolenoides*, *P. pogonipensis*, from the zone. Adrain and McAdams (2012) also demonstrated that *Psephosthenaspis glabrior* extends upward into the zone from the underlying zone which bears its name.

The zone is mainly represented by one prolific bed 1.5 m above the base of the Kanosh Formation. This is locality K-1 of Hintze (1953, table 11) at section K-South. The bed is not found in outcrop, but is represented by small lumps of limestone densely scattered and weathering in place along strike (now mostly collected). The same interval at Section J has not yielded abundant silicified fossils, but did yield Hintze's (1953) articulated holotype of *P. dilectus*.

***Pseudoolenoides acicaudus* Zone**

This zone is as outlined by Hintze (1953, pp. 20–23). Hintze's main collection was made at Section CP 150 feet (45.7 m). This level features sparse limestone nodules in an olive shale with very limited lateral outcrop on the side of a small gully. New sampling has yielded very few fossiliferous nodules and it appears most were removed during the original collection. A few more were recovered slightly higher at CP 48.8 m and these yielded all of the material of *P. acicaudus* illustrated herein. We have since found another exposure of this zone along strike to the east, but silicification is very sporadic in the rocks. The fauna is as listed by Hintze (1953, p. 42), with the addition of a large effaced bathyurid.

***Pseudoolenoides fossilmountainensis* Zone (new)**

This zone characterizes the upper part of the Kanosh Formation and possibly the lower part of the overlying Lehman Formation, with which the lithological transition is gradual. It consists of a monospecific fauna containing only abundant *Pseudoolenoides fossilmountainensis*.

Phylogenetic analysis

Taxa.

The ingroup includes all species which have been assigned to *Pseudoolenoides*, with the exception of *Pseudoolenoides* cf. *dilectus*, described herein, which is known only from three pygidia. Plesiomorphic species of *Pseudoolenoides* are very similar in overall morphology to species currently assigned to *Acidiphorus* Raymond, 1925, most of which are upper Floian in age. Any of these species would likely serve as a suitable outgroup for *Pseudoolenoides*. We have elected to use the species briefly illustrated by Adrain and McAdams (2012, fig. 6) as

"*Acidiphorus* n. sp.". This species is stratigraphically close to the oldest known species of *Pseudoolenoides*, as it occurs in nearly highest Floian strata at Ibex Section J 40.0 m, and illustrations of properly associated examples of its cranidium, librigena, and pygidium are available.

Characters.

The taxon-character matrix used in the analysis is shown in Table 1. All characters were treated as unordered.

Cranidium

1. Expression of S1 in large specimens: 0, not directly impressed, visible as smooth area or lateral notch; 1, deep, posteromedially directed furrow.

A deep and prominent S1 is a very unusual feature in bathyurids, and is unknown in any other *Acidiphorus* group (*sensu* McAdams and Adrain, 2007) taxa.

2. Glabellar sculpture: 0, dominated by tubercles; 1, dominated by raised lines; tubercles subdued or absent.

An anastomosing raised line sculpture is fairly widely distributed within Bathyuridae, and may even be the basal condition for the group. Raised line sculpture is obvious on many Floian species of *Acidiphorus*, but all have their sculpture dominated by tubercles, as do basal species of *Pseudoolenoides*. Elsewhere in *Acidiphorus* group taxa, tubercles are secondarily subdued or lost and raised line sculpture is dominant in derived species of *Aponileus* Hu, 1963, and *Psephosthenaspis* Whittington, 1953 (see Adrain and McAdams, 2012, for both).

3. Presence of transverse ridge/raised line on frontal area: 0, absent; 1, present.

This feature is unique to a derived subset of species within *Pseudoolenoides*. Where present, it connects across the anterior section of the facial suture with a similar ridge on the librigenal field (character 15) and hence this might seem like redundant coding. The characters are separate, however, as it is possible for the ridge to be expressed on the librigena, but not on the frontal area, as in *P. dilectus*.

4. Raised boss anterior to junction of eye ridge and axial furrow: 0, absent; 1, present.

In most species of *Acidiphorus* there is a small oblique ridge cutting across the axial furrow and connecting the librigena with the anterior glabella in front of the adaxial contact of the eye ridge. In many species of *Pseudoolenoides* this structure is replaced by a prominent boss on the fixigena which is apparently uniquely derived within the *Acidiphorus* group.

5. Size of palpebral lobes: 0, large; 1, small.

The palpebral lobes of the more derived species of *Pseudoolenoides* are by far the smallest developed within the *Acidiphorus* group. Whereas the large lobes typical of the group are more than twice as long (exsag.) than the sagittal length of LO, derived species of *Pseudoolenoides* have lobes only slightly more than one and a half times as long as LO.

6. Expression of eye ridge: 0, subdued; 1, prominent raised and inflated ridge bounded by associated furrows.

In species of *Acidiphorus* in which the interocular fixigena is wide enough, the eye ridge is often expressed, but always as a subdued ridge. In derived species of *Pseudoolenoides*, the ridge is elaborate and completely set off from the fixigena by bounding furrows.

7. Width of fixigena opposite anterior edge of palpebral lobe: 0, at most subequal to, usually less than, sagittal length of LO; 1, considerably wider than sagittal length of LO.

In many members of the *Acidiphorus* group the anterior edge of the palpebral lobe nearly abuts the glabella, and at most the fixigena here is as wide as LO is long. In derived species of *Pseudoolenoides* the fixigena is strikingly broad.

8. Position of palpebral lobe: 0, anterior; transverse line connecting rear edges clearly cuts across substantial portion of rear part of glabella; 1, posterior; transverse line connecting rear edges cuts across very rear margin of glabella and front of SO; 2, very posterior; transverse line connecting rear edges cuts across front of LO.

Most species of *Acidiphorus* have large palpebral lobes set opposite approximately the middle third to three-fifths of the glabella. In no case does the rear of the palpebral lobe not cut across the main part of the glabella.

9. Anterior outline of glabella: 0, distinctly pointed, with obvious angular change in course in front of adaxial termination of eye ridge; 1, anteriorly evenly arcuate, furrow nearly straight in front of adaxial termination of eye ridge to rear of anterior border furrow.

The anterior glabella of species of *Acidiphorus* is typically bluntly pointed and this is true of stratigraphically early species of *Pseudoolenoides*. A blunt, evenly arcuate condition is also developed independently within *Aponileus*.

10. Depth of SO: 0, similar in depth laterally as medially; 1, much deeper laterally than medially, lateral portions

transverse slot-like pits.

There is no comparison elsewhere in the *Acidiphorus* group for the deeply impressed lateral SO seen in derived species of *Pseudoolenoides*.

11. Semicircular or crescentic fixigenal alae abutting L1: 0, absent; 1, present.

This feature can be subtle, especially in earlier species. Its expression can be variable within species; if it is expressed in any specimens, the species is assigned to state 1. In *P. fossilmountainensis*, for example, some specimens have the semilunate region inflated laterally into a crescentic ridge (Pl. 21, fig. 8) whereas others show just a faint semilunate depression (Pl. 21, fig. 1) similar to that seen in the holotype of *P. dilectus* (Pl. 11, fig. 1).

12. Sculpture along anterior edge of L1: 0, not substantially differentiated; 1, inflated rim topped by prominent tubercle row; 2, with raised line sculpture prominently bowed around adaxial end of S1 and forming raised complex ridge along front of L1.

Separating the style of sculpture among the three species which exhibit any prominent sculpture in this position risks discarding a potential synapomorphy, and the tuberculate species *P. derbyi* augments its librigenal and frontal area raised line with tubercles. Nevertheless, it is not clear that the concentration of tubercles along L1 in *P. derbyi* reflects the distinct, sharp ridge composed of joined raised lines seen in *P. fossilmountainensis* and *P. carterensis*.

13. Narrow longitudinal ridge running anteriorly from front of L1 along axial furrow, flanking L2 abaxially: 0, absent; 1, present.

This very unusual feature is best seen in *P. acicaudus* (e.g., Pl. 17, figs 3, 10) but variations of it are plain in all of the more derived species of *Pseudoolenoides*. Similar ancillary structures are also visible in some specimens opposite SO (e.g., Pl. 17, fig. 10) and opposite the anterior region of the glabella (e.g., Pl. 21, fig. 3).

Librigena

14. Lateral edge of librigenal lateral border and genal spine: 0, rounded and inflated; 1, flattened to a distinct edge.

Some species of *Acidiphorus* flatten their genal spine somewhat, and species of both *Aponileus* and *Psephosthenaspis* develop a laterally sharp, blade-like spine. Only *Pseudoolenoides*, though, shows the parallel very sharp lateral edge of both the librigenal lateral border and genal spine. Other *Acidiphorus* group species which flatten the genal spine typically retain at least the anterior part of the lateral border with ventrolateral rounding and inflation.

15. Presence of a prominent raised, arcuate line running across the librigenal field beneath the eye: 0, absent; 1, present.

See discussion of Character 3.

16. Tuberculate sculpture on librigenal field: 0, present, even if subdued; 1, absent (except associated with raised line arc).

While Character 2 also codes for dorsal cephalic expression of tubercles (on the glabella), the characters code independently of one another as both *P. dilectus* and *P. derbyi* display glabellar tubercles but lack librigenal field tubercles.

17. Inflation of librigenal posterior border: 0, inflated, semicylindrical in section; 1, flattened, with faint secondary furrow near posterior edge.

It is debatable whether this character should be regarded as independent of Character 14, and both characterize all species of *Pseudoolenoides*. The modifications of the lateral border and posterior border are not structurally identical, and in particular the small secondary furrow developed on the posterior border has no counterpart on the lateral border. Hence we regard them provisionally as separate modifications.

18. Shape of posterior edge of librigenal posterior border: 0, straight; 1, posteriorly arced to lobate.

Again, as for Characters 14 and 17, this is a feature of the modified librigenal border which is shared by all species of *Pseudoolenoides*. Once more, it is not obviously structurally correlated with the modifications involved in either of those characters, so we elect to code it separately.

19. Relationship of base of genal spine to librigenal field: 0, gently gradational, lateral border furrow shallowed out, but no independently inflated structure; 1, connected by distinct, independently inflated girder-like structure, reflected as furrow on internal surface.

The relationship of the base of the genal spine to the librigenal field is modified in many different bathyurid taxa, with some kind of broad and inflated connection common, often with prominent raised line sculpture. Such a feature is developed in some species currently assigned to *Acidiphorus*. The basal condition in *Pseudoolenoides*, however, is that seen also in the outgroup, in which there is only a broad but subdued connection. The

development of a narrow but prominent girder-like connection within *Pseudoolenoides* has no obvious comparison in other *Acidiphorus* group taxa.

20. Length of librigenal field behind eye: 0, with some extent; eye separated from posterior border furrow, even if by very narrow strip of field; 1, field completely reduced, rear of eye abutting posterior border furrow.

This character is potentially redundant with Character 8, state 2, as both are associated with a posterior eye position. However, Character 8, state 1, also codes for a posterior eye in which a strip of field is retained on the librigena.

21. Librigenal lateral border furrow: 0, with simple morphology of continuously deep furrow; 1, with irregular, scalloped, pseudo-pitted bottom.

It is unclear exactly what is responsible for the irregular bottom of the librigenal lateral border furrow in derived species of *Pseudoolenoides* (seen well, e.g., in Pl. 23, fig. 14). In other trilobite taxa where this occurs it is usually associated with caecal sculpture and involves caecal trunks crossing the furrow. No prominent caecal structure is expressed within the *Acidiphorus* group, however.

Hypostome

22. Spine on shoulder of hypostome: 0, absent; 1, present.

Hypostomes of species of *Pseudoolenoides* seem likely to be highly informative. Unfortunately, they are only known with certainty for four species (*P. dilectus*, *P. pogonipensis*, *P. ludificatus*, and *P. fossilmountainensis*). A hypostome associated with *P. aspinosus* (see discussion below) by Fortey and Droser (1996) is accepted for purposes of coding, but is entirely plesiomorphic in its morphology.

23. Spines on posterolateral corners of hypostome: 0, absent; 1, present.

The hypostomes we have associated with several upper Floian species of *Acidiphorus* (work in progress) have rounded posterolateral corners lacking spines. The number and morphology of the spines in this position is likely informative but as noted above hypostomes are lacking for many species (unknown for *P. derbyi*, *P. acicaudus*, *P. oilcreekensis*, and *P. carterensis*). We have coded the hypostome of *P. pogonipensis* (Pl. 10, fig. 1) as lacking spines (forcing a reversal to state zero) but this is debatable as it has a strongly modified, shelf-like posterior border with acute lateral corners which could well be the homologue of the spines seen in other species. *Pseudoolenoides ludificatus* has a single pair of spines, while both *P. dilectus* (see Hintze, 1953, pl. 27, fig. 4) and *P. fossilmountainensis* (Pl. 24) have two pairs of spines.

Pygidium

24. Number of pairs of pygidial pleural spines: 0, zero; 1, one; 2, five; 3, four.

These features are likely associated with paedomorphosis (see discussion below) and no similar spines are known anywhere else in the *Acidiphorus* group.

25. Pygidial margin: 0, complete; 1, interrupted by pleural spines.

This character is potentially entwined with Character 24, and if paedomorphic processes are responsible for generating the spinose morphology, then this character codes for the shared property of derivation from the initial paedomorphic event. If that is the case, then strictly speaking Character 24 ought to be coded reductively, with state 0 instead changed to "?". While we are convinced that paedomorphosis is involved, it remains process-based speculation. Regardless, a double zero coding would only be an issue in the case of a reversal, which does not affect these characters.

26. Length of pygidial posteromedian spine; 0, moderately short; 1, extremely long.

At least superficially, the polarity of this character could be affected by which species of *Acidiphorus* is chosen as outgroup (and this is the only character in the analysis in which this choice potentially makes a difference). Many species of *Acidiphorus*, such as *A. brighti* (Hintze, 1953), have a long, robust posteromedian pygidial spine. Others, such as the selected outgroup species, do not. Most species of *Pseudoolenoides* have a short spine similar to that of the chosen outgroup, and only the two youngest, *P. fossilmountainensis* and *P. carterensis*, have a long spine. This spine has quite different morphology from most of those known in Floian *Acidiphorus*. It is slender and does not taper strongly posteriorly, whereas those of species of *Acidiphorus* tend to have a broad base and display a marked posterior taper, beginning immediately posterior to the pygidial posterior margin. Nevertheless, the specific root of *Pseudoolenoides* within "*Acidiphorus*" remains to be determined, and the long spine of *P. fossilmountainensis* and *P. carterensis* could legitimately be considered a reversal.

27. Rear of pygidial axis: 0, clearly circumscribed posteriorly by uninterrupted union of axial furrows, strongly set

off from post-axial region with significant break in slope; 1, partially or wholly gradational into subtriangular post-axial region and base of posteromedian spine; axial furrows posteriorly effaced, rear of axis with only slight and gentle change in slope to post-axial region.

A strongly posteriorly circumscribed axis independently inflated versus the post-axial region is present in virtually all Floian *Acidiphorus*, including the outgroup species.

28. Shape of pygidial axis or equivalent in species with pleural spines: 0, axial furrows straight, rear of axis slightly swollen; 1, axial furrows laterally bowed around entire equivalent; 2, small and subtriangular.

The shape of the progressively reduced axis of the region homologous with the full holaspid pygidium in *Acidiphorus* is probably shaped by paedomorphosis and hence there might be concern about redundancy with character 24. Number of spine pairs and shape of axis, however, vary independently.

Results

The matrix was analyzed using exact algorithms (implicit enumeration in TNT and branch and bound in PAUP*), with all characters treated as unordered. The result was a single tree of length 36, with consistency index 0.91 and retention index 0.95. The cladogram is shown with character-states mapped using the ACCTRAN assumption in Figure 3. Nodal support was assessed using Bremer support via constrained branch and bound searches using TreeRot and PAUP*; Bremer support values are given as the upper value at each node on Figure 3. Support was also assessed with nonparametric bootstrapping, in which 10,000 implicit enumeration pseudoreplicates were run using TNT. Scores shown as the lower value at each node in Figure 3 are bootstrapping GC metrics (Goloboff *et al.*, 2003).

Analysis yielded a hypothesis of relationship completely congruent with sampled stratigraphic order (to the extent known, as the precise relative stratigraphic positions of the Utah vs Oklahoma species are impossible to confirm). The tree is generally very well supported and low in homoplasy. Some groupings are extraordinarily well supported whereas resolution of relationships within the most derived group of species is somewhat tenuous. There is good support for the notion, as advanced by Fortey and Droser (1996), that *P. aspinosus* is the basal species of the clade. Characters shared by the remaining species but excluding *P. aspinosus* are the development of fixigenal alae (Character 11(1)) and a hypostome with a spinose shoulder (22(1)). *Pseudoolenoides pogonipensis* is sister to the remaining group, all of which display a raised boss on the anterior cranidial fixigena (4(1)) and spinose posterior corners of the hypostome (23(1)). *Pseudoolenoides ludificatus* is then sister to an extraordinarily well supported clade which shares 11 unreversed synapomorphies. This is the group probably shaped by paedomorphic processes (see genus discussion). *Pseudoolenoides dilectus* is recovered as the basal member of this derived clade, and this node is also strongly supported. *Pseudoolenoides acicaudus* is sister to the remaining three species, which share a reduced, triangular tagmatized pygidial region (28(2)) and a long, slender posteromedian pygidial spine (26(1)). *Pseudoolenoides fossilmountainensis* and *P. carterensis* are retrieved as sister species on the basis of their shared ridge-like raised line sculpture on the anterior edge of L1 (12(2)). Support for the internal structure of the clade comprising the most derived four species, however, is relatively weak, with nodes having Bremer support of one and GC metrics of 28% and 17%.

Systematics

Repositories. Figured material is housed in the Paleontology Repository, Department of Geoscience, University of Iowa, Iowa City, with specimen number prefix SUI; the American Museum of Natural History, New York, with specimen number prefix AMNH; the Oklahoma Museum of Natural History, University of Oklahoma, Norman, with specimen number prefix OU; and the United States Museum of Natural History, Smithsonian Institution, Washington, D.C., with specimen number prefix USNM.

Family Bathyuridae Walcott, 1886
Pseudoolenoides Hintze, 1953

Type species. *Pseudoolenoides dilectus* Hintze, 1953, Kanosh Formation, western Utah, USA.

Other species. *Pseudoolenoides acicaudus* Hintze, 1953, Kanosh Formation, western Utah; *P. aspinosus* Fortey and Droser, 1996, Juab Formation, western Utah; *P. carterensis* Shaw, 1974, Oil Creek Formation, Oklahoma; *P. derbyi* Shaw, 1974, Oil Creek Formation, Oklahoma; *P. fossilmountainensis* n. sp., Kanosh Formation, western Utah; *P. pogonipensis* n. sp., Kanosh Formation, western Utah; *Goniotelus*? *ludificatus* Hintze, 1953, Kanosh Formation, western Utah; *P. oilcreekensis* n. sp, Oil Creek Formation, Oklahoma; *Pseudoolenoides* cf. *dilectus* Hintze, 1953, Kanosh Formation, western Utah.

Hintze (1953, p. 226) pointed out that *Symphysurus* ? *goldfussi* Walcott, 1884, from the "Pogonip group" near Eureka, Nevada, is certainly a species of *Pseudoolenoides*, but the unique holotype cranidium is both too poorly preserved for meaningful comparison and also lost. Hence the species should be restricted to its missing holotype.

Diagnosis. Librigenae with entire lateral border and abaxial edge of genal spine flattened into very sharp ventrolateral edge; posterior border flattened and with faint accessory furrow near posterior edge; posterior margin of posterior border posteriorly arcuate to lobate.

Discussion. No diagnosis has previously been provided for *Pseudoolenoides*. As often happens once notions of phylogenetic relationship are made explicit, there is an obvious, well supported group which forms the derived core of the taxon. This is the group which Hintze (1953) and Shaw (1974) recognized as *Pseudoolenoides*. However, following Fortey and Droser (1996) and with the addition of *P. pogonipensis* herein, there is also a series of successive, less derived, sister species on the stem leading to the derived group. At issue is how to treat these less derived species and where to draw the basal node of the genus.

The question is placed more sharply in relief for *Pseudoolenoides* by the extreme morphological novelty of the derived group. The multiple unreversed changes at this node (encompassing *P. dilectus*, *P. derbyi*, *P. acicaudus*, *P. oilcreekensis*, *P. fossilmountainensis*, and *P. carterensis*) affect all sclerites, but seem largely to be associated with the initiation of paedomorphosis. Information from articulated specimens is not as extensive as one would like within Bathyuridae, but there are strong indications that the basic body plan involves 14 well expressed thoracopygidial segments plus a terminal piece which does not usually display additional segmentation. Where known within the *Acidiphorus* group, the plan is 10 thoracic segments and a pygidium with four well expressed rings plus a terminal piece [e.g., *Aponileus aasei* Adrain and McAdams, 2012, pl. 2; *Platyantyx arcuata* (Billings, 1865) (Whittington, 1953, pl. 68, fig. 28); *Acidiphorus kindlei* (Whittington, 1963, pl. 14, fig. 4)]. Pygidia of early (lower Tulean) species generally have four axial rings, so this arrangement may be basal for the family. Within the taxa with more or less fan-shaped pygidia, it is common to reduce the number of thoracic segments to nine (e.g., *Uromystrum validum* (Billings, 1865) (Whittington, 1953, pl. 67, fig. 10); *Punka nitida* (Billings, 1865) (Whittington, 1963, pl. 11, fig. 11)). In these species there appear to be five pygidial axial rings, though it can be difficult to count due to effacement and the generally small photographs available in the literature.

The derived group of *Pseudoolenoides* species appears to have evolved via progressive retention of posterior thoracic segments as part of the adult pygidium. That is, the pygidium in holaspids represents an arrested transitory pygidium including the fully tagmatized portion, which is homologous with the adult pygidium of other members of the *Acidiphorus* group, plus one or more unreleased thoracic segments fused to the anterior margin. The number of unreleased segments ranges from one (*P. dilectus* and *P.* cf. *dilectus*) to four (*P. fossilmountainensis*, *P. carterensis*, *P. derbyi*, *P. oilcreekensis*) to five (*P. acicaudus*). If the apparently universal body segment count of 14 is maintained, this hypothesis makes predictions about thoracic segment counts in these species: the number of unreleased thoracic segments incorporated into the adult pygidium should concomitantly reduce the number of thoracic segments.

While the evidence is sparse, such predictions are borne out. *Pseudoolenoides dilectus* retains one unreleased segment, predicting a nine segment thorax, and in fact this what it possesses (Pl. 11, fig. 1). *Pseudoolenoides fossilmountainensis* retains four unreleased segments in the adult pygidium, predicting a (highly unusual) six segment thorax. While no fully articulated individual is known, we have recovered a well preserved thoracopygidium (pl. 27, figs 18–26) which displays six thoracic segments. Of course, the thorax of this specimen could be incomplete, but the pleural spines of the first segment are reduced to small nubs, which is a common alteration of the anteriormost segment of laterally spinose forms to facilitate enrolment (cf. the first thoracic segment of *P. dilectus*, Pl. 11, fig. 1). Hence, as far as the available data indicate, the evolution of the derived group involved neotenic paedomorphosis.

Cephalic modifications are difficult to evaluate in terms of paedomorphosis, as no relevant ontogenies are known in any detail. Ontogenetic information is poor for bathyurids in general, and those developmental series that are at least partially known (e.g., *Bathyurus ulu* Ludvigsen, 1979; see Chatterton, 1980, pl. 6, figs 1–15) do not

represent taxa of the *Acidiphorus* group. Cephalic modifications in derived *Pseudoolenoides* involve reduction in the relative area of the glabella, broadening of the fixigena, emphasis of the eye ridge, reduction in eye size, and migration of the eye to a more posterior position. A hypothesis of paedomorphosis predicts the presence of at least some of these features earlier in the ontogeny of less derived species, which can be tested via discovery of well preserved life histories. In the present state of knowledge, only the presence of a deeply impressed S1 is supported as paedomorphic based on available data, as S1 is transformed from well impressed in small individuals to weakly impressed or effaced in large specimens in several of the species of *Bathyurus* described by Ludvigsen (1979; e.g., *B. platyparius*, cf. pl. 2, figs 23, 20).

Following Hintze (1953) and Shaw (1974), the basal node of *Pseudoolenoides* would be taken as that subtending the derived and probably paedomorphic group, which was recovered on all 10,000 bootstrap pseudoreplicates (Fig. 3). Fortey and Droser (1996) named an older species from the Juab Formation, *P. aspinosus*, and pointed out its affinities to the derived group. These authors were also first to point out that *Goniotelus*? *ludificatus* Hintze, 1953, also has clear affinity with the derived group, and they advocated an expanded concept of the genus. As is the case with Hintze (1953) and Shaw (1974), they did not diagnose this expanded genus. We here describe a third plesiomorphic species, *P. pogonipensis*, which also lies outside the derived group. The situation is very similar to that encountered in the bathyurid genus *Psalikilopsis* Ross, 1951, discussed by Adrain *et al*. (2011). In both cases there is a highly autapomorphic derived group which includes the type species, along with a set of plesiomorphic species retrieved as successive sister species in a pectinate basal region of the cladogram. The options are to classify the basal species in a paraphyletic group of convenience (in the present case, presumably by assigning them to the currently broadly conceived *Acidiphorus*), to erect new monotypic genera to receive them, or to draw the basal node of *Pseudoolenoides* to include them. As with *Psalikilopsis*, we consider the latter option the most informative and least disruptive course of action.

Electing to include the plesiomorphic species within *Pseudoolenoides* however, means that the striking features of the derived group cannot feature in the genus diagnosis. Nevertheless, the modifications to the cephalic margin and genal spines shared by all species, involving flattening, the development of sharp, blade-like ventrolateral margins, and posteriorly extended posterior borders with small accessory furrows between the posterior border furrows and the posterior margins, are all uniquely derived within the *Acidiphorus* group and serve to effectively diagnose the taxon.

Pseudoolenoides ludificatus **(Hintze, 1953)**

Plates 1–7

1953 *Goniotelus* ? *ludificatus* Hintze, p. 161, pl. 27, figs 12–19.
1996 *Pseudoolenoides ludificatus* (Hintze); Fortey and Droser, p. 88.

Material. Holotype, cranidium, AMNH-FI 26498, and paratypes AMNH-FI 26499–26505, and assigned specimens SUI 129972–130020, 130111–130115, from Section K-South 1.5T m, Kanosh Formation (Dapingian; *Pseudoolenoides dilectus* Zone), southern Confusion Range, Ibex area Millard County, western Utah, USA.

Diagnosis. Hypostome with large subtriangular spines at shoulder and posterolateral corner; anterior lobe of middle body set off from anterior wing by distinct inflated ridge; pygidium strongly dorsally vaulted; posteromedian pygidial spine very short in large specimens.

Description. Cranidial measurements were made on the most complete specimens of Pl. 1–2. In cases where only the right or left side of the specimen was preserved, the distance to the sagittal line from this side was doubled. Cranidium weakly vaulted; sculpture of closely spaced raised lines covers glabella, fixigena, and LO; sculpture of prominent tubercles also present on glabella, LO, and anterior and posterior areas; sculpture of fine raised lines present on anterior border; width across midlength of palpebral lobes 117.7% (115.1–121.5%) sagittal length, width across posterior projections 157.0% (Pl. 2, fig. 2) sagittal length; anterior border about half as long (sag.) as LO (sag.), abaxially tapered, anterior margin strongly peaked medially, posterior margin less peaked medially and bowed around anterior margin of glabella, in anterior view dorsal margin nearly transverse, slightly ventrally bowed medially, ventral margin broadly "U" shaped, in lateral view border forms a ventrally sloping shelf; sculpture of fine raised lines arranged in anastomosing pattern present on posterior part of anterior border and arranged subparallel to margin present on anterior part; anterior border furrow is short, dorsally concave,

moderately shallow almost along entire course, developed into short deeper slit on either side of anterior glabellar margin (Pl. 1, fig. 2); anterior sections of facial sutures laterally convex opposite anterior border, very slightly laterally concave opposite rear of anterior border furrow, and strongly laterally bowed opposite frontal areas, width across maximum point of divergence (β) 84.8% (81.1–86.6%) cranidial sagittal length; frontal areas weakly dorsally inflated, strongly sloped downward from interocular fixigena; palpebral lobes large, distance across γ 73.9% (71.7–74.9%) cranidial sagittal length, distance across ε 81.4% (80.0–84.3%) cranidial sagittal length; lobe strongly but unevenly laterally bowed, anterior curve shallower than posterior curve, so lobe slung posteriorly; lobe with prominent, inflated border around margin with sculpture of fine raised lines arranged in anastomosing pattern that continues from fixigena; palpebral furrow well defined, running inside inflated rim, furrow subdivided into distinct anterolateral and posterior sections that overlap posterolaterally (Pl. 1, figs 2, 3), anterolateral section deepest opposite lateral margin of lobe, shallow, but distinct opposite anterior margin of lobe, posterior section much shallower; interocular fixigena held at oblique angle above horizontal plane, with almost no dorsal inflation, sloping toward glabella (Pl. 1, fig. 8); preocular field subtriangular, with inflation similar to that of interocular fixigena, sloped down anteriorly from horizontal plane toward anterior border furrow, with sculpture of fine anastomosing lines, scattering of prominent tubercles present on anterolateral corner of preocular field; very weak eye ridge present, developed as continuation of palpebral border running to S3; posterior fixigena with inflation similar to that of frontal area, sloped down toward posterior border furrow; posterior section of facial suture nearly transverse, extended laterally beyond lateral extent of palpebral lobe; posterior border furrow long (exsag.) and deep medially, shallower adaxially, distal tip significantly shallower and nearly effaced at contact with posterior facial suture, sharp contact medially with posterior border and posterior fixigena; posterior border moderately dorsally inflated, moderately short (exsag.) proximally, longer distally, strongly directed downward from horizontal plane, distal tip nearly subquadrate; entire border covered with small prominent tubercles, of about the same size as those on adjacent posterior fixigena; posterior margin of posterior border directed slightly anteromedially to fulcrum, nearly transverse from fulcrum adaxially; glabella with maximum width opposite γ 50.2% (47.9–52.3%) sagittal length excluding LO; glabella bullet shaped in dorsal view, sagittal length (excluding LO) 70.8% (69.7–73.4%) that of cranidium, moderately dorsally inflated with slight peak medially (Pl. 1, fig. 2), sitting below maximum height of fixigena in anterior view; lateral profile weakly curved, with portion anterior to palpebral lobes strongly downturned from horizontal plane; axial furrows nearly effaced and slightly laterally bowed around LO, width across posterior contact of furrows with posterior margin 51.5% (50.2–53.2%) cranidial sagittal length; axial furrows confluent with SO; axial furrows deepest adjacent to portion of glabella posterior to S1, much shallower anteriorly from S1, of nearly equal width from posterolateral corner of glabella anteriorly to S3 and running nearly parallel to sagittal axis, anterior to S3 furrows slightly narrower and directed strongly anteromedially, running without obvious distinction into anterior border furrow; fossula expressed dorsally as small round swelling situated adjacent to axial furrow opposite S3 (Pl. 1, figs 1, 6), expressed ventrally as small pit (Pl. 1, fig. 7); S1 visible in dorsal view (Pl. 1, figs 1, 2), expressed as smooth area lacking sculpture, straight, anterolaterally directed, in contact with axial furrows; S2 and S3 faintly visible on some specimens in dorsal view as short indentation along lateral margin of glabella; L1 defined partially by S1, with weak independent inflation; L2 not prominent, also with very weak independent inflation; uniformly strong tubercles on part of glabella posterior to S3 give way to progressively finer tubercles on anterior portion of glabella; LO long, sagittal length 15.5% (14.0–16.1%) that of cranidium, longer sagittally than exsagittally, posterior margin strongly posteriorly bowed, anterior margin nearly transverse, with sculpture of scattered prominent tubercles similar to those on glabella, sculpture of prominent anastomosing lines continues from glabella onto anterior portion of LO (Pl. 1, fig. 1); median node weakly expressed on larger specimens (Pl. 1, fig. 2) and more prominent on smaller specimens (Pl. 2, fig. 2), set just anterior to midpoint of LO; SO deep and broad (sag.; exsag.), anterior and posterior edges with sharp contact with rear of main glabella and anterior edge of LO respectively, nearly transverse to slightly anteriorly bowed medially, joining axial furrow in smooth curve so that it resembles confluent continuation of axial furrow, slightly deeper at this contact; doublure of broad, lenticular articulating surface underlying LO (Pl. 1, fig. 7, Pl. 2, fig. 10), with sculpture of fine, closely spaced raised lines set mainly transversely; rear margin of posterior border with ventral transverse groove to receive anterior edge of first thoracic segment; small triangle of doublure at distal tip of anterior border.

Librigenal measurements were made on the specimens of Pl. 4, figs 7, 11, 13, 15. Main body of librigena (excluding anterior projection and genal spine) with maximum width behind eye 51.7% (48.5–53.4%) exsagittal length; anterior section of facial suture with length 55.3% (43.8–64.6%) exsagittal length of main body and

posterior section of facial suture with length 42.1% (34.7–52.7%) exsagittal length of main body; anterior section nearly transverse opposite field, slightly curved across lateral border; posterior section "L"-shaped, curved very slightly across posterior border; visual surface rarely preserved intact, but long, relatively tall, and bulbous, bounded by shallow circumocular furrow (Pl. 4, fig. 9); field with prominent background sculpture of fine raised lines arranged in anastomosing pattern; distinct broad, raised band just below visual surface, set off from main part of field by sculpture running perpendicular to that of sculpture on main part of field, change in slope, and narrow band of prominent tubercles present on main part of field; lateral border furrow moderately broad and deep, slightly shallower anteriorly, does not meet posterior border furrow due to disruption by prominent ridge running from genal angle onto field; posterior border furrow slightly deeper than lateral border furrow, but otherwise similar; lateral border broad, with lateral margin gently and nearly evenly arcuate, curve strongest at midlength, border flattened and moderately inflated forming a ridge along lateral margin (Pl. 4, fig. 6), slightly wider posteriorly than anteriorly, with sculpture of fine raised lines running subparallel to margin, oriented more linearly anteriorly and abaxially, pattern more irregular along abaxial margin and posteriorly, lines more closely spaced and oriented subparallel to margin on lateral and ventrolateral aspects of border; posterior border with sculpture of raised lines oriented in anastomosing pattern on anterior part, sculpture much finer on posterior part; sculpture from lateral and posterior borders continuous across lateral and posterior border furrows up to genal field (Pl. 4, fig. 11); genal spine apparently long (Pl. 4, fig. 4), but not completely preserved on any recovered specimens, curved, inflation similar to that of lateral border, with sculpture of fine raised lines running down length of spine on all aspects, arranged in a "V"-shaped pattern, sculpture appears to be more subdued posteriorly; area in front of base of genal spine (confluence of lateral and posterior borders) swollen, developed into prominent ridge that cuts across posterior portion of genal field, sculpture of fine raised lines continues from genal field over ridge; anterior projection with subparallel raised lines continuous from lateral border; doublure differentiated into ventrally curved sector and flat, slightly upturned adaxial sector anteriorly beneath anterior part of lateral border and anterior projection, upturned portion flatter beneath posterior border; doublure beneath posterior border with faint fine raised lines set subparallel to posterior margin on posterior portion, sculpture more effaced anteriorly, doublure widens toward base of genal spine where sculpture joins that on doublure beneath lateral margin and continues onto ventral surface of genal spine in "V"-shaped pattern; inner margin of doublure describes smooth continuous arc, with curve strongest posteriorly at intersection of lateral and posterior borders and opposite posterior border; small Panderian notch (Pl. 4, figs 14, 20) developed along doublure beneath posterior border just adjacent to base of genal spine.

Rostral plate relatively narrow, very long, hourglass shaped in outline (Pl. 5, fig. 1); anterior part (Pl. 5, figs 4, 27) significantly longer (sag. and exsag.) than doublural portion, trapezoidal outline in anterior view; doublural portion short (sag. and exsag.), slightly shorter abaxially, distal tips reach beyond distal extent of anterior section, subsemilunate shaped in ventral view (Pl. 5, fig. 8) with posterior margin describing broad, gently curved arc; connective sutures set at strongly oblique angle, chevron shaped (Pl. 5, fig. 1), articulate with anterior projection of librigena; in lateral view describe strongly curved arc (Pl. 5, figs 17, 24); sculpture of fine, raised lines covers external surface of rostral plate, transversely oriented on majority of rostral plate to slightly upwardly arched medially on anterior portion, interior surface largely smooth with very faint expression of external sculpture (Pl. 5, fig. 22).

Hypostomal measurements were made on specimens of Pl. 3, figs 1, 6, 12, 16. Hypostome with maximum width (excluding anterior wings) across middle middle body 100.2% (97.0–106.1%) sagittal length; ventral surface covered with sculpture of raised lines, arranged in anastomosing pattern on middle body, aligned subparallel with margins on borders and anterior wings; middle body with maximum width 78.0% (71.8–84.0%) maximum length of middle body; sculpture on middle body with lines broken up into closely spaced, short segments; anterior margin turned up at nearly 90° angle to form anterior-facing wall, with sculpture of subparallel raised lines oriented subparallel to margin becoming progressively effaced toward margin; anterior area grades into middle body across sharp break and distinct change in sculpture, lines oriented subparallel to margin change to being oriented in anastomosing pattern at change in slope; anterior wing best preserved on a single specimens (Pl. 3, figs 1, 5), extended dorsolaterally, lacking sculpture of raised lines on anterior portion, set off from anterior lobe of middle body by distinct inflated ridge; lateral border directed obliquely from anterior wing forming shoulder, strongly bowed inward from shoulder to posterior margin; lateral border furrow initiated opposite posterior margin of anterior wing; lateral and posterior border forming rim-like ridge enclosing middle body, weakly inflated, strongly ventrally flexed, with sculpture of very closely spaced raised lines oriented subparallel to hypostomal margin; lateral and posterior border furrows shallow, expressed largely as a change in slope between middle body and border, forming deep pit opposite inward bow of lateral border; distinction between lateral and posterior border

clearly defined as posterolateral corner of posterior border is developed into a short posteriorly directed spine; posterior margin of posterior border broadly bowed anteriorly, with weak posteriorly directed peak developed medially; middle furrow set at about two-thirds distance posteriorly on middle body, expressed as pair of very slightly anterolaterally directed, deep, hook-shaped furrows, with distal tip forming hook, separated from lateral border furrow by strip of inflated middle body; macula small but prominent, lacking sculpture of fine raised lines; middle body with moderate ventral inflation, pinched slightly at middle furrow; doublure moderately broad behind anterior wings and posterior projection at posterolateral corner of posterior border; doublure behind posterior border narrows posteromedially; entire doublure with sculpture of several fine raised lines similar to that on anterior wing, sculpture less prominent along internal margin of doublure.

Thorax incompletely known; width of axis slightly greater than that of articulating half ring; general construction of segments consists of a tuberculate, highly dorsally inflated axial ring, generally with larger, linearly arranged tubercles with smaller tubercles scattered between,
a long, deep ring furrow, a large lenticular and smooth articulating half ring, very shallow axial furrows, a prominent pleural furrow that is long (exsag.) and shallow adaxially and deep and short at distal tip, an anterior pleural band composed of short (exsag.) inflated strip, with sculpture of small scattered tubercles present at and adjacent to fulcrum, anterior margin forming narrow ridge that sets off short anterolateral tongue with a short spike (Pl. 4, fig. 1) which articulates with a narrow ventral notch beneath the lateral edge of the pleurae of the next segment anteriorly (or the posterior border of the cranidium) (Pl. 5, fig. 26), a posterior pleural band slightly longer (exsag.) than anterior band, posterior margin slightly sinuous, with sculpture of prominent tubercles generally linearly arranged subparallel to posterior margin of pleurae, sculpture of anastomosing lines present beneath tubercles on both anterior and posterior pleural bands, continues across pleural furrow with exception of deepest distal tip, across articulating tongue and spike, and across pleural spine; large pleural spine derived from both anterior and posterior pleural bands, directed posteriorly to posterolaterally depending on position of segment in thorax, lateral margin slightly abaxially bowed opposite posterior margin of pleurae,very small projection is set at the anterior margin of the axial furrow; ventrally, the doublure forms a lenticular articulating surface beneath the axial ring with sculpture of fine, very subdued, closely spaced raised lines (Pl. 5, fig. 5), sculpture is nearly effaced abaxially; doublure also present beneath pleural spine, with additional thin strip continuing along posterior margin of pleural region to fulcrum, with sculpture of fine, widely spaced raised lines; fulcrum is set close to the axis, and the portion of the pleura distal to the fulcrum is turned down from about 40° to about 45° from horizontal.

Pygidial measurements were made on the specimens of Pl. 6, figs 1, 4, 5, 11. Pygidium with maximum width across posterior margin of second segment 185.6% (183.0–188.6%) sagittal length (excluding articulating half ring and post-axial spine); axis of four segments and long terminal piece, maximum axial width across first ring 36.6% (36.3–37.1%) maximum pygidial width; width across fourth segment 73.8% (69.7–78.7%) width across first segment; length of axis excluding articulating half ring equal to sagittal length of pygidium; articulating half ring short (sag.), sagittal length 9.8% (9.4–10.3%) pygidial length, anterior margin subsemicircular, ring sits below first segment in general sagittal profile of axis, gently dorsally convex in sagittal profile, sculpture of very fine and faint granules arranged in anastomosing pattern; first ring furrow moderately long (sag. and exsag.), transverse, shallowest medially, progressively deeper abaxially and ending in deep slit at intersection with axial furrow; subsequent ring furrows similarly transverse to very slightly posteriorly bowed, progressively shorter and shallower than first ring furrow; first axial ring slightly shorter sagittally than exsagittally, with sculpture of medium and small densely spaced tubercles, tubercles less dense medially, tubercles absent on distal portion of axial ring (Pl. 6, figs 6, 8) and replaced with sculpture of fine, raised anastomosing lines; posterior rings progressively smaller and with essentially the same morphology, except that tubercles are densely spaced across entire ring in dorsal view; axis terminated by broad posteriorly rounded terminal piece, sculpture of medium and small densely spaced tubercles covers terminal piece, tubercles become smaller and less densely spaced posteriorly, sculpture of fine, raised anastomosing lines covers posterior and posterolateral portions of terminal piece; axis distinctly terminated in dorsal view, in lateral view posterior margin of axis forms distinct almost vertical scarp; articulating facet on first segment developed into short spine-like point with a medial ridge directed anterolaterally, covered with sculpture of fine raised lines, densely spaced on adaxial portion, more widely spaced abaxially; first segment with maximum exsagittal pleural length 27.1% (22.5–30.4%) sagittal axial length, anterior margin slightly anteriorly bowed to fulcrum, which is set near axis, margin directed posterolaterally distal to fulcrum; anterior margin of first pleural band set off from margin by prominent posterolaterally directed accessory furrow, well inflated, with sculpture of scattered medium and small tubercles arranged in irregular transverse rows

covering majority of pleural band, sculpture of fine raised lines present on proximal and distal tips of pleural band; pleural furrow longest (exsag.) medially, proximal and distal tips pinch out, with distal tip less dramatically pinched, terminated at border; subsequent pleural furrows with generally same morphology as first but becoming slightly shorter overall; first interpleural furrow expressed as moderately deep, elongated pit at distal end of pleurae, subsequent interpleural furrows very weakly or not expressed; morphology of pleurae of second and third segments generally similar to those of segment one, but progressively narrower and directed more posterolaterally; fourth and fifth segments with no associated expression of inflated pleural bands, pleural region adjacent to fourth ring and fifth ring fused to terminal piece is broadly triangularly shaped and depressed (Pl. 6, fig. 12); pleural bands and furrows terminated by weakly inflated, flattened border, with sculpture of prominent raised lines, oriented roughly parallel to transverse axis, moderately densely spaced; border runs from posterior margin of anterior pleural band of first segment to posterior spine; border slightly bowed outward opposite first and second pleural bands, bowed very slightly inward opposite terminal piece; border set off from pleurae by very shallow furrow and change in slope and inflation between pleurae and border; posterior median spine short (Pl. 6, fig. 1), anteriorly broad (tr.) at intersection with posterior margin of pygidium, but drastically narrows posteriorly to form a distinct narrow point, subcircular in cross section (Pl. 6, figs 3, 10), in lateral view spine is slightly upturned from horizontal plane, sculpture of fine, densely spaced anastomosing lines covers spine, lines are slightly more coarse and less densely spaced on lateral margins of spine; in ventral view relatively broad doublure visible (Pl. 6, fig. 22), widest opposite first and second pleural segments, tapers posteriorly, prominent sculpture of raised lines oriented roughly parallel to inner margin of doublure, sculpture continues posteriorly meeting in a "V" medially and continuing onto ventral surface of median spine.

Ontogeny. The glabella becomes much more rounded anteriorly (cf. Pl. 1, figs 2, 20); a very short preglabellar field is present medially (Pl. 1, fig. 20) on the smallest specimen, but the anterior margin of the glabella increasingly comes into contact with the anterior border furrow; S1 becomes less well impressed; palpebral lobes reduce in size compared to the rest of the cranidium, and the angle at which they are held relative to a horizontal plane increases from almost level with glabella in smallest specimens (Pl. 1, fig. 22); sculpture of tubercles and raised lines more prominent; median node of LO becomes less prominent.

Tubercles on pygidial axial rings arranged in two distinct rows on either side of axis on very small specimens (Pl. 7, fig. 20), become more coarse and dense and less clearly arranged in distinct rows, while scattering of background tubercles become more prominent, and there is overall fining of the axial tubercles in largest specimens; pleural bands with sculpture of single row of tubercles along anterior and posterior margins of segments changes to more densely spaced scattering of finer tubercles; pygidial border becomes broader; articulating flange becomes more prominent; posteromedian spine becomes significantly shorter, but retains upturn from horizontal plane.

Discussion. *Pseudoolenoides ludificatus* compares most closely with the other two plesiomorphic species, *P. pogonipensis* and *P. aspinosus*. Collectively, these species differ from the derived group in a large suite of characters (discussed above) and there is little point in attempting detailed comparisons between species drawn from either group. *Pseudoolenoides ludificatus* differs from *P. aspinosus* in the possession of an anterior border that is only faintly nasute, versus distinctly anteriorly pointed, a fixigenal boss anterior to the eye ridge, versus the faint oblique ridge (best seen on Pl. 8, fig. 1, right side) which characterizes *Acidiphorus*, less prominent eye ridge, medially slightly shorter SO, longer LO, faint fixigenal alae opposite L1, slightly smaller palpebral lobes, much smaller tubercles on the librigenal field, a narrower and less posteriorly lobate librigenal posterior border, a longer, narrower field, a better impressed lateral border furrow, a longer genal spine; a hypostome with quite radically different morphology (assuming that of *P. aspinosus* is correctly assigned; see below), with large subtriangular spines at the shoulder and posterolateral corners and more transverse, anteriorly convex middle furrows; a much more dorsally vaulted pygidium, with an anteriorly broader, more laterally lobate border, a shallower border furrow, and a shorter posteromedian spine.

Pseudoolenoides ludificatus differs from *P. pogonipensis* in having a relatively larger, more anteriorly pointed glabella, more distinct, oblique S1, narrower interocular fixigenae, a less prominent eye ridge; librigenae with a much less lobate posterior margin of the posterior border, with only a subtle versus very prominent accessory furrow; a hypostome that is broader relative to its length, with distinct spines on the posterolateral corners versus a broad posterior shelf; and a pygidium that is much more dorsally vaulted, narrower relative to its length, dominated by fine tuberculate versus fine raised line sculpture, with less inflated pleural bands, and with a very short versus apparently very long posteromedian spine.

Pseudoolenoides ludificatus occurs together at K-South 1.5T m with *P. pogonipensis* and *Pseudoolenoides* cf. *dilectus* (and apparently also with *P. dilectus*, though we did not encounter it in our sampling). There is little difficulty with sclerite associations, however, as *P. ludificatus* is very common, whereas *P. pogonipensis* is quite rare, and *Pseudoolenoides* cf. *dilectus* is very rare (only three specimens found).

Pseudoolenoides aspinosus Fortey and Droser, 1996

Plate 8

1996 *Pseudoolenoides aspinosus* Fortey and Droser, p. 87, fig. 12.1, 12.3, 12.5, 12.7 (only; fig. 12.2, 12.4, 12.6 = *Pseudoolenoides pogonipensis* n. sp.?).
1999 *Pseudoolenoides aspinosus* Fortey and Droser; Fortey and Droser, p. 189.

Material. Holotype, cranidium, USNM 481341 (Pl. 8, figs 1, 4, 5), and paratypes USNM 481344–481346, along with an unnumbered specimen, all from a single bedding plane, 36 m above *Hesperonomiella minor* bed ("K"), Juab Formation (Dapingian; *Psephosthenaspis pseudobathyurus* Zone), Thomas Range section, Juab County, western Utah, USA.

Diagnosis. Cranidial anterior border slightly nasute and pointed; librigena with tubercles on anterior part of field and raised lines on posterior part; raised lines prominent on upper surface of genal spine; pygidium with well impressed border furrow.

Discussion. Fortey and Droser (1996, p. 87) described the species on the basis of six specimens. Four of the specimens, including the holotype cranidium, were from a single bedding surface in the *Psephosthenaspis pseudobathyurus* Zone in their Thomas Range section. The other two specimens, both cranidia, were from the *Psephosthenaspis glabrior* Zone at Ibex Section J. The Ibex specimens, of younger age than the Thomas Range material, also show clear morphological differences. The glabella and occipital ring are more coarsely tuberculate, the glabella does not expand anteriorly to nearly the same extent as the holotype, the anterior border is not bowed forward medially nearly as much, and SO is considerably shorter both sagittally and exsagittally. Although the Ibex cranidia are smaller than the Thomas Range holotype, the silicified samples of *Pseudoolenoides* species documented herein (as well as many unpublished species of the *Acidiphorus* group) demonstrate that changes of this nature and magnitude do not occur through ontogeny.

In a later paper, Fortey and Droser (1999) named *Acidiphorus*? *lineotuberculatus* from basal Whiterockian strata at Whiterock Canyon, Nevada. They recognized that the small Section J cranidia they had previously assigned to *P. aspinosus* were unlikely to belong, illustrated a third example (Fortey and Droser, 1999, fig. 4.20), and assigned these specimens to *A.*? *lineotuberculatus*. We agree that the specimens do not belong to *P. aspinosus*, but they do appear to represent a plesiomorphic species of *Pseudoolenoides*, and they do not represent *A.*? *lineotuberculatus*. Among the obvious differences are a coarsely tuberculate glabella and occipital ring versus sparsely tuberculate with fine raised lines, and the absence of a preglabellar field, with the frontal lobe of the glabella intruding on the anterior border, versus the unambiguous presence of a field in all (three) known specimens. We have discovered a similar species, *P. pogonipensis*, at Section K-South 1.5T m. The Ibex cranidia are tentatively referred to this new species (see discussion below).

The hypostome assigned to *P. aspinosus* (Pl. 8, figs 2, 3, 8) is unlike those definitely belonging to species of *Pseudoolenoides*, which have their lateral and posterior borders developed into spines or broad shelves. In its simple morphology, this hypostome closely resembles those firmly associated with species of *Acidiphorus* in our collections. Fortey and Droser (1996) assigned the hypostome on the basis of its association on a bedding plane with the other Thomas Range specimens. The possibility that it belongs to a cooccurring species of *Acidiphorus* is difficult to exclude. On the other hand, *Pseudoolenoides aspinosus* is a stratigraphically low and plesiomorphic species and could plausibly lack the modifications to the hypostome. *Pseudoolenoides ludificatus* is also generally plesiomorphic, however, and a close comparison for *P. aspinosus* in the morphology of other sclerites, yet it has a spinose hypostome.

With the younger Ibex specimens excluded and the association of the hypostome at least somewhat tentative, *P. aspinosus* is known from only four definitely assigned specimens (one newly illustrated herein), which limits the degree to which it can be interpreted. Nevertheless, the single known cranidium, while incomplete, is nearly as large as the typical large holaspid specimens of *P. ludificatus*, *P. acicaudus*, and *P. fossilmountainensis*. The pygidium, however, is small (though holaspid), and less than half the size of the largest *P. ludificatus* specimens.

Fortey and Droser (1996, p. 87) diagnosed *P. aspinosus* on the basis of what it lacked (features of the derived group such as unreleased spines in the pygidium and a deep S1) and on its tuberculate sculpture. All of the features listed in their diagnosis are symplesiomorphies shared with all species of *Acidiphorus*. The species, insofar as it is known, does appear to have a few autapomorphies associated with the librigenal sculpture and the pygidial border furrow, and these are what constitute the present diagnosis. *Pseudoolenoides aspinosus* was compared with *P. ludificatus* above and is compared with *P. pogonipensis* below.

***Pseudoolenoides pogonipensis* n. sp.**
Plate 9, figs 1–5?, 6–19, Plate 10

1996 *Pseudoolenoides aspinosus* Fortey and Droser, p. 87, fig. 12.2, 12.4, 12.6 (only; fig. 12.1, 12.3, 12.5, 12.7 *Pseudoolenoides aspinosus*).
1999 *Acidiphorus*? *lineotuberculatus* Fortey and Droser, p. 189, fig. 4.20 (only; fig. 4.14–4.19 = *Acidiphorus lineotuberculatus*).

Material. Holotype, pygidium, SUI 130116 (Pl. 10, figs 10–12, 15, 16), and assigned specimens SUI 130116–130119, 30021–130025, 130035–130037, 132146, from Section K-South 1.5T m, Kanosh Formation (Dapingian; *Pseudoolenoides dilectus* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. Tentatively assigned specimens USNM 481342, 481343, and 495718, from 38 m above *Hesperonomiella minor* bed ("K"), Juab Formation (Dapingian; *Psephosthenaspis glabrior* Zone), Section J, southern Confusion Range, Ibex area, Millard County, western Utah, USA.

Etymology. From the Pogonip Group.

Diagnosis. Cranidium with nearly straight-sided glabella with relatively small area; librigena with strongly posteriorly lobate posterior margin of posterior border and strong accessory furrow on border near margin; hypostome with large subtriangular spine at shoulder and broad shelf posteriorly; pygidium broad, with dorsal sculpture dominated by raised lines; pygidial border furrow weakly impressed; posteromedian spine robust and apparently long.

Description. Cranidium moderately vaulted; sculpture of raised anastomosing lines covers fixigena and LO; sculpture of prominent tubercles present on glabella and LO; anterior border with sculpture of fine raised lines arranged subparallel to margin; anterior border about half as long (sag.) as LO (sag.), abaxially tapered, anterior margin describing gently curved arc with slight peak medially, in anterior view dorsal margin slightly ventrally bowed and ventral margin broadly "U"-shaped, in lateral view border forms a strongly upwardly flexed sinuous shelf; anterior border furrow is long, dorsally concave, deep along entire course, slightly deeper and slit-like distally; frontal areas weakly dorsally inflated, strongly sloped downward from interocular fixigena, with sculpture of prominent, relatively widely spaced anastomosing lines; interocular fixigena held at very slight angle above horizontal plane, with almost no dorsal inflation, sloping slightly toward glabella, sculpture of anastomosing lines continues from frontal area, but lines are less prominent and more closely spaced; palpebral lobes not preserved; posterior fixigena incomplete, but with inflation similar to that of frontal area, sloped downward toward posterior border furrow; posterior border incomplete, but appears to be dorsally inflated (Pl. 9, fig. 10), set off adaxially by shallow border furrow, sculpture of very fine and closely spaced anastomosing line present on adaxial portion; glabella with maximum width opposite γ 79.9% sagittal length excluding LO; glabella bullet-shaped in dorsal view, sagittal length (excluding LO) 64.2% that of cranidium, moderately strongly vaulted, with apex sitting high above maximum height of fixigena in anterior view; lateral profile moderately curved, with anterior portion strongly downturned from horizontal plane; axial furrows faint and slightly laterally bowed around LO, width across posterior contact of furrows with posterior margin 43.5% cranidial sagittal length; axial furrows confluent with SO, forming deeper pit at intersection; axial furrows deepest opposite inferred anterior margin of palpebral lobe, slightly shallower posteriorly, of nearly equal width along entire course, slightly sinuous, running without obvious distinction into preglabellar furrow; preglabellar furrow and anterior border furrows confluent medially; fossula very faintly expressed dorsally as small swelling situated adjacent to axial furrow opposite S3; S1 very faintly impressed, directed posteromedially, in contact with axial furrows; S2 and S3 expressed dorsally as very small areas lacking sculpture; L1 defined partially by S1, with very weak independent inflation; prominent large tubercles present posteromedially, giving way to progressively finer tubercles on anterior portion of glabella, tubercles absent on small strip situated in middle of glabella, tubercles absent on lateral margins of glabella;

background sculpture of fine, raised anastomosing lines present on anterior portion and lateral margins of glabella; LO long, sagittal length 16.2% that of cranidium, semi-lunate, longer sagittally than exsagittally, posterior margin strongly posteriorly bowed with median portion nearly transverse, anterior margin nearly transverse, sculpture of scattered prominent tubercles similar to those on glabella, very faint background sculpture of anastomosing lines continues from glabella onto LO; SO deep and very broad (sag. and exsag.), distal tips slightly shorter (exsag.), anterior and posterior edges with sharp contact with rear of main glabella and anterior edge of LO respectively, nearly transverse; doublure underlying LO broken, but with sculpture of fine, closely spaced raised lines set transversely.

Librigenal measurements were made on specimens of Pl. 9, figs 9, 11. Main body of librigena (excluding anterior projection and genal spine) with maximum width behind eye 38.6% (33.2–44.1%) exsagittal length; anterior section of facial suture nearly transverse opposite field, slightly curved across lateral border; posterior section of facial suture extremely short, strongly sinuous across posterior border; visual surface not preserved on any recovered specimens, but long, apparently occupying large portion of length (exsag.) of genal field, bounded at base by narrow and shallow circumocular furrow (Pl. 9, figs 6, 9); field with prominent sculpture of fine raised lines arranged a scrobiculate pattern; triangular band of small tubercles present on field below visual surface, tubercles not prominent, band broadest anteriorly, spanning entire width of field, narrows posteriorly; lateral border furrow narrow and deep, does not meet posterior border furrow; posterior border furrow similar to lateral border furrow, ending in deep pit at base of genal spine; lateral border broad, with lateral margin gently flexed upward, border flattened and moderately inflated, with sculpture of fine raised lines running subparallel to margin; posterior border with sculpture of raised lines oriented in anastomosing pattern adjacent to border furrow, sculpture is rearranged into a series of lines running parallel to external margin toward margin, prominent flange present on posterior border from base of genal spine toward posterior facial suture, does not intersect posterior facial suture, flange less than half as wide as posterior border, flange separated from border by shallow, but distinct accessory furrow; sculpture from lateral and posterior borders continuous across lateral and posterior border furrows onto genal field (Pl. 9, fig. 9); genal spine apparently long (Pl. 9, fig. 11), but incompletely preserved on an recovered specimens, curved, inflation similar to that of lateral border, with sculpture of fine raised lines running down length of spine on all aspects, arranged in a "V"-shaped pattern with apex of "V" along external lateral margin of spine; area in front of base of genal spine (confluence of lateral and posterior borders) flat, merges smoothly into genal field, sculpture of fine raised lines continues from base of spine onto genal field, but becomes arranged in a more anastomosing pattern; anterior projection long, with subparallel raised lines continuous from lateral border; doublure strongly upturned anteriorly beneath anterior part of lateral border and anterior projection, remains strongly upturned, but broader beneath posterior border; doublure with sculpture of faint, fine raised lines set subparallel to external margin, sculpture more effaced medially on widest portion of doublure just behind base of genal spine; inner margin of doublure describes smooth continuous arc, with curve strongest posteriorly opposite intersection of lateral and posterior borders; small Panderian notch (Pl. 9, fig. 15) developed along adaxial end of doublure beneath posterior border.

Hypostome with maximum width (excluding anterior wings) across shoulder 92.5% sagittal length; ventral surface, including furrows, covered with sculpture of raised lines, arranged in anastomosing pattern on middle body, aligned subparallel with margins on borders, sculpture subdued on anterior wing; middle body with maximum width 49.9% maximum length of middle body, maximum width of anterior lobe 116.9% maximum width of posterior lobe; sculpture on middle body composed of densely spaced anastomosing raised lines; anterior margin describing broadly curved arc, medial portion opposite hypostomal suture turned upward at nearly 90° angle to form short anterior-facing rim, with sculpture of subparallel raised lines continuing from anterior lobe of middle body and arranged in a way that outlines the lateral and anterior margins of the anterior lobe of the middle body; anterior wing extended dorsolaterally, lacking sculpture of raised lines on anterior portion, posterior portion with sculpture of subdued raised lines; lateral notch also smooth (Pl. 10, fig. 5); shoulder developed into a prominent, pointed, and posterolaterally and ventrally directed spine (Pl. 10, fig. 5), anterior margin describing convex outward arc, posterior margin describing concave outward arc, sculpture of prominent raised lines running parallel to margin of spine on ventral surface and cutting across spine on dorsal surface; lateral and posterior borders weakly inflated, dorsoventrally flattened, enclosing middle body, with sculpture of closely spaced raised lines oriented subparallel to hypostomal margin; lateral border furrow separated into two portions, both are deep, slit like, directed posteromedially, with the posterior portion nearly effaced opposite posterolateral corner of middle body, not confluent with posterior border furrow; posterior border furrow shallow, deepest abaxially, nearly effaced

medially, describing broadly curved arc around posterior margin of middle body; intersection of lateral and posterior borders forming rounded corner and meeting at nearly 90º angle; posterior border long (sag. and exsag.), with sagittal length 16.3% length of hypostome, posterior margin describing very gently curved arc, ventrally flexed, but less so than shoulder spine; middle furrow set at about two thirds distance posteriorly on middle body, expressed as pair of short, deep, posteromedially directed furrows, which do not meet medially, separated from posterior portion of lateral border furrow by narrow strip of inflated middle body, confluent with anterior portion of lateral border furrow; macula small; middle body with strong ventral inflation, strongly pinched at middle furrow; doublure present behind shoulder spines, posterior portion of lateral border, and posterior border, broadest exsagittally behind posterior border, narrows slightly medially; entire doublure with sculpture of several fine raised lines similar to that on posterior border.

Rostral plate and thorax unknown.

Pygidial measurements were made on specimens of Plate 10 and doubled from the sagittal line if specimen is incomplete. Pygidium with maximum width across anterior margin of third axial segment 244.5% (242.3–243.4%) sagittal length of axis (excluding articulating half ring); axis of three clearly defined segments and fourth poorly expressed (although clearly expressed ventrally) segment fused with terminal piece, maximum axial width across first ring 30.0% (29.9–30.0%) maximum pygidial width; width across third segment 78.7% (78.7–78.7%) width across first segment; length of axis excluding articulating half ring slightly shorter than sagittal length of pygidium; articulating half ring incomplete, but appears short (sag.; exsag.), maximum width slightly less than that of first axial segment; articulating furrow well defined (sag. and exsag.), transverse, slightly deeper abaxially; first ring furrow well defined (sag. and exsag.), transverse, deepest of ring furrows, slightly shallower medially, deep and slit-like abaxially; second and third ring furrows similarly transverse, progressively shorter and more effaced than first ring furrow, with fourth furrow completely effaced dorsally; first axial ring of nearly equal length sagittally and exsagittally, length (sag.) 13.4% (12.6–14.1%) axial length (sag.), with sculpture of raised posterolaterally directed lines present along anterior and lateral portions, sculpture of very faint medium sized tubercles present medially forming a semicircle of tubercles emanating from the posterior margin and in a row along posterior margin; second and third rings progressively smaller and with essentially the same morphology, except that tubercles are completely absent along posterior margin of third ring with only a few present medially in a smaller semicircle; poorly expressed fourth segment fused with terminal piece, clearly visible in ventral view (Pl. 10, figs 6, 15) by expression of fourth inter-ring furrow; axis terminated by anteriorly broad terminal piece that tapers posteriorly, sculpture of raised lines continues from axial rings onto terminal piece, becoming more granular on medial portion of terminal piece; axis distinctly terminated in dorsal view by narrow, shallow furrow outlining terminal piece, in lateral view posterior margin of axis forms very slight change of slope before emergence of posterior median spine; articulating facet small, triangular with short, spike-like projection developed at anterolateral corner (Pl. 10, fig. 3), short ventrally directed spine-like point developed at lateral corner (Pl. 10, figs 16, 17), covered with sculpture of fine raised lines oriented subparallel to anterior margin; first segment with anterior margin slightly anteriorly bowed to border furrow, directed posterolaterally at about 19º angle; anterior margin of first pleural band set off from margin by shallow, posterolaterally directed accessory furrow; anterior margin of first pleural band developed into anterolaterally directed ridge, narrow strip of pleurae along either side of first pleural furrow smooth; first pleural furrow of similar length sagittally and exsagittally, slightly deeper abaxially, nearly effaced adaxially at intersection with axial furrow (Pl. 10, fig. 11), distal tip terminated just past lateral border furrow; subsequent pleural furrows of similar length and depth sagittally and exsagittally, shallower than deepest portion of first pleural furrow, meet axial furrow, terminate at lateral border furrow, progressively more posterolaterally directed than first pleural furrow with fourth furrow nearly parallel to sagittal axis; first interpleural furrow expressed as very shallow depression at intersection of pleurae with border furrow, subsequent interpleural furrows not expressed; morphology of subsequent segments generally similar to segment one, but directed more posterolaterally and without strong inflation of anterior margin; pleural bands terminated by weakly inflated, flattened border, with sculpture of densely spaced raised lines oriented roughly parallel to pygidial margin, border broadest anteriorly, tapers posteriorly; border slightly bowed outward opposite first and second pleural bands, bowed very slightly inward opposite terminal piece and base of posterior spine; border set off from pleurae by very shallow furrow, almost no change in slope and inflation between pleurae and border, in posterior view border is medially arched upward below posterior spine (Pl. 10, figs 10, 14); posterior median spine apparently long (Pl. 10, fig. 11), but full length unknown, anteriorly broad (tr.) at intersection with posterior margin of pygidium, narrows posteriorly, circular in cross section (Pl. 10, figs 10, 14), in lateral view spine is upturned from

horizontal plane, sculpture of fine, densely spaced lines arranged in a chevron pattern aligned with sagittal axis covers dorsal and ventral surface of spine, point of chevrons directed anteriorly on dorsal surface and directed posteriorly on ventral surface, sculpture nearly effaced on ventral surface of spine at intersection with posterior margin of pygidium (Pl. 10, fig. 15); in ventral view broad doublure visible (Pl. 10, figs 6, 15), widest opposite first and second segments, tapers dramatically posteriorly, with proximal portion strongly upturned toward ventral surface of pygidium, prominent sculpture of raised lines oriented roughly parallel to inner margin of doublure present along interior and external margins, sculpture of more widely spaced anastomosing lines present medially on widest portion of doublure.

Discussion. As discussed above, sclerites assigned to *P. pogonipensis* are unlikely to be confused with those of the cooccurring *P. ludificatus* as the latter species is much more common. The pygidia described below as *Pseudoolenoides* cf. *dilectus* also cooccur, but comparison of the cranidium, librigenae, and pygidia grouped as *P. pogonipensis* to those of the broadly similar *P. aspinosus* reveals essential similarity and permits considerable confidence in the association. Also as discussed above, three cranidia from high in the Juab Formation at Ibex illustrated by Fortey and Droser as *P. aspinosus* (1996, fig. 12.2, 12.4, 12.6) and *Acidiphorus*? *lineotuberculatus* (1999, fig. 4.20) are very similar to the cranidium of *P. pogonipensis*. We have previously demonstrated (Adrain and McAdams, 2012) that *Psephosthenaspis glabrior* Fortey and Droser, 1996, occurs at both of the same horizons, albeit with some minor morphological differences on the pygidium. The situation is similar for *Pseudoolenoides pogonipensis*. Only one cranidium has been found at the type horizon (Pl. 9, figs 7, 8, 10, 13) and, while it is quite small, it is certainly holaspid. The main difference between it and the upper Juab specimens is that its glabella is shorter and slightly more expanded laterally, and clearly stops short of the anterior border furrow, while in the older specimens the front of the glabella overhangs the rear of the border. The Juab specimens also have somewhat coarser tuberculate sculpture. Apart from these differences the specimens are very close in all other respects, and if they are not conspecific, it seems certain that the upper Juab material represents a species very similar to *P. pogonipensis*. For the present we tentatively assign them to the species. More material from both horizons would be required to assess the relationship with greater confidence.

Pseudoolenoides pogonipensis was compared with *P. ludificatus* above. It differs from *P. aspinosus* in the possession of a much smaller glabella, an anterior border which is nearly evenly curved on its anterior margin, versus clearly nasute, slightly sparser tuberculate sculpture on the glabella, frontal areas mostly lacking tuberculate sculpture versus with prominent tubercles, a less well impressed eye ridge, a weakly expressed fixigenal boss in front of the eye ridge, a shorter SO but longer LO; a librigena with finer tuberculate sculpture and a much more posteriorly lobate posterior border with a strong accessory furrow; and a pygidium with a broader border anteriorly, shallower border furrow, and much longer posteromedian spine.

Pseudoolenoides dilectus Hintze, 1953

Plate 11

1951	"*Symphysurus* ? *goldfussi*" Walcott; Ross, p. 64, pl. 15, figs 16–18.
1953	*Pseudoolenoides dilectus* Hintze, p. 228, pl. 27, figs 1–6.
1973b	*Pseudoolenoides dilectus* Hintze; Hintze, text-fig. 28.
1974	*Pseudoolenoides dilectus* Hintze; Shaw, p. 22.
1991	*Pseudoolenoides dilectus* Hintze; Ross and Ethington, p. 160.
1991	*Pseudoolenoides dilectus* Hintze; Church, fig. 2.
1996	*Pseudoolenoides dilectus* Hintze; Fortey and Droser, p. 87.
2003	*Pseudoolenoides dilectus* Hintze; Jell and Adrain, p. 434.

Material. Holotype, AMNH-FI 26492 (Plate 11), from Section J, Locality J-22 of Hintze (1951, 1953), and paratypes AMNH-FI 26490, 26491, 26493–26495, from Section K-South 1.5T m, Kanosh Formation (Dapingian; *Pseudoolenoides dilectus* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

Diagnosis. Faint raised arc of sculpture on librigenal field but not continued across facial suture onto frontal area; glabella with subdued tuberculate sculpture; thorax of nine segments; pygidium incorporating one unreleased thoracic segment, terminal piece showing distinct segmentation; posteromedian spine very short and nearly ventrally directed.

Discussion. In addition to Hintze's (1953) holotype specimen from Section J, he assigned two large cranidia, a hypostome, and two pygidia from Section K-South 1.5T m. While there is no reason to doubt these assignments,

we have not encountered the species in our resampling of this horizon. Instead we have found very common *P. ludificatus* (which Hintze also found in profusion) and *P. pogonipensis* (which Hintze did not find). We did encounter three pygidia which are similar in morphology to those of *P. dilectus*, but they seem clearly to represent a different, related species (see *Pseudoolenoides* cf. *dilectus* below). It is difficult to explain this discrepancy, as the fauna we retrieved from K-South 1.5T m in all other respects matches that reported by Hintze, and there is no question that we sampled the same bed in the same place. As explained above, however, the bed is not in outcrop but rather represented by small talus lumps strewn in place along strike. Sclerites of *P. dilectus* must have been restricted to one or a few small lumps removed by Hintze during the original sampling.

Pseudoolenoides dilectus is the oldest species of the derived group, and is retrieved as the basal member of that group by parsimony analysis (Fig. 3). It retains only a single unreleased thoracic segment in a pygidium that is otherwise quite comparable to that of *P. ludificatus*. *Pseudoolenoides dilectus* is distinguished from all of the other species of the derived group in the lack of a raised line across the frontal area, retention of a standard deep and uninterrupted librigenal lateral border furrow, retention of only one versus four or five unreleased pygidial segments, and retention of a pygidial axis of normal, parallel-sided shape, which is fully circumscribed posteriorly and well elevated above the post-axial region. It shares with this derived group a suite of 11 synapomorphies (see Fig. 3 and Table 1) which serve to distinguish it from the plesiomorphic species *P. aspinosus*, *P. pogonipensis*, and *P. ludificatus*.

Ross (1951, pl. 15, figs 16–18) illustrated three cranidia of a species of *Pseudoolenoides* from two localities in the Swan Peak Formation in southeastern Idaho and northern Utah. As recognized by Hintze (1953, p. 226), these most likely represent *P. dilectus*, though more material, particularly of other exoskeletal parts, would be required to be certain.

Pseudoolenoides cf. *dilectus* Hintze, 1953

Plate 16, figs 24–35

Material. Assigned specimens SUI 130026–130028 from Section K-South 1.5T m, Kanosh Formation (Dapingian; *Pseudoolenoides dilectus* Zone), southern Confusion Range, Ibex area Millard County, western Utah, USA.

Description. Pygidial measurements were made on the three figured specimens. For measurement of the distance across the pygidium of Pl. 16, fig. 34, the distance to the sagittal line from the left side was doubled. Pygidium strongly vaulted, with maximum width across anterior margin of third segment 224.9% (212.8–239.9%) sagittal length (excluding articulating half ring and post-axial spine); axis of four segments and terminal piece, maximum axial width across first ring 46.1% (45.3–46.6%) maximum pygidial width; width across fourth segment 63.1% (61.5–65.3%) width across first segment; length of axis excluding articulating half ring just shorter than sagittal length of pygidium; articulating half ring nearly as long (sag.) as first axial segment, sagittal length 15.0% (14.4–15.6%) pygidial length, anterior margin subsemicircular, ring sits just below first segment in sagittal profile of axis, gently dorsally convex in sagittal profile, sculpture of very fine and faint granules arranged in anastomosing pattern, pattern stronger along posterior margin and merges smoothly onto lateral portion of first axial segment; articulating furrow short (sag. and exsag.), very deep, slit-like, and transverse medially, with distal ends shallow, almost effaced, and directed anterolaterally; first ring furrow short (sag. and exsag.), nearly transverse with a slight posterior bow medially, deepest medially, progressively shallower abaxially, terminating in a deep pit at intersection with axial furrow; second and third ring furrows similarly transverse with median posterior bow becoming more prominent, about same length (sag. and exsag.) as first, distal tips of third ring furrow almost completely effaced; first axial ring of equal length sagittally and exsagittally, subtrapezoidal in outline, wider across anterior margin than posterior margin, sculpture composed of a band of prominent medium to small sized tubercles arranged along anterior margin, a prominent medium sized median tubercle separate from the anterior band, and a row of smaller tubercles located medially along the posterior margin, background sculpture of fine raised anastomosing lines also present, in lateral view distal portion of ring covered only with sculpture of anastomosing lines and granules arranged in similar pattern; second and third rings progressively smaller and with essentially the same morphology, except that anterior and posterior margins are more similar in width, bands of tubercles are more closely spaced across entire ring, and distal portion of third ring is almost completely smooth in lateral view (Pl. 16, fig. 32); fourth segment poorly expressed, fused with terminal piece, can be identified in dorsal

view by median tubercle, also expressed in lateral view by smooth area on distal portion of segment (Pl. 16, fig. 32); axis terminated by broad, posteriorly rounded terminal piece, sculpture of prominent medium and small widely spaced tubercles form band along posterior margin of terminal piece, tubercles less dense medially, background sculpture of fine, raised anastomosing lines present between tubercles; axis distinctly terminated in dorsal view, in lateral view posterior margin of axis forms gentle scarp compared to post-axial region that is nearly horizontal (Pl. 16, fig. 30); post-axial region strongly downturned from horizontal plane, very short in dorsal view and slightly longer in lateral view, in posterior view sculpture of raised lines crosses region horizontally; facet developed into strongly ventrally downturned and posterolaterally directed wing-like flange, with short spike-like point along anterior margin (Pl. 16, fig. 34), adaxial portion covered with sculpture of fine granules arranged in anastomosing pattern, abaxially sculpture of granules changes to prominent raised lines also arranged in anastomosing pattern; first segment longest (exsag.), anterior margin nearly transverse to fulcrum, which is set very close to axis, anterior margin directed posterolaterally distal to fulcrum, strongly laterally bowed forming rounded corner; first pleural band set off from margin by very faint and shallow posterolaterally directed accessory furrow, inflated, distal tip extended into short posteriorly directed spine, spine formed primarily from posterior pleural band, sculpture of raised anastomosing lines present on entire band including pleural furrow and spine; pleural furrow longest (exsag.) medially, anterior margin forming distinct break with anterior pleural band, posterior margin gradually merging into posterior pleural band, distal tip forming deep slit-like pit oriented almost parallel to sagittal axis, terminated at border; second pleural furrow with generally same morphology as first, but slightly shorter, directed more strongly posteriorly, and with distal tip not terminating in deep slit-like pit; first interpleural furrow expressed as small, deep pit at distal end of pleurae, subsequent interpleural furrows not expressed; morphology of second pleural segment generally similar to first segment, but progressively narrower, directed more posterolaterally, and distal tip terminating at border and not forming short spine; third and fourth segments with no associated expression of pleural bands, pleural region adjacent to third ring and fourth ring fused to terminal piece with segments not expressed; border flattened, with no dorsal inflation, external margin forming narrow rolled rim (Pl. 16, fig. 31), sculpture of prominent raised lines continues without disruption from pleurae, border slightly concave anterior to pleural spine, also slightly concave between pleural spine and posterior median spine, in posterior view border strongly peaked medially at posterior median spine (Pl. 16, figs 31, 33, 35); border set off from pleurae in lateral and posterior view by change in slope, in dorsal view distinction is less apparent; posterior median spine short, thorn-like, widest (tr.) at intersection with posterior margin of pygidium, narrows posteriorly to form a distinct point, in lateral view spine is slightly upturned from horizontal plane, sculpture of densely spaced anastomosing lines covers spine, lines are slightly coarser and less densely spaced on lateral margins of spine, in dorsal view lines form a "V" along sagittal axis of spine; in ventral view relatively broad doublure visible (Pl. 16, figs 25, 26), widest opposite first and second pleural segments, tapers posteriorly, sculpture of raised lines oriented roughly parallel to inner margin of doublure.

Discussion. Three pygidia from Section K-South 1.5T m clearly represent a species closely related to *P. dilectus*, which was collected from the same horizon, but which we did not encounter in our sampling. The pygidia just as clearly are not conspecific with *P. dilectus*. While they possess a single pair of pleural spines, in common with *P. dilectus*, which implies a single unreleased thoracic segment, they show only two axial rings behind the first, and a very short, wide terminal piece showing no evidence of segmentation. They are smaller than Hintze's pygidia of *P. dilectus*, but not markedly so, and are definitely holaspid. There is no possibility that ontogenetic change could transform one to the other. Pygidia of *P. dilectus* (e.g., Pl. 11, figs 6, 8, 9) have four well expressed rings behind the first, and have a much longer terminal piece behind these five rings. The posterior axis is fully circumscribed posteriorly and exhibits a strong break in slope to the post-axial area. That of the pygidia of *Pseudoolenoides* cf. *dilectus* is gently merged posteriorly with the post-axial area, with only a gentle break in slope. Overall, they are also much wider relative to their length than those of *P. dilectus*. They certainly represent a distinct unnamed species of *Pseudoolenoides* and for that reason are given extended written description above.

***Pseudoolenoides derbyi* Shaw, 1974**

Plate 12, figs 1–14, 16–19, Plates 13–15

1974 *Pseudoolenoides derbyi* Shaw, p. 26, pl. 1, figs 23, 25–28.
1996 *Pseudoolenoides derbyi* Shaw; Fortey and Droser, p. 87.

Material. Holotype, cranidium, OU 7952 (Pl. 12, figs 1, 4, 7), and assigned specimens OU 7948–7950, 13961–13963, 38881, 38884–38886, 38888–38890, 38894, 38897, 38899, 38902, 38904, 38905, 38912, 38914, 38917–38921, from Section WSC 46.3–51.5 m, Oil Creek Formation (Darriwilian), West Spring Creek, Murray County, Oklahoma, USA. Assigned specimen OU 7951, from Section N 1 161.5 m, Oil Creek Formation (Darriwilian), Carter County, Oklahoma, USA.

Diagnosis. Glabella strongly and fairly coarsely tuberculate; line of tubercles on slightly swollen anterior edge of L1; eye ridge very prominent; raised line arc on librigenal field and frontal area surmounted by line of partially merged tubercles; pygidium with four unreleased segments, but pleural spines relatively small; pygidium with strong dorsal convexity, especially of pleurae; posteromedian spine short.

Discussion. Shaw's (1974, p. 26) list of autapomorphic features of *Pseudoolenoides derbyi* is accurate, and is supplemented in the diagnosis above. *Pseudoolenoides derbyi* is a distinctive species with its combination of a strongly tuberculate glabella with mostly nontuberculate fixigenae and librigenae and a raised librigenal field/frontal area arc that features aligned, partially merged tubercles. Parsimony analysis retrieves it as sister to a clade including *P. acicaudus*, *P. oilcreekensis*, *P. fossilmountainensis*, and *P. carterensis* (Fig. 3). The tuberculate glabella of *P. derbyi* is a plesiomorphic feature and is transformed in the more derived group to a sculpture composed entirely of raised lines. *Pseudoolenoides derbyi* also retains a forward eye position whereas the derived group are characterized by a posteriorly placed eye (though this is reversed in *P. carterensis*).

Among known species, *P. derbyi* is most similar to *P. acicaudus*, which is retrieved as the basal species of its derived sister group. Pygidia of the species are closely comparable, except that those of *P. acicaudus* feature an extra unreleased segment, have slightly longer pleural spines, have a completely smooth axis versus a sculpture of subdued scattered small tubercles, and have an apparently longer posteromedian spine, though this structure is broken at the base in most specimens of *P. derbyi* (but see the internal mold of Pl. 15, fig. 14, which seems to give an indication of a short, narrow spine). Librigenae differ in that those of *P. derbyi* have an acute versus obtuse angle between the rear margin of the posterior border and the inner margin of the genal spine, have a distinctly broader field with a prominent tuberculate raised arc versus very subdued and non-tuberculate sculpture, have a posterior border that widens versus narrows adaxially, and which appears to lack the posterior point at the contact with the facial suture seen in *P. acicaudus*. Cranidia are similar in proportions, but differ in the tuberculate sculpture and anterior eye position of *P. derbyi*, as well as its somewhat deeper anterior border furrow.

Almost all of the material of this species is from a narrow stratigraphic interval at the West Spring Creek section in Murray County, where its highest occurrence is some 56 metres below the occurrence of *P. carterensis*. The exception is a single cranidium (Pl. 12, figs 11, 12) from a section in Carter County, which Shaw (1974, p. 26) listed as occurring in the same collection as *P. carterensis*. The occurrence seems anomalous, given the wide stratigraphic separation of the species at West Spring Creek, but was taken by Shaw (1974, p. 26) to indicate a much longer range for *P. derbyi*.

***Pseudoolenoides acicaudus* Hintze, 1953**

Plate 16, figs 1–23, Plates 17–19

	1953	*Pseudoolenoides acicaudus* Hintze, p. 229, pl. 27, figs 7–11.
	1973b	*Pseudoolenoides acicaudus* Hintze; Hintze, text-fig. 28.
non	1974	*Pseudoolenoides acicaudus* Hintze; Shaw, p. 22, pl. 1, figs 13–22, 24 (=*Pseudoolenoides oilcreekensis* n. sp.).
	1991	*Pseudoolenoides acicaudus* Hintze; Ross and Ethington, p. 158.
	1991	*Pseudoolenoides acicaudus* Hintze; Church, fig. 2.
	1996	*Pseudoolenoides acicaudus* Hintze; Fortey and Droser, p. 87.

Material. Holotype, pygidium, AMNH-FI 26497, and paratype AMNH-FI 26496 from Section CP 45.7 m, and assigned specimens SUI 130038–130060 from Section CP 48.8 m, Kanosh Formation (Dapingian; *Pseudoolenoides acicaudus* Zone), Crystal Peak Hills, Ibex area, Millard County, western Utah, USA.

Diagnosis. Librigena with very narrow field with very subdued transverse raised line arc; librigenal posterior border with prominent posterior point at contact with facial suture; pygidium with five unreleased segments.

Description. Cranidial measurements were made on the most complete specimens of Pl. 16–17. Measurements were doubled from the sagittal line when necessary, e.g., for specimens with a single intact

palpebral lobe. Cranidium broad and fairly long, moderately vaulted (sag., tr.), widest across palpebral lobes (δ), 136.2% (130.4–144.3%) sagittal length, consistently wide posteriorly, with width across β 110.9% (104.4–116.6%) length, width across γ 107.1% (99.8–112.9%) length, width across ε 111.6% (105.0–115.7%) length, and width across posterior projections 128.4% (121.9–134.8%) length, sculpture somewhat effaced, but generally of semi-anastomosing ridges running subparallel to axis on fixigenae and more anastomosing ridges on glabella, scrobiculate where curving around anterior end of glabella; anterior branch of facial suture long, moderately laterally bowed, curvature strongest at mid-length of course along fixigena, more gently bowed anteriorly along exsagittal ends of anterior border; posterior branch of facial suture short (oblique), runs only along very short posterior fixigena and posterior border; anterior border short to very short, longest anterior to anterolateral corners of glabella, shorter sagittally and strongly tapered exsagittally, moderately inflated, anterior margin strongly anteriorly bowed, particularly medially, ventral margin forms very shallow "M"-shape (anterior view), sculpture of a few fine ridges near margin, running parallel to it; doublure only a rim ventrally, mainly expressed as median anterior face, very short, with a few transverse ridges; anterior border furrow short, fairly deep, with sharper contact anteriorly with border than posteriorly with frontal areas, shortest and most distinct just exsagittal to glabella, less distinct medially on all but largest specimen (Pl. 17, fig. 1), longer and shallower, grading posteriorly toward glabella, leading into very short, deeper preglabellar furrow observable on some specimens (e.g., Pl. 16, fig. 3, Pl. 17, fig. 10), course broadly anteriorly bowed, more strongly bowed around anterior of glabella where overlying preglabellar furrow on most specimens; glabella elongate, anteriorly tapered, bullet-shaped, with maximum width across L2 75.2% (72.1–79.9%) sagittal length, moderately vaulted (sag., tr.), with vaulting decreasing anterior to ocular ridge and far posteriorly over L1, with distinct L1 but other lobes unclearly defined, glabellar sculpture of fine, semi-anastomosing ridges running subparallel to axis for most of length, and strongly curved to match anterior curvature of glabella, with small, fairly widely spaced tubercles concentrated posteromedially, and with fine scrobiculate ridge on anteromedian rim of L1; L1 moderately independently inflated, strongly anterolaterally directed, short adaxially, lengthened abaxially, wide; S1 disconnected from axial furrows by very narrow strip of inflated glabella running from front of L1 to L2, moderately long, longer posteromedially, somewhat shorter anterolaterally, deep, deepest at anterolateral end; L2 poorly defined by either furrows or inflation, extremely short near axial furrows, very long medially; S2 expressed as extremely narrow and fairly short deep point just inside axial furrows midway between end of eye ridge and S1 (best observed on Pl. 17, fig. 10); L3 likewise poorly defined, very short and narrow, anteromedially directed; S3 deep, fairly short, very strongly anteromedially directed, located along sagittal end of eye ridge; LF extremely large, nearly half length of entire glabella, strongly anteriorly tapered; SO long and moderately deep, deeper laterally toward axial furrows, but effaced just adjacent to axial furrows, with transverse anterior margin and "W"-shaped posterior margin, ridge sculpture of glabella carries through SO to LO; LO moderately inflated, long medially, slightly shorter laterally, 16.4% (14.8–17.6%) sagittal length of cranidium, broad, with width across junction of axial furrows and posterior margin of cranidium 53.7% (49.9–57.9%) sagittal length of cranidium, lobe with shallowly "W"-shaped anterior margin, and with sculpture of very small, fairly widely spaced tubercles, line of tubercles along posterior edge, and with slightly larger median node located slightly anterior to mid-length, tubercles overlie fine, anteromedially angled semi-anastomosing ridges; doublure long medially, short and pinched out far exsagittally, with shallowly "W"-shaped anterior margin, and with sculpture of very fine, very closely spaced transverse ridges; axial furrows fairly shallow and narrow, wider and deeper along midlength of L1, across from posterior part of median end of ocular ridge (but effaced over anteriormost part of ridge), and along LF, course very slightly waisted along L1, gently laterally bowed around L2, then strongly anteriorly convergent; frontal areas trapezoidal, long and broad, with strongly posterolaterally sloped anterior and posterior margins, moderately anteroventrally sloped and gently anteriorly bowed (lateral view), with anastomosing ridge sculpture directed posteromedially anterior to fine scrobiculate ridge extending from a little posterior and exsagittal to junction of axial and anterior border furrows to β, ridges then directed more posteriorly, slightly laterally bowed posterior to scrobiculate ridge, frontal areas also with small raised bump near anteromedian end of ocular ridge indicating fossula for hypostome (visible ventrally, Pl. 17, fig. 12); ocular ridge relatively long, moderately inflated, posterolaterally directed at about 30º below horizontal, with moderately short, shallow furrows along anterior and posterior margins; palpebral furrow shallow, broad (long at anterior and posterior tips), very strongly laterally bowed, confluent with furrow along posterior margin of ocular ridge; palpebral lobes located far posteriorly on cranidium, across from L1, slightly anteroventrally and ventromedially sloped, small relative to cranidium overall, a little larger than semicircular in area, but closer to half-teardrop shaped, with anterior end of lobe extending slightly further adaxially and lobe more

strongly curved posteriorly, with broad, slightly inflated lateral margin, margin broadest a little posterior to midlength of lobe; interocular fixigena trapezoidal, broad and fairly long, with strongly posterolaterally sloped anterior margin defined by ocular ridge, fixigena held nearly horizontally (anterior, lateral views), with weakly swollen crescentic rim outlining weakly depressed ala adjacent to L1; posterior fixigena relatively broad, very short, only a strip along anterior edge of posterior border, with extremely short laterally tapered section along projection of border, fixigena strongly posteroventrally downturned, with sculpture like that of frontal areas (continuous over entire fixigena); posterior border furrow short, very shallow and almost effaced adaxially, longer and deeper abaxially, then abruptly shallowed far abaxially along tips of posterior projections, course roughly transverse; posterior border narrow, short, slightly posteriorly lengthened along and just adaxial to posterior projections, moderately inflated, effaced, with short, very shallow furrow along posterior margin of projection for thoracic articulation (best seen on specimens of Pl. 17, figs 2, 17); doublure extremely short, only a rim until expanded into short wedge far exsagittally, effaced.

Hypostome unknown.

Librigenal measurements were made on the specimens of Pl. 18. Librigena of narrow, relatively elongate main body and very long genal spine; anterior branch of facial suture long (oblique), section along librigenal field slightly shorter than that along anterior projection of lateral border, suture forms smooth obtuse angle of about 120º at border, section along anterior projection of border cuts border, exposing wedge of inner surface; posterior branch of facial suture extremely short, only crosses posterior border, steeply sloped, with tiny recurved hook on posterior end to fit with posterior projection of cranidium; visual surface strongly convex, large, long and wide, reniform, composed of numerous tightly packed lenses, lenses smaller and less distinctly defined toward bottom of eye (Pl. 18, fig. 9); circumocular furrow narrow, deep (deeper posteriorly; shallower overall in larger specimens), more strongly curved anteriorly, intersects posterior border furrow approximately even with intersection of opposite end with anterior branch of facial suture; librigenal field trapezoidal, narrow (longer anteriorly and posteriorly) and relatively long, with minimum width under midpoint of eye 22.2% (18.9–27.7%) exsagittal length along lateral border furrow, field weakly laterally convex (exsag., tr.), with sculpture of narrow, scrobiculate ridge running in shallow arc from junction of circumocular and posterior border furrows anterolaterally to approximately mid-width of field along anterior branch of facial suture (joins ridge on frontal area of cranidium), and with fine anastomosing ridge sculpture feeding into scrobiculate ridge; sculpture abaxial to ridge directed anteromedially and sculpture adaxial to ridge directed anterolaterally (seen well on Pl. 18, fig. 8); lateral border furrow narrow and deep, course almost straight, only very slightly laterally bowed, furrow appears almost pitted in larger specimens (e.g., Pl. 18, fig. 2), separated from posterior border furrow by raised extension of base of genal spine running onto librigenal field; lateral border with sculpture near border furrow of fine, semi-anastomosing ridges directed posteromedially, effaced at mid-width, and with slightly thicker ridges parallel to arc of margin abaxially (these continue into spine sculpture), border moderately inflated, dorsoventrally flattened, bladed, with wedge-shaped cross-section, relatively broad, almost same width as narrowest part of librigenal field except in largest specimens, narrower along long anterior projection, with external side cut by facial suture and strongly anteriorly tapered down to point not quite at tip of projection, border merges posteriorly into genal spine; genal spine with short, semicylindrical, inflated base extending from genal angle anteromedially to a little less than half-width of field, main part of spine flattened and bladed similar to lateral border, very long, none complete, but at least 184.8% length of main body of librigena (Pl. 18, fig. 1), slightly broader than lateral border at genal angle, gradually tapered, smoothly and gently posteromedially curved, with sculpture of fine ridges forming herringbone chevrons, vertices of chevrons located near abaxial margin of spine and point anteriorly, sculpture continues on internal side of spine as other diagonal of chevrons; posterior border furrow short and deep, very incised where overlapped with circumocular furrow, shallower over border, course straight along field, then curved to cut across border at raised base of genal spine; posterior border similar to lateral border, but about 2/3 as long as width of former (shorter adaxially) and slightly more inflated, mostly effaced, with a few anastomosing ridges near furrow and a few linear ridges on posterior margin; doublure of posterior border long at genal angle, tapered sagittally to about half length of border, flattened (slopes anteriorly) and effaced, with shallow Panderian notch expressed mainly as indented anterior margin a little exsagittal of ω; lateral border doublure broad, just slightly narrower than border, of even width until tip of anterior projection, where cut by diagonal suture, doublure moderately inflated, with inflation highest just exsagittal from mid-width, with sculpture of fine ridges parallel to margin.

Measurements of thoracic segments were made on the specimens of Pl. 16 and were doubled as necessary for broken axial rings and pleurae. Total number of thoracic segments unknown; segments short and relatively broad,

axis very broad, 46.4% (45.4–47.3%) total width of segment, moderately vaulted, more from axis than pleurae; articulating half ring lens-shaped, long medially and pinched out laterally, inset into axial ring such that anterior margin of segment is almost transverse, with only slight anterior bowing across half ring, with anastomosing line sculpture subparallel to sagittal axis on posterior portion (connected to furrow and axial ring sculpture), anterior part of ring effaced; articulating furrow fairly long and shallow medially, deeper and shorter laterally along taper of half ring, broadly posteriorly bowed, with line sculpture from axial ring extending into furrow; axial ring broad and relatively short, very slightly narrower posteriorly, moderately inflated, a little higher posteriorly, moderately dorsally arched, with sculpture of roughly transverse to posterolaterally directed anastomosing ridges and with small, flattened tubercles concentrated medially; doublure forms large articulating surface, roughly crescentic in shape, longest medially and strongly laterally tapered, effaced; axial furrows narrow, shallow anteriorly, much deeper posteriorly, approximately parallel-sided; inner pleurae horizontal, a little wider than outer pleurae; outer pleurae narrow, ventrolaterally sloped from fulcral angle of about 135º; anterior and posterior pleural bands about equal in length, anterior band a little shorter, particularly adaxially, with triangular (longer exsagittally) articulating wedge along outer pleurae; pleural furrow fairly long and shallow, a little deeper at fulcrum; posterior pleural band lengthened adaxially compared to anterior band, posterior margin transverse along inner pleurae and posteriorly bowed along outer pleurae; both bands nearly effaced, merged into spine at end of outer pleurae; spine incompletely preserved, roughly triangular, moderately wide, a little shorter than pleurae, base centered at about midlength of pleurae, with fine anastomosing ridges running along margins; doublure extremely narrow, just a rim curled in dorsomedially from base of pleural spine.

Pygidial measurements were taken from the specimens of Pl. 19 excluding the smallest specimen (Pl., 19, fig. 28). Measurements were doubled from the sagittal line if necessary, e.g., for specimens with only one side of the pleurae fully preserved. Pygidium composed of five segments with pleurae, plus additional two poorly expressed axial rings, moderately strongly vaulted (sag., tr.), lower posteriorly, very broad and fairly long, with width across first segment (excluding pleural spines) 143.3% (138.6–148.5%) sagittal length (excluding articulating half ring and furrow); articulating half ring broad and relatively short, 9.1% (8.5, 9.7%) sagittal length of pygidium, mostly effaced, with a little anastomosing ridge sculpture posteriorly; articulating furrow deep, long medially and shorter laterally, with transverse anterior margin and posteriorly bowed posterior margin; axis very long, almost equal to sagittal length of pygidium (94.6 [87.9–98.2%] length), wide anteriorly, with width of first axial ring 46.6% (44.9–48.8%) width across first segment, strongly posteriorly tapered, with width across fourth axial ring 72.4% (71.3–73.4%) width across first ring, strongly vaulted anteriorly, lower posteriorly; anterior two axial rings well independently inflated, posterior rings less inflated, with fifth ring only slightly raised above ring furrows, rings six and seven much less distinct, poorly independently inflated, mainly indicated by arrangement of weak inter-ring furrows and tuberculate sculpture, all rings short, particularly medially, with medially concave anterior margins and very slightly anteriorly bowed posterior margins on rings 1–4, all rings relatively broad, with sculpture of small tubercles concentrated medially, flanked by fine anastomosing ridges running subparallel to sagittal axis, and increasingly anteromedially directed on more anterior rings; inter-ring furrows long medially, likely include small pseudo-articulating half rings on at least segments 2–4, short near axial furrows, deep, particularly exsagittally, furrows 4–7 increasingly short and shallow (best visible on Pl. 19, fig. 3), course generally transverse, but exsagittal ends gently posterolaterally curved, sculpture of axis-subparallel anastomosing ridges carries through furrows from axial rings, median part of furrows more effaced, with a few granules posteriorly; rear of axis poorly defined (best seen on Pl. 19, fig. 3), a little shorter than wide, moderately convex (sag., tr.), with posterior margin steeply sloped down toward posteromedian spine, with sculpture similar to axial rings, except anteromedian anastomosing ridges wrap around posterior margin and more posterolateral ridges continue posteriorly onto spine; axial furrows mostly moderately narrow and deep, shallower along posterior rings and posterior of axis, strongly anteriorly divergent in course, posterior tips curve inward slightly to meet poorly expressed post-axial furrow, also abruptly shallowed anteriorly along first axial ring; inner pleurae broad and transverse, separated from steeply sloping outer pleurae of nearly equal width by fulcral angle of about 130º (Pl. 19, fig. 12), pleurae mostly effaced, with just sparse, faint, axis-subparallel anastomosing ridge sculpture sagittally on some specimens, and stronger ridge sculpture on short, posteriorly tapered, unfurrowed pleural region adjacent to posterior of axis; anterior pleural bands very slightly independently inflated, a little longer abaxially than adaxially, posterolaterally directed, with fairly large triangular articulating facet on outer pleurae of first segment; pleural furrows long and deep, shallower just adjacent to axial furrows (distinctly so in larger specimens), proportionately shorter posteriorly, posterolaterally directed, increasingly so posteriorly; posterior pleural bands similar to anterior bands, but longer

adaxially than abaxially; interpleural furrows moderately short, very shallow, very nearly effaced in some specimens, similar in course to pleural furrows but a little more laterally and less posteriorly angled; pleural spines produced from just above base of outer pleurae, extend posterolateroventrally, with posterior spines increasingly posteriorly directed (fourth pair subparallel, fifth pair posteromedially directed), long at base and strongly tapered to sharp point, a little narrower than corresponding pleural band, with sculpture of anastomosing ridges roughly following contours of spine on dorsal aspect, ridges more widely spaced than those on main body of pygidium, with some sculpture at base of spines extending onto outer pleurae, mostly effaced ventrally; posteromedian spine moderately long, with free length 50.3% sagittal length of pygidium (Pl. 19, fig. 1), robustly conical, with fairly broad base separated from axis by distinct break in slope and moderately long, shallow post-axial furrow, spine posteriorly tapered to blunt point, held roughly horizontally, or slightly posterodorsally directed, with concentric sculpture of fine ridges forming inverted “V”-shapes dorsally and “V”-shapes ventrally, with some anastomosing ridge segments; pygidial border mainly expressed ventrally, partially visible as posterior margin of pygidium from fifth pleural spine pair back to underneath base of posteromedian spine, moderately inflated, extends vertically beneath bases of pleural spines on sides of pygidium, then rises up posteriorly to merge with pleural region into base of posteromedian spine, with sculpture of concentric ridges a little coarser than those of pygidial axis following shape of border; doublure only visible in anterior view (Pl. 19, fig. 12), held roughly vertically, shallowly "W"-shaped, longest medially over rounded dorsal extension into hollow at base of posteromedian spine, then anterolaterally tapered, with sculpture of subparallel fine ridges following shape of margin.

Ontogeny. Cranidia of *P. acicaudus* (cf. Pl. 16, fig. 2 and Pl. 17, figs 1, 10) broaden overall; the anterior border shortens, particularly medially, as does the anterior border furrow, although the furrow appears to lengthen initially before shortening again (cf. Pl. 16 figs 2 vs 1, 3 and Pl. 17, figs 1–3); the glabella inflates and becomes more vaulted (sag.; transverse convexity remains similar), broader, and its sparse tuberculate sculpture effaces, particularly anteriorly; L1 becomes longer and larger; SO lengthens and shallows medially; LO shortens, inflates, and the tubercles become less prominent; the lateral margins of the frontal area (anterior branch of the facial suture) become less laterally bowed and straighter; the fixigenal boss above the fossula becomes more prominent; the eye ridge inflates; the palpebral lobes become smaller (both shorter and narrower) relative to rest of cranidium; and the posterior fixigena narrows relative to the glabella.

Librigenal changes (cf. Pl. 18, figs 2, 15) include shallowing of the circumocular furrow, significant widening of the librigenal field, stronger expression of the scrobiculate line sculpture on the field, stronger inflation and further adaxial extent of the base of the genal spine on the field, widening/lengthening of the lateral and posterior border furrows, and effacement of the linear and herringbone chevron sculpture of the lateral border and genal spine.

Thoracic segments are insufficiently known for discussion of ontogeny.

Pygidia (cf. Pl. 19, figs 1, 22, 28) become relatively narrower and more elongate; the anterior and posterior margins of the first axial ring curve toward each other with increasing expression of pseudoarticulating half ring and shorten axial ring medially; tuberculation develops on axis, and anastomosing line sculpture on axis, pleurae, and margin strengthens; the pleural furrows deepen slightly; and the posteromedian spine shortens and thickens.

Discussion. Hintze's (1953, pl. 27, figs 9, 10) holotype pygidium and an associated cranidium came from surface specimens at Section CP 45.7 m. All of the material illustrated herein came from a small, highly fossiliferous limestone nodule collected *in situ* in shale at CP 48.8 m. The fauna is overwhelmingly dominated by *P. acicaudus*, but also contains rare sclerites of the associated species documented by Hintze (1953).

Resolution of relationships between the most derived four species of *Pseudoolenoides* is the least well supported region of the tree. *Pseudoolenoides acicaudus* is very similar to *P. oilcreekensis* (which Shaw (1974) identified as *P. acicaudus*) and differences between these species are discussed below. It is also quite similar in many details to *P. fossilmountainensis*. *Pseudoolenoides acicaudus* is the only species which retains five unreleased thoracic segments, which differentiates it from all other species. In cranidial features, it differs from *P. fossilmountainensis* in a complete lack of glabellar tubercles versus a medially concentrated scattering of small tubercles, less posteriorly bowed anterior sections of the facial suture, more anteroposteriorly oriented, less anastomosing, more widely spaced, and generally more subdued raised line sculpture, and distinctly smaller palpebral lobes. In anterior view, the palpebral lobes are less elevated and more nearly horizontal. Librigenae of the species are very similar, and share a small posterior point where the posterior border meets the facial suture, but that of *P. acicaudus* is larger and more prominent. The librigenal field is also narrower and the raised line arc less well expressed. The species are most different in their pygidial morphology. In addition to retaining an extra unreleased segment, the pygidium of *P. acicaudus* has a much broader posterior axis, axial furrows which converge

posteriorly to a much lesser degree, and a relatively short, tapering posteromedian spine versus long and nontapering (at least proximally).

Pseudoolenoides oilcreekensis n. sp.

Plate 12, figs 15, 20, Plate 20

1974 *Pseudoolenoides acicaudus* Hintze; Shaw, p. 22, pl. 1, figs 13–22, 24.
1975 *Pseudoolenoides acicaudus* Hintze; Derby, p. 26.

Material. Holotype, cranidium, OU 7939 (Pl. 20, figs 1, 4), from Section SP 1 126.8 m, and assigned specimens OU 7940–7947, from Section SP 1 104.5 m and 126.8 m, Highway 77 section, Oil Creek Formation (Darriwilian), Carter County, Oklahoma, USA.

Etymology. From the Oil Creek Formation.

Diagnosis. Eye ridge with highly oblique course; fixigena relatively narrow; pygidium with raised pleural regions; anterior pleural band with distinct distal node.

Description. This species is very similar in cephalic morphology to *P. acicaudus*, with which it was originally identified (Shaw, 1974). Hence, it is described via comparison with that species, noting all observable differences. Cranidium with eye ridge set more obliquely (very clear in Pl. 20, figs 1, 2, but Pl. 20, fig. 3 approaches the attitude seen in *P. acicaudus*); interocular fixigenae distinctly narrower (transverse line from maximum lateral point of glabella to exsagittal line running through γ is 27–31% sagittal distance from front of LO to front of glabella in *P. oilcreekensis*, versus 35–40% in *P. acicaudus*); anteromedian portion of LO set forward as distinct subtrapezoidal protrusion of anterior margin versus margin nearly transversely straight with only slight anterior projection in a few specimens (e.g., Pl. 17, fig. 17); pygidium with four versus five unreleased segments; raised pleural regions, anterior pleural band with swollen node on distal part, axis tapers more rapidly, rear of axis much narrower; posteromedian spine much more robust proximally and apparently longer.

Discussion. In cephalic morphology, *P. oilcreekensis* is differentiated from *P. acicaudus* to an extent which leaves no doubt it is a distinct species. The differentiation is still very subtle, and given the very close similarity of the cranidia and pygidia one would expect the pygidia also to be close. This is not the case, as the single pygidium occurring in the Oil Creek Formation with the cephalic material (Pl. 20, fig. 15) is quite radically different from that of *P. acicaudus*, and instead more closely resembles those of *P. carterensis* and *P. fossilmountainensis*. Given this, one must at least consider the possibility of misassociation. There is apparently no cephalic material associated with the pygidium other than figured herein, but the overall sample size is very small and the possibility exists that the pygidium belongs to a second, rare, species. For this reason we have selected one of the larger heads (Pl. 20, fig. 1) which displays the cranidial differentia well as the holotype, even though if correctly associated the pygidium is the much more distinctive sclerite. *Pseudoolenoides oilcreekensis* occurs a comparable distance beneath *P. carterensis* in the Oil Creek Formation (48.8 m at the Highway 77 section) as *P. acicaudus* does beneath *P. fossilmountainensis* in the Kanosh Formation (approximately 68 m) and the pairs of species are each other's closest comparison.

Pseudoolenoides fossilmountainensis n. sp.

Plates 21–27

Material. Holotype, cranidium, SUI 130061 (Pl. 22, figs 1–3, 5, 7), and assigned specimens SUI 130062–130110, from Section K-South 152.4T m and 159.7T m, Kanosh Formation (Darriwilian; *Pseudoolenoides fossilmountainensis* Zone), southern Confusion Range, Ibex area Millard County, western Utah, USA.

Etymology. From Fossil Mountain.

Diagnosis. Glabella with fine, scattered tubercles with distinct backwardly-raked, subtriangular shape; glabella narrow anteriorly; pygidium with distinct laterally flared border protruding from tagmatized region behind fourth pleural spine; posterior pygidial region narrow, not tapering broadly into posteromedian spine base.

Description. Cranidial measurements were made on the most complete specimens of Pl. 21–23. Measurements were doubled from the sagittal line if necessary, e.g., for specimens with a single intact posterior projection. Cranidium moderately vaulted (sag., tr.), broad and fairly long, with maximum width across palpebral

lobes (δ) 135.2% (127.1–140.1%) sagittal length, width across β 112.0% (103.6–117.3%) length, width across γ 103.7% (96.0–115.3%) length, width across ε 104.4% (92.5–119.8%) length, and width across posterior projections 128.2% (124.1–132.8%) length, with sculpture of anastomosing ridges running generally subparallel to axis, slightly posteromedially directed, sculpture more scrobiculate toward anterior and lateral edges of cranidium; anterior branch of facial suture moderately laterally bowed along frontal areas, slightly anterolaterally bowed along lateral parts of anterior border; posterior branch of facial suture very short (obliquely), extends posterolaterally, but only to even with palpebral furrow; anterior border short, longest medially, particularly anterior to pits at anterolateral corners of LF, laterally tapered, broad, but narrower than fixigena, broadly and unevenly anteriorly bowed, with median section breaking arc of curve with nearly transverse anterior margin, median section gently anteriorly downturned, lateral sections roughly horizontal, border with sculpture of very fine anastomosing ridges roughly parallel to curvature; doublure very slightly turned under medially, but just a rim, mainly exposed as anterior face of border, with fine transverse ridge sculpture; anterior border furrow short, moderately deep, arcuate like border laterally, overlying preglabellar furrow medially and more strongly and narrowly anteriorly bowed, also slightly shallower medially, convergent with axial furrows in small, deep pits; frontal areas large, long, fairly wide, narrower posteriorly, trapezoidal, with posterolaterally slanted anterior and posterior margins, gently anteriorly bowed along mid-length and anteroventrally sloped at about 30–35º angle from horizontal (lateral view), with small, ovoid swelling located adjacent to axial furrow and ocular ridge, reflecting position of fossula on ventral surface, and with sculpture of anastomosing ridges forming small polygons overlain by short scrobiculate ridge situated at about 1/4 length of frontal area, scrobiculate ridge sloped posterolaterally at about 30–35º from horizontal, slightly steeper than anterior border furrow, steeper abaxially, intersects cranidial margin at β, stops short of intersecting axial furrows near their junction with anterior border furrow, polygonal sculpture of frontal areas smaller anterior to ridge and more equant, more elongate posterior to ridge; ocular ridge moderately inflated, lower ad- and abaxially, directed posterolaterally from just anterior to S3 to palpebral lobe at about 30–35º below horizontal; palpebral lobes relatively small in proportion to cranidium, slightly greater than semicircular in area, strongly laterally bowed, but unevenly arcuate, with posterior end closer to sagittal axis, lobes with broad, slightly more inflated lateral margin, margin wider and longer from midlength of lobe posteriorly, tapered far posteriorly, shorter/narrower anteriorly into connection with ocular ridge, lobes elevated to roughly half height of glabella, with lateral edge slightly ventrally bent (anterior view), lobes also anteroventrally sloped (lateral view), and with anastomosing line sculpture differentiated from that of fixigenae by forming small polygons; palpebral furrow best expressed on small specimens (e.g., Pl. 22, fig. 1), short and narrow, shallow, shallowest along mid-course (mid-length of palpebral lobe), course strongly laterally bowed, "U"-shaped, arc of curve uneven (extends further anteromedially), furrow connects anteriorly to shallow furrow along posterior edge of ocular ridge, stops abruptly posteriorly at edge of lobe; interocular fixigena trapezoidal, broad and fairly long, with posterolaterally sloped anterior margin due to strike of ocular ridge, roughly horizontal, only slightly anteroventrally sloped, with far abaxial section slightly raised toward palpebral lobe (anterior, lateral views), with sculpture like that of posterior part of frontal areas (continuous across ocular ridge), and with narrow, short, crescentic slight swelling across from L1 (more prominent on smaller specimens, e.g., Pl. 22, figs 1–3) surrounding small, depressed alae; posterior fixigena very short and relatively wide, rectangular except for lateral extension of posterior margin along posterior projection, strongly posteroventrally sloped (lateral view), with sculpture like that of interocular fixigena; posterior border furrow short, nearly effaced adjacent to glabella and shallow adaxially, much deeper abaxially starting at about half-width, but abruptly effaced just short of cranidial margin, course nearly transverse, very shallowly posterolaterally angled; posterior border narrow, with distance across posterior projections less than distance across palpebral lobes, border short, not quite as long as anterior border, very slightly longer adjacent to LO than at lateral tip, moderately inflated, with shallow furrow (most apparent adaxially and far abaxially) along posterior margin for articulation with thorax, with sculpture like that of fixigenae but a little more effaced; doublure very short, just a rim curled underneath posterior margin, slightly longer far abaxially; axial furrows moderately wide, of varying depth, deepest along L1, shallower posteriorly and anteriorly until deeper again along LF, gently anteriorly divergent until mid-length of glabella, then bowed laterally around L2 and L3, then more strongly anteriorly convergent toward junction with anterior border furrow; glabella with distinct L1 and less distinct L2 and L3, overall elongate and fairly narrow, with maximum width across L2 (even with inner end of ocular ridge) 73.7% (68.7–78.6%) sagittal length excluding LO, bullet-shaped, with strongly tapered and bowed anterior end and straight-sided posterior end (along L1; gently laterally expanded along L2 and L3), strongly transversely vaulted posterior to mid-length, less vaulted anteriorly, moderately strongly sagittally vaulted, with sculpture of fine

anastomosing ridges, ridges form rough, strongly anteriorly bowed concentric arcs with subparallel lateral segments, ridges overlain by small, posteriorly-raked, triangular tubercles, tubercles concentrated medially; L1 broad, short adaxially and elongated abaxially, moderately independently inflated, with fine scrobiculate ridge on anterior margin leading into S1, ridge stops after half-width of lobe but before meeting axial furrow; S1 very long and shallow adaxially, short and deep abaxially, extends far adaxially but just separated from axial furrows by very narrow ridge of raised glabella running from L1 to L2 (shown well on Pl. 21, figs 1, 9), strongly anterolaterally directed; L2–LF and sulci poorly defined on all but smallest specimens (e.g., Pl. 22, fig. 1), L2 and L3 very weakly independently inflated; L2 (as defined by furrows) wedge-shaped, very short near axial furrows, with wide posterior margin along S1 and narrow anterior margin along S2, lobe generally posteromedially directed; L3 very short and narrow (as defined by furrows), anteromedially directed; S2 and S3 short and narrow, barely extend out of axial furrows, shallow, anteromedially directed, S3 located at median end of ocular ridge, S2 located halfway between lateral ends of S3 and S1; LF very large, long and fairly wide, strongly anteriorly tapered, decreasingly convex (tr.) anteriorly; LO moderately inflated, wide, with width across junction of axial furrows and posterior margin 49.7% (44.5%–53.7%) sagittal cranidial length, lobe short laterally, rounded longer extension medially creating wavy anterior margin, LO 16.1% (14.5–17.5%) sagittal length of cranidium at maximum, with evenly arcuate posterior margin, and with sculpture of anastomosing ridges anteriorly, connected to SO ridges, fewer ridges posteriorly on lobe, with small median node situated even with lateral anterior margin (so at slightly anterior to half length medially), and with triangular backwardly-raked tubercles like those of glabella concentrated medially on most specimens; doublure long medially, reaches posterior margin of SO, strongly tapered and short laterally, with shallowly "W"-shaped anterior margin, slightly raised posterior rim, and sculpture of very fine transverse ridges; SO moderately deep, deeper abaxially, long, with roughly transverse anterior margin and shallowly "W"-shaped posterior margin, crossed by ridges of anastomosing, but generally axis-parallel sculpture medially, and with weaker anastomosing sculpture laterally.

Rostral plate unknown.

Hypostomal measurements were made on specimens of Pl. 24–25. Hypostome broad and relatively long, with maximum width across anterior wings 109.2% (106.8–114.0%) sagittal length, with sculpture of fine, closely spaced anastomosing ridges on middle body and more curvilinear fine ridges on borders and doublure; hypostomal suture very shallowly "W"-shaped, gently anteriorly bowed medially, and anteriorly recurved far laterally; anterior border of a very short, inflated rim, with short, shallow furrow behind it; anterior wings triangular, very large, strongly upturned, with anterolateral margin steeply posterolaterally sloped away from anterior border, and with raised rim on posterior margin leading into lateral border, effaced except for a few fine ridges near anterolateral margin and fine ridges following curvature of raised posterior margin; middle body ovoid, elongate and fairly narrow, with width at lateral notch 78.6% (76.1–82.1%) sagittal length, distinctly divided into anterior and posterior lobes by short middle body furrow with strongly posteromedially directed course; furrow discontinuous medially and confluent with lateral border furrow along anterior wings, depth of furrow slightly irregular, with pitted appearance, shallowed at lateral notch where posterior lobe of middle body pinches out; anterior lobe of middle body moderately ventrally inflated (sag., tr.; most of transverse convexity of hypostome due to large anterior wings), ovoid, with lateral bounds undefined by furrow along wings, demarcated instead by effacement of wings vs complex anastomosing ridge sculpture of middle body (as well as change in slope onto wings), sculpture forms small polygons anteromedially, larger, wider polygons medially with more transverse ridges, fewer polygons and more ridges posteriorly, and more widely spaced ridges running approximately parallel to sagittal axis anterolaterally; posterior lobe broadly crescentic, about 1/3 length of anterior lobe at medial maximum, anterolaterally tapered, pinched out at lateral notch, moderately strongly inflated, slightly higher laterally than medially, with sculpture of fine anastomosing ridges roughly transversely directed across lobe, connects to sculpture of anterior lobe and lateral and posterior borders; maculae small, ovoid, positioned just posterior of inner end of middle body furrow, effaced and raised slightly above anterior edge of posterior lobe, less noticeable on larger specimens; lateral border furrow short and deeply impressed along posterior margin of anterior wings (where confluent with middle body furrow), slightly anterolaterally but almost transversely directed along wings, much shallower and curved posterolaterally around lateral notch, then very shallow, narrow, and gently posteromedially directed along posterior lobe of middle body; lateral border very narrow, just an inflated (strongest at lateral notch), downturned rim with fine ridges running parallel to length, with pair of small, finely tapered and pointed spines at shoulders; posterior border furrow arcuate, strongly posteriorly bowed, forms smooth arc in most specimens, but deflected around median projection of posterior lobe of middle body in some (e.g., Pl. 24, figs 1, 15), deep

medially and far anterolaterally, shallower between these points (across from base of posterior border spines), meets shallow lateral border furrow about halfway between shoulder and posterolateral corner; posterior border slightly inflated, highest posteromedially on very short part of border, longer and less inflated exsagittally, merging into triangular base of two pairs of spines similar to those of lateral border at posterolateral corners, spines triangular and somewhat dorsoventrally flattened, but with narrow ridge running anteroposteriorly down longer, slightly thicker adaxial spine, abaxial spine much shorter and narrower, border with sculpture of fine, concentric, semi-anastomosing ridges following contours of border; doublure of lateral and posterior borders narrow and short respectively, dorsomedially upturned, with small, triangular posterior wings at posterior end of very deep (considered from anterior side), fairly long lateral notch, doublure widest and longest at posterolateral corners over bases of spines, reaches posterior border furrow, with sculpture of roughly concentric fine ridges.

Librigenal measurements were made on the most complete specimens of Pl. 23. Librigena of small main body and large genal spine; anterior branch of facial suture very long, approximately equally split along field and along anterior projection of lateral border, very steeply sloped along field, gently anteromedially curved along border, cuts border such that anterior face of doublure is exposed in triangular slice, sections form approximately 125º angle at border; posterior branch of facial suture extremely short, extends only along eye and across posterior border; visual surface composed of numerous tiny, closely packed lenses (more clearly seen ventrally), reniform, long and moderately wide, tall, with rounded dorsal surface and steeply sloped lateral surface (ventrolateral view); circumocular furrow strongly posterolaterally curved, moderately narrow, deep, incised; librigenal field small, trapezoidal, narrow and fairly short, with narrowest width under midlength of eye 32.6% (27.6–37.3%) exsagittal length of field along lateral border furrow, gently laterally convex, with densely spaced anastomosing line sculpture (e.g., Pl. 23, fig. 16) or scrobiculate sculpture (e.g., Pl. 23, fig. 6), and with distinct raised, semi-anastomosing ridge cutting across field from about mid-width of anterior edge to mid-width of posterior edge (diagonal and closer to eye posteriorly due to wider anterior edge); lateral border furrow narrow and fairly deep (shallower on some, e.g., Pl. 23, figs 14, 17–19), shallower posteriorly, only very slightly laterally bowed (moreso posteriorly), separated from posterior border furrow by swollen base of genal spine, includes sculpture of field; lateral border moderately inflated, dorsoventrally flattened into bluntly bladed edge, fairly narrow, narrower anteriorly, anterior projection almost equal in length to remainder of border, with shallowly curved rostral suture at tip (Pl. 23, figs 6, 16, 17), projection gently anteroventrally curved (ventrolateral view), whole border with chevron-shaped ridge sculpture, vertices of chevrons roughly at half width of border, more adaxial anteriorly onto projection and pointed anteriorly, sculpture continuous with, but more anastomosing than, similar sculpture of genal spine, border merged into base of spine; genal spine with similar inflation as lateral border, but less flattened, with ovoid cross-section, base slightly more inflated than librigenal field, spine moderately wide, gradually posteriorly tapered, incomplete on all specimens, but very long, at least 343.2% length of field (Pl. 23, fig. 11), with chevron line sculpture, vertices located at lateral margin posteriorly, move adaxially anteriorly and onto lateral border, ventral sculpture of posteromedially sloped diagonal lines continuous with abaxial branches of dorsal sculpture; posterior border furrow short and deep, longer and deepest adaxially, nearly perpendicular to lateral border furrow, much shallower and curved along base of spine on field; posterior border moderately short, narrower than length of lateral border (excluding anterior projection), reaches to approximately mid-width of eye (separated by overlapping section of posterior border and circumocular furrows), tapered far laterally around base of genal spine and merged onto spine, nearly effaced, with faint ridges roughly parallel to anterior margin; doublure wide laterally, reaches lateral border furrow, raised such that border has ovoid cross-section, with sculpture of subparallel ridges following arc of border and merging into dorsal sculpture of border and spine, shorter posteriorly, and tapered adaxially, effaced or with faint ridge sculpture near posterior edge, with very small Panderian notch expressed mainly as slightly swollen rim located almost at ω.

Total number of thoracic segments unknown, at least six present (Pl. 27, fig. 22). Thoracic measurements were made on specimens of Pl. 25. Thoracic segments fairly shallowly vaulted, axis more vaulted than pleurae, with moderately narrow axis and broad pleurae, axial width 47.1% (43.2–50.3%) width across anterior pleural band; articulating half ring short, a little shorter than axial ring, laterally tapered, with anastomosing line sculpture posteriorly; articulating furrow of varying length and depth (likely from position in thorax), short and deep (e.g., Pl. 25, fig. 17) to long and shallow (Pl. 25, fig. 9), shorter laterally, course posteriorly bowed to very shallowly "W"-shaped, with line sculpture roughly parallel to sagittal axis concentrated medially, extends anteriorly onto posterior part of articulating half ring and posteriorly onto anterior face of axial ring as more transversely oriented lines; axial ring moderately inflated, higher medially, fairly short, shallowly arcuate, longer laterally near axial

rings, with sculpture of small tubercles, points of tubercles raked posteriorly, and of fine ridges near anterior margin, swept back posterolaterally on some specimens (e.g., Pl. 25, fig. 1); doublure similar to that of LO, with shallowly "W"-shaped anterior margin, long medially, reaches to articulating furrow, sharply tapered and very short laterally, with very fine transverse ridge sculpture; axial furrows narrow, moderately deep, subparallel to slightly anteriorly divergent, with tips tucked around margins of ring; inner pleurae broad, about twice as wide as outer pleurae (excluding spine), horizontal; outer pleurae sloped ventrolaterally from fulcrum at about 55–60º below horizontal; anterior and posterior pleural bands of approximately equal short lengths, both effaced on most specimens (but see Pl. 25, fig. 9); anterior band with extremely short articulating ridge on inner pleurae defined posteriorly by fine furrow, and with small, sharp, triangular articulating facet near ventral margin; pleural furrow long and shallow, shorter at ad- and abaxial ends, course roughly transverse to gently posterolateral, with sculpture of fine ridges roughly parallel to sagittal axis; posterior pleural band with margin of inner pleurae turned ventrally to articulate with ridge on anterior band of other segments, with small posterior bulge near fulcrum; pleural spine formed from both pleural bands, triangular, fairly long adaxially, anterior margin curved and strongly posteriorly tapered, posterior margin less strongly tapered, spine gently slopes ventrolaterally from base just above ventrolateral margin of segment with tip below margin of segment, with sculpture of fine ridges following shape of spine; pleural doublure not present on anterior margin of inner pleurae, only a rim on posterior margin of inner pleurae, very narrow laterally near base of spine, just curled in dorsomedially as a rim.

Pygidial measurements were made on the best preserved specimens of Pl. 26–27. Pygidium composed of four distinct axial rings with spinose pleurae, with fifth ring lacking pleural spines more weakly expressed on most specimens, and sixth–seventh rings visible on some (e.g., Pl. 26, fig. 2, Pl. 27, figs 1, 3, 4), and with very small terminal piece, pygidium moderately vaulted (sag., tr.), main body broad and strongly posteriorly tapered, with maximum (excluding spines) width across first segment 154.6% (137.9–169.8%) sagittal length excluding articulating half ring and spine; articulating half ring short, tapered laterally, lens-shaped; articulating furrow fairly short, shallower anteriorly and deeper posteriorly, transverse to gently posteriorly bowed in course, with fine ridges parallel to axis crossing furrow onto articulating half ring; axis moderately strongly vaulted, lower posteriorly, long, 87.3% (82.4–96.0%) sagittal length of main body (both measurements excluding articulating half ring), broad anteriorly, with width across first axial ring 48.4% (46.5–51.2%) width across first segment, strongly posteriorly tapered, with sixth ring approximately 1/3 width of first ring and fourth ring 64.3% (62.0–68.8%) width of first ring; axial rings independently inflated, but first four much more distinctly so than subsequent rings, first 4–5 rings short medially, much longer exsagittally, with anteriorly bowed posterior margin and more gently posteriorly bowed median anterior margin, subsequent rings with transverse margins, ring sculpture of small and moderately large tubercles medially, with ridges subparallel to sagittal axis (some more transverse) connecting tubercles, ridges become posterolaterally angled far laterally; inter-ring furrows deep, deeper exsagittally near axial furrows, very long, with anteriorly bowed anterior margin, possibly include poorly differentiated pseudo-articulating half rings, furrows with sculpture similar to that of thoracic ring furrows, with ridges running roughly parallel to sagittal axis crossing furrows and running onto rings, but discontinuous over rings, also with some anastomosing ridge segments; sliver-like terminal piece posterior of axial rings 5–7 (shown well on specimens of Pl. 27; posterior rings weakly defined by shallow inter-ring furrows and transverse lines of tubercles on crest of rings); posterior margin of axis poorly posteriorly defined by post-axial furrow, with weakly inflated median ridge leading onto posterior spine in some specimens (e.g., Pl. 26, figs 1, 2); axial furrows moderately wide, slightly wider anteriorly, deep, much shallower far anteriorly over first segment and posteriorly along rear of axis, course strongly anteriorly divergent; posterior furrow weakly expressed in most specimens (but see Pl. 26, fig. 11, Pl. 27, fig. 3), strongly posteriorly bowed, very short, moderately–very shallow; pleurae moderately long, slightly longer than corresponding axial rings, maximum length of pleurae on first segment 25.9% (22.2–31.2%) sagittal length of pygidium, pleurae moderately narrow, about half width of axis, with relatively broad, transverse inner pleurae, sharp fulcral angle of about 120º, and narrower, strongly laterally downturned outer pleurae, pleurae mainly effaced, with a few granules and segments of fine ridges, with anterior and posterior bands of approximately equal length, bands increasingly posterolaterally directed posteriorly, merged and indistinct along rear of axis, tapering posteriorly into base of posterior spine; anterior pleural bands longer abaxially, slightly broader than corresponding posterior band, moderately inflated, more strongly inflated than posterior bands, with short articulating tongue (inner pleurae) and triangular flange (outer pleurae, anterolateral edge of lateral border) on first segment; pleural furrows long, moderately deep, shorter and deeper exsagittally on outer pleurae, with sculpture of fine, closely spaced, partially anastomosing ridges running roughly perpendicular to gently posterolateral course of furrow;

posterior pleural bands similar to anterior bands, but longer adaxially and less inflated; interpleural furrows mostly effaced, very short (Pl. 26, fig. 2), shallow, increasingly posterolaterally directed; pleural spines on first four segments, posterolaterally curved, blade-like, dorsoventrally flattened with distinct anterior and posterior edges, spines as long as pleurae adaxially, gradually tapered to blunt point at posteriorly- or posteromedially-directed tip, a little broader (oblique) than pleurae, with sculpture of fine, semi-anastomosing ridges running mostly subparallel to curvature of spines on dorsal surface, and fewer, very fine ridges concentrated near edges on ventral surface; slightly widened and very slightly flattened, bluntly laterally curved area of merged pleurae just posterior to fourth spine; posterior spine conical, long, full length unknown; at least 125–126% length of main body (Pl. 27, fig. 1), moderately wide, gradually posteriorly tapered, raised about 15º above horizontal, with fine ridge sculpture shaping very closely spaced inverted chevrons dorsally and chevrons ventrally, individual ridges connected laterally; pygidial border expressed mainly ventrally along sides of pygidium, also partially visible posteromedially in posterior view along rear of axis, forms moderately narrow, inflated rim with subparallel ridge sculpture, merged posteromedially into ventral base of posterior spine, anterior tips turned out laterally into articulating flange on anterior pleural band of first segment; pygidial doublure held subvertically, only visible anteriorly (Pl. 26, fig. 18), short, slightly longer medially and slightly anterolaterally tapered, with fine ridge sculpture like that of border.

Ontogeny. Cranidia of *P. fossilmountainensis* (cf. Pl. 21, fig. 1, Pl. 23, fig. 1) become broader overall; the anterior part of the cranidium (in front of the ocular ridges) becomes longer relative to the posterior part; anastomosing ridge sculpture overall becomes finer and a little more widely spaced; the anterior border shortens, especially medially; all cranidial furrows (except S1) become shallower; the anterior branch of the facial suture becomes longer and more weakly laterally bowed; the fixigenal bosses above the fossulae become more prominent; the eye ridges become relatively shorter and a little less inflated; the palpebral lobes become smaller, with wider, less inflated rims; the glabella broadens and inflates; S1 deepens and lengthens, and the scrobiculate sculpture of the posterior rim develops; glabellar tuberculation develops anteriorly, becomes more densely spaced overall; individual tubercles shrink in size and become posteriorly raked; anastomosing ridge sculpture develops on the glabella; SO lengthens; LO shortens a little and the anterior margin becomes "W"-shaped; and the median LO node becomes smaller, but not less prominent.

The hypostome (cf. Pl. 24, figs 3, 15) broadens overall; all furrows become shallower; the sculpture becomes finer and more closely spaced; the posterior lobe of the middle body shortens; the middle body overall becomes less inflated, and the posterior lobe becomes particularly less independently inflated; the lateral border spines at the shoulder shrink to nubs and those at the posterolateral corners become shorter; and the posterior border spines become shorter and narrower.

Librigenal ontogenetic changes (cf. Pl. 23, figs 3, 16) include enlargement of the eye (it becomes distinctly wider, although not relative to the size of the librigenal field), while the individual lenses become smaller; the circumocular furrow shallows and widens; the librigenal field shortens and broadens; the scrobiculate ridge sculpture on the field develops and strengthens; the anastomosing ridge sculpture of the field develops; the lateral and posterior borders inflate slightly; and the anterior projection of the lateral border lengthens relative to the field.

The thorax is not sufficiently well known to evaluate most ontogenetic changes, but comparison of the thoracic segments attached to the juvenile thoracopygidium (Pl. 27, fig. 22) with individual segments (Pl. 25) shows that the tuberculate sculpture of the axial ring becomes more densely distributed and the tubercles grow into the characteristic posteriorly-raked form.

Pygidial ontogenetic changes (cf. Pl. 26, figs 1, 14, Pl. 27, figs 15, 24) include overall broadening of the main body; median shortening of the axial rings; the first four inter-ring furrows lengthen, particularly the first one, but the fifth shortens; the ring furrows become shallower medially and deeper laterally; the rear of the axis lengthens and narrows; axial ring tubercles become less prominent; anastomosing ridge sculpture becomes more prominent; pleural furrows lengthen and deepen; and the median posterior spine becomes relatively thinner.

Discussion. *Pseudoolenoides fossilmountainensis* is closely similar to *P. carterensis*, and is compared in detail with that species below.

Pseudoolenoides carterensis **Shaw, 1974**

Plates 28–30

1974 *Pseudoolenoides carterensis* Shaw, p. 25, pl. 1, figs 1–12.

1996 *Pseudoolenoides carterensis* Shaw; Fortey and Droser, p. 87.

Material. All specimens are from the Oil Creek Formation (Darriwilian), Oklahoma. Holotype, cranidium, OU 7932 (Pl. 28, figs 3, 6, 9, 12), and illustrated specimens OU 7928, 7930, 7934, 7936–7938, 30122–30125, 30128, 30139, from Section SP 1 175.6 m, and OU 7931 from Section SP 1 171.0 m, Highway 77 section, Carter County; illustrated specimen OU 7935 from Section AW 1, approximately 122 m, north end of Criner Hills, Carter County; illustrated specimens OU 7927, 7929, 7933 from Section N 1 161.5 m, Carter County; illustrated specimens OU 38926–38928, 38930 from Section WSC 107.6 m, West Spring Creek, Murray County.

Diagnosis. Anterior portion of glabella bulbous and entirely lacking sculpture; raised line arc on frontal area more irregular than in any other species; S1 very deep; pygidium lacking flared border behind fourth pleural spine, but with posterior region flared and expanded, forming broad posterolateral extension which merges with the broad base of the posteromedian spine.

Discussion. *Pseudoolenoides carterensis* is very similar to its sister species, *P. fossilmountainensis*. However, the species are clearly differentiated, with multiple pervasive differences on each sclerite. Compared with those of *P. carterensis*, cranidia of *P. fossilmountainensis* have a significantly shallower anterior border furrow, particularly in the region in front of the glabella; an anteriorly narrower, more anteriorly tapering glabella; less prominent transverse raised line sculpture on the frontal area, lacking forward extensions toward the anterior border and lacking a posterior extension along the facial suture toward the eye ridge; interocular and posterior fixigenae covered with fine, scrobiculate raised line sculpture versus mostly smooth; and less deeply impressed S1. Librigenae of *P. fossilmountainensis* differ in having a narrower lateral border; a raised line on the field beneath the eye which carries on anteriorly on a straight course, versus bending adaxially; dense but fine raised line sculpture on the field versus mostly smooth; a slightly wider field; and a much narrower and deeper posterior border furrow. Pygidia of *P. fossilmountainensis* differ in the possession of faint tubercles on the axis versus completely smooth; the presence of a distinct lateral flange of the border behind the fourth pleural spine (see particularly ventral views, Pl. 26, figs 9, 13, to confirm this is a distinct structure), a posterior axis that is much more merged with the post-axial region (in many specimens of *P. carterensis*, the axis is nearly fully circumscribed posteriorly: Pl. 30, figs 1, 3, 10); and in particular a posterolateral region of the pleura which is small and does not extend posteriorly, versus broad and extended posteriorly to merge with an expanded base of the posteromedian spine.

Acknowledgements

We are grateful to Steve Westrop and Roger Burkhalter for loan of material from the University of Oklahoma and providing OU specimen numbers, to the staff of the United States Museum of Natural History for loan of material from the Smithsonian Institution, and to Tiffany Adrain for assistance with curation, facilitating loans, and specimen numbers. We thank Lisa Amati and an anonymous reviewer for helpful comments which improved the paper.

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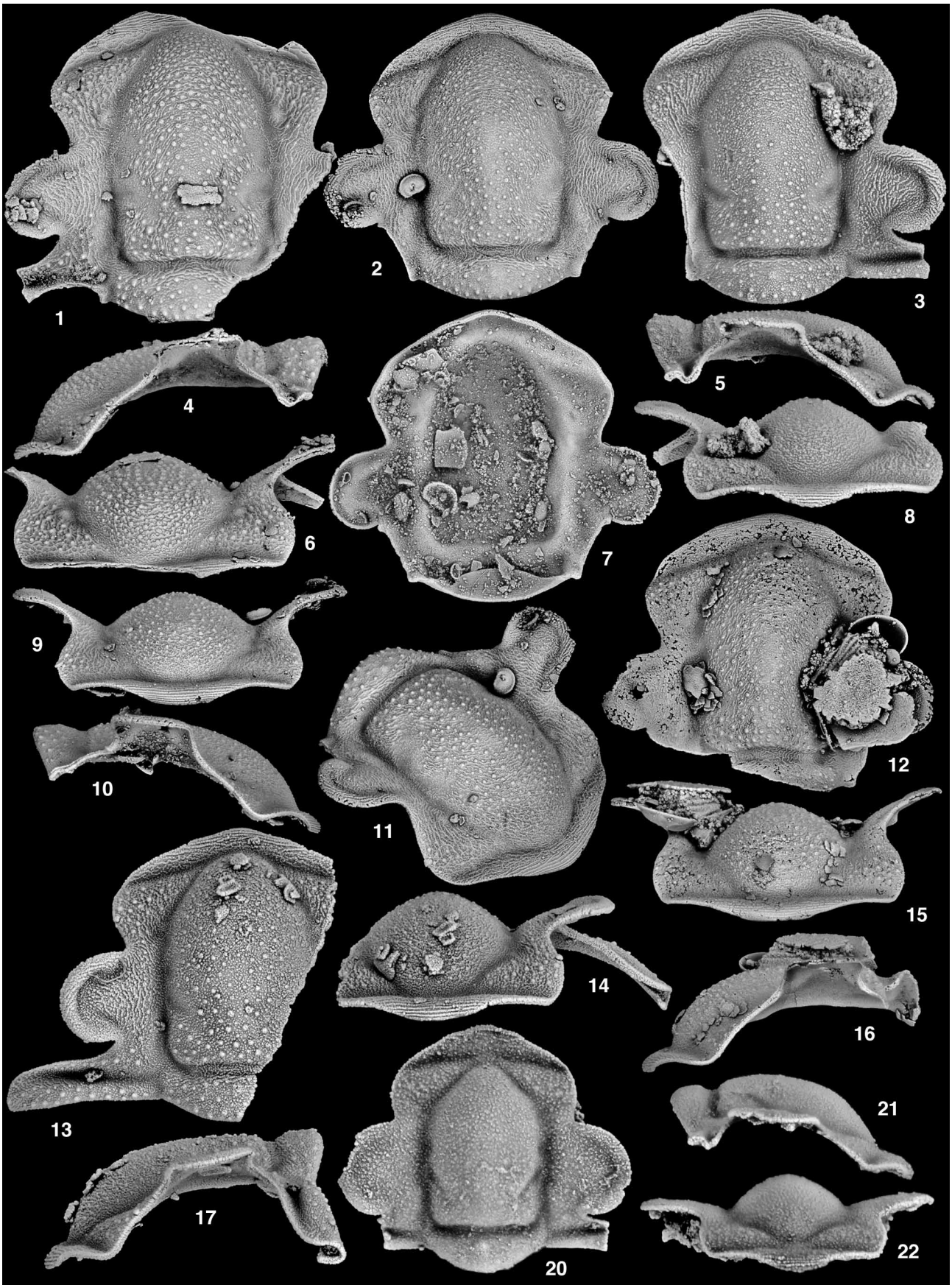

PLATE 1

Pseudoolenoides ludificatus (Hintze, 1953), from Section K-South 1.5T m, Kanosh Formation (Dapingian; *Pseudoolenoides dilectus* Zone), southern Confusion Range, Ibex area Millard County, western Utah, USA.

1, 4, 6. Cranidium, SUI 129972, dorsal, left lateral, and anterior views, x9.
2, 7, 9–11. Cranidium, SUI 129973, dorsal, ventral, anterior, right lateral, and oblique views, x9.
3, 5, 8. Cranidium, SUI 129974, dorsal, right lateral, and anterior views, x15.
12, 15, 16. Cranidium, SUI 129975, dorsal, anterior, and left lateral views, x9.
13, 14, 17. Cranidium, SUI 129976, dorsal, anterior, and left lateral views, x15.
20–22. Cranidium, SUI 129977, dorsal, right lateral, and anterior views, x30.

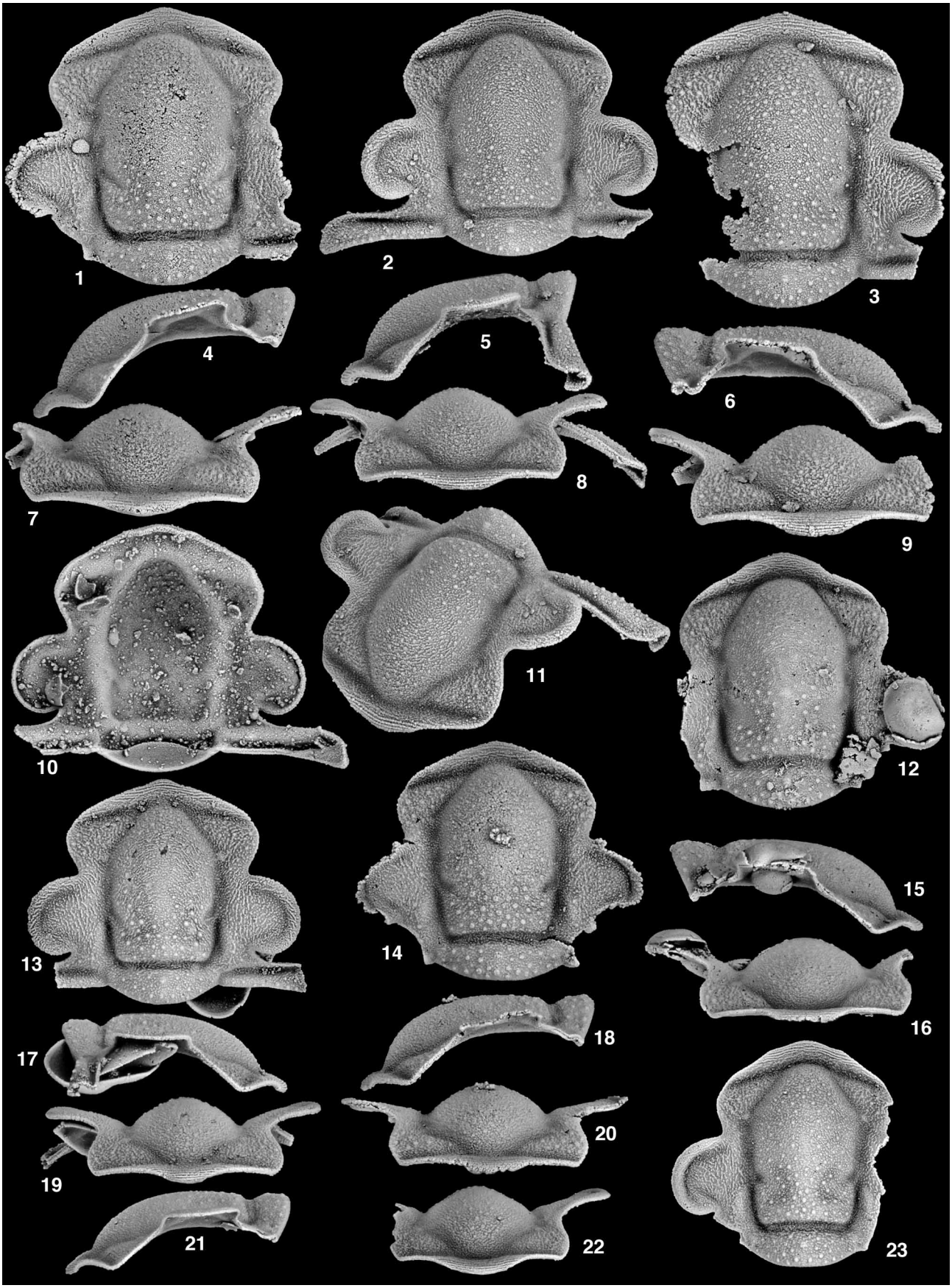

PLATE 2

Pseudoolenoides ludificatus (Hintze, 1953), from Section K-South 1.5T m, Kanosh Formation (Dapingian; *Pseudoolenoides dilectus* Zone), southern Confusion Range, Ibex area Millard County, western Utah, USA.

1, 4, 7. Cranidium, SUI 129978, dorsal, left lateral, and anterior views, x15.
2, 5, 8, 10, 11. Cranidium, SUI 129979, dorsal, left lateral, anterior, ventral, and oblique views, x15.
3, 6, 9. Cranidium, SUI 129980, dorsal, right lateral, and anterior views, x15.
12, 15, 16. Cranidium, SUI 129981, dorsal, right lateral, and anterior views, x15.
13, 17, 19. Cranidium, SUI 129982, dorsal, right lateral, and anterior views, x17.
14, 18, 20. Cranidium, SUI 129983, dorsal, left lateral, and anterior views, x17.
21–23. Cranidium, SUI 129984, left lateral, anterior, and dorsal views, x15.

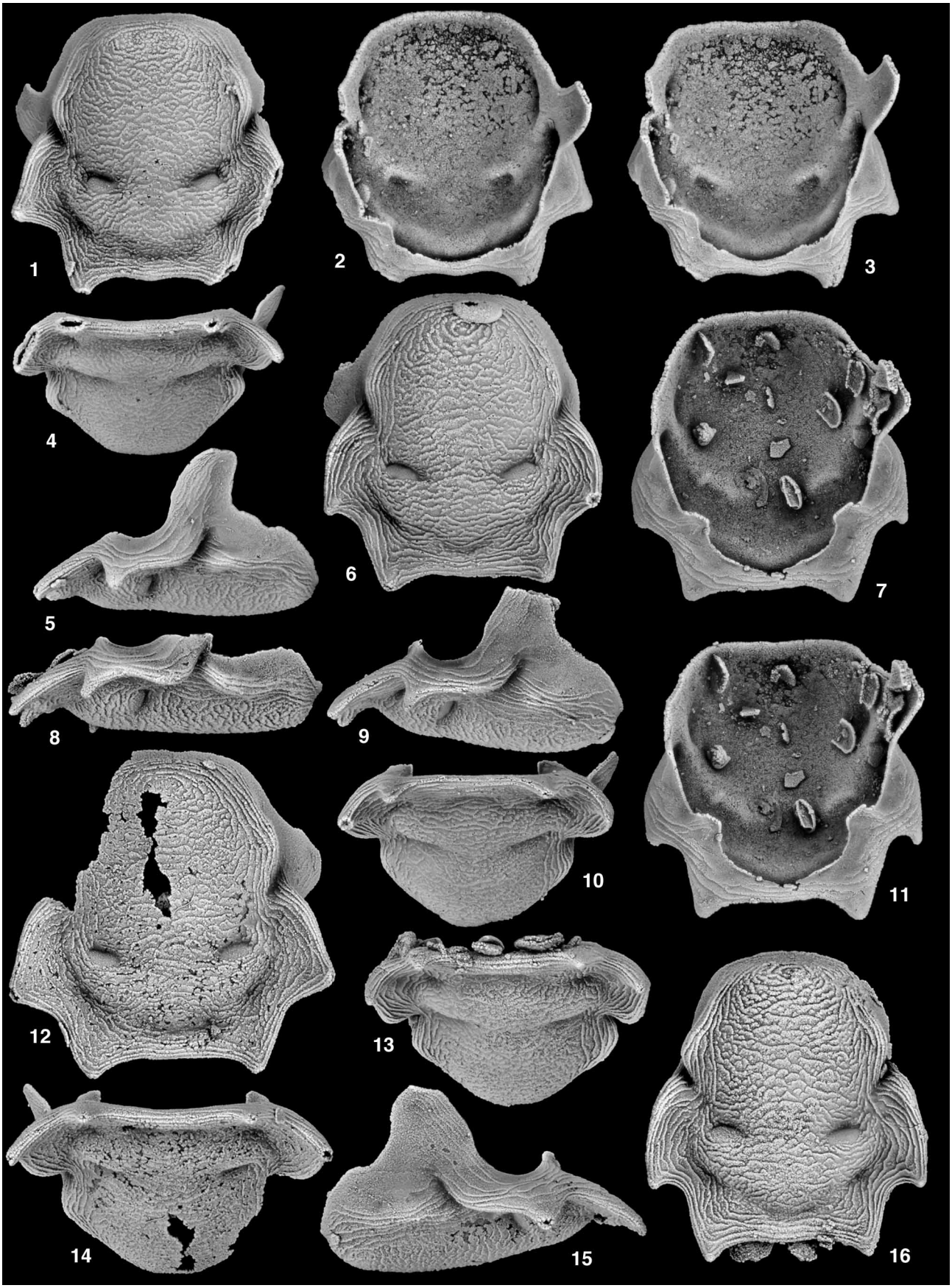

PLATE 3

Pseudoolenoides ludificatus (Hintze, 1953), from Section K-South 1.5T m, Kanosh Formation (Dapingian; *Pseudoolenoides dilectus* Zone), southern Confusion Range, Ibex area Millard County, western Utah, USA.

1–5. Hypostome, SUI 129985, ventral, dorsal, doublural, posterior, and right lateral views, x17.
6, 7, 9–11. Hypostome, SUI 129986, ventral, dorsal, right lateral, posterior, and doublural views, x17.
8, 13, 16. Hypostome, SUI 129987, right lateral, posterior, and ventral views, x14.
12, 14, 15. Hypostome, SUI 129988, ventral, posterior, and left lateral views, x14.

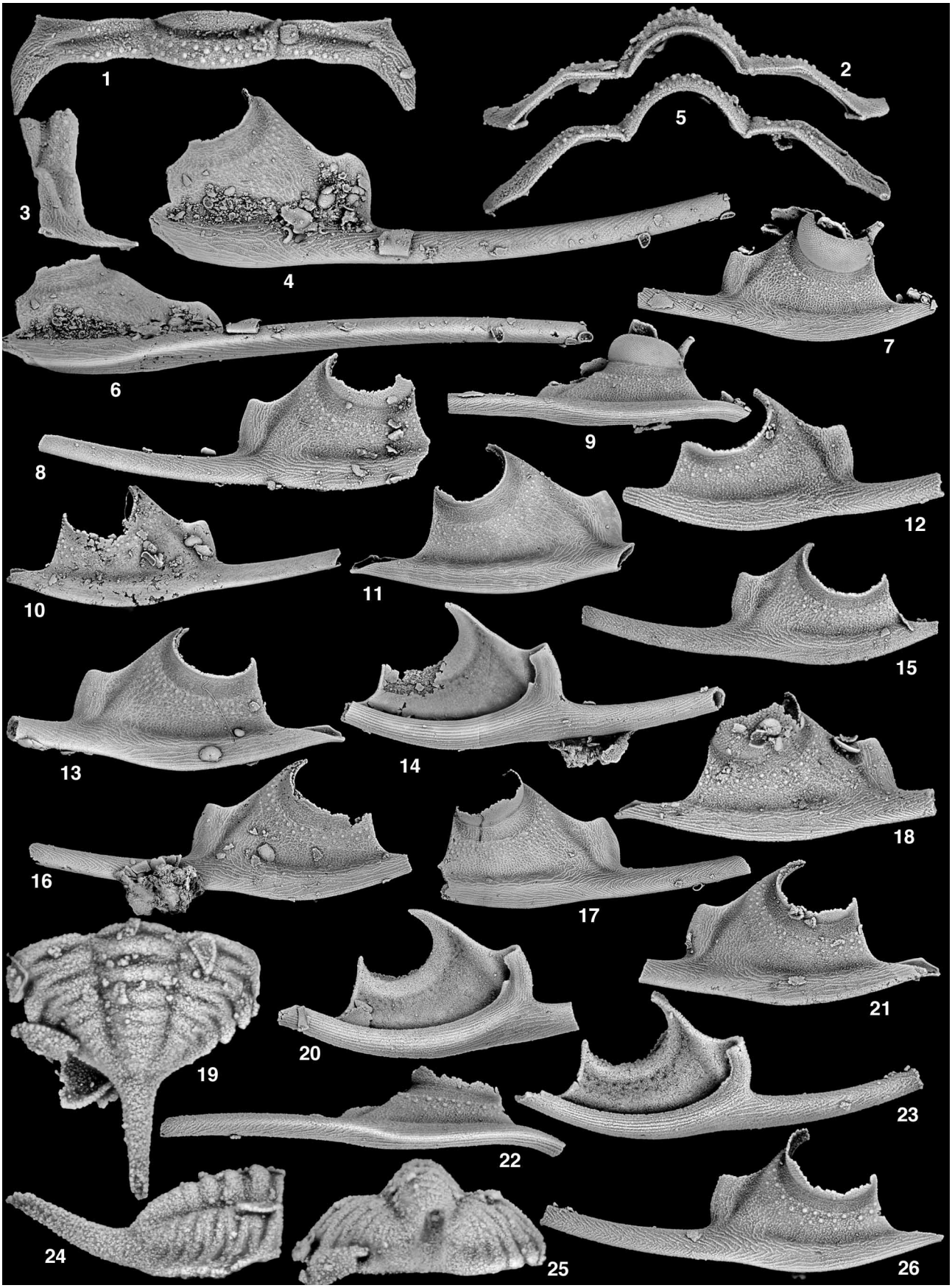

PLATE 4

Pseudoolenoides ludificatus (Hintze, 1953), from Section K-South 1.5T m, Kanosh Formation (Dapingian; *Pseudoolenoides dilectus* Zone), southern Confusion Range, Ibex area Millard County, western Utah, USA.

1, 2, 3, 5. Thoracic segment, SUI 129989, dorsal, anterior, left lateral, and posterior views, x15.
4, 6. Left librigena, SUI 129990, external and ventrolateral views, x7.5.
7, 9. Right librigena, SUI 129991, external and ventrolateral views, x8.
8. Right librigena, SUI 129992, external view, x10.
10. Left librigena, SUI 129993, external view, x10.
11. Left librigena, SUI 129994, external view, x5.
12. Left librigena, SUI 129995, external view, x15.
13. Right librigena, SUI 129996, external view, x8.
14, 16. Right librigena, SUI 129997, internal and external views, x8.
15. Right librigena, SUI 129998, external view, x12.
17. Left librigena, SUI 130111, external view, x6.
18. Left librigena, SUI 130112, external view, x12.
19, 24, 25. Transitory pygidium, SUI 130113, dorsal, right lateral, and posterior views, x30.
20, 21. Right librigena, SUI 130114, internal and external views, x9.
22, 23, 26. Right librigena, SUI 130115, ventrolateral, internal, and external views, x14.

PLATE 5

Pseudoolenoides ludificatus (Hintze, 1953), from Section K-South 1.5T m, Kanosh Formation (Dapingian; *Pseudoolenoides dilectus* Zone), southern Confusion Range, Ibex area Millard County, western Utah, USA.

1, 4, 8, 17. Rostral plate, SUI 129999, anteroventral, anterior, ventral, and right lateral views, x15.
2, 5, 7, 9, 15. Thoracic segment, SUI 130000, dorsal, ventral, right lateral, anterior, and posterior views, x12.
3, 6, 14. Thoracic segment, SUI 130001, dorsal, posterior, and left lateral views, x15.
10, 11, 13, 18, 20. Thoracic segment, SUI 130002, posterior, ventral, left lateral, anterior, and dorsal views, x10.
12, 16, 19, 22, 24, 30. Rostral plate, SUI 130003, anteroventral, anterior, ventral, posterior, right lateral, and posteroventral views, x12.
21, 27, 28, 31–33. Rostral plate, SUI 130004, anteroventral, anterior, right lateral, posterior, ventral, and slightly anteroventral views, x12.
23, 25, 26. 29, 34. Thoracic segment, SUI 130005, dorsal, right lateral, ventral, anterior, and posterior views, x12.

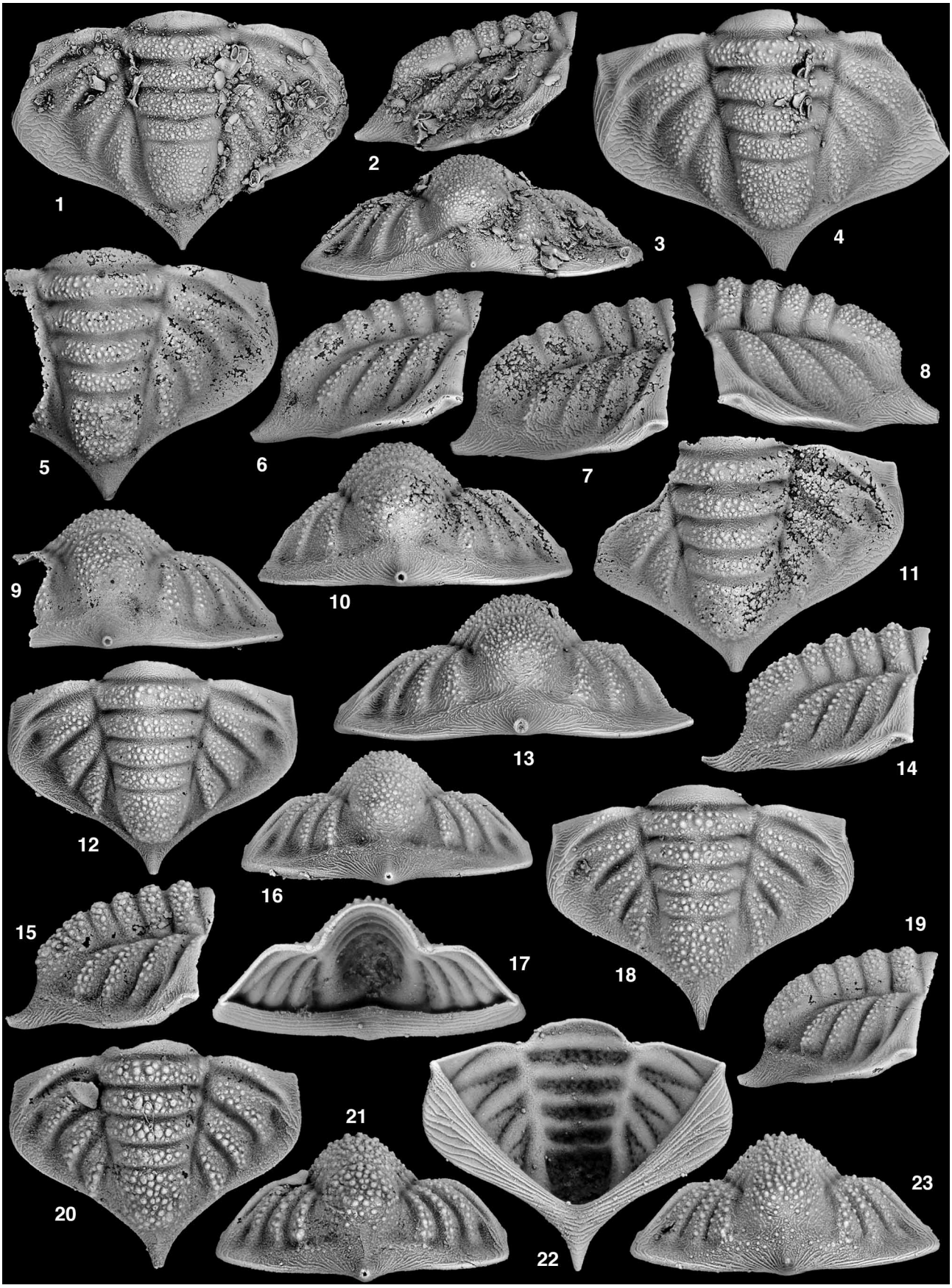

PLATE 6

Pseudoolenoides ludificatus (Hintze, 1953), from Section K-South 1.5T m, Kanosh Formation (Dapingian; *Pseudoolenoides dilectus* Zone), southern Confusion Range, Ibex area Millard County, western Utah, USA.

1–3. Pygidium, SUI 130006, dorsal, right lateral, and posterior views, x5.
4, 8, 13. Pygidium, SUI 130007, dorsal, left lateral, and posterior views, x7.5.
5, 6, 9. Pygidium, SUI 130008, dorsal, right lateral, and posterior views, x8.
7, 10, 11. Pygidium, SUI 130009, right lateral, posterior, and dorsal views, x9.
12, 15, 19. Pygidium, SUI 130010, dorsal, posterior, and right lateral views, x10.
14, 17, 18, 22, 23. Pygidium, SUI 130011, right lateral, anterior, dorsal, ventral, and posterior views, x13.
15, 20, 21. Pygidium, SUI 130012, right lateral, dorsal, and posterior views, x14.

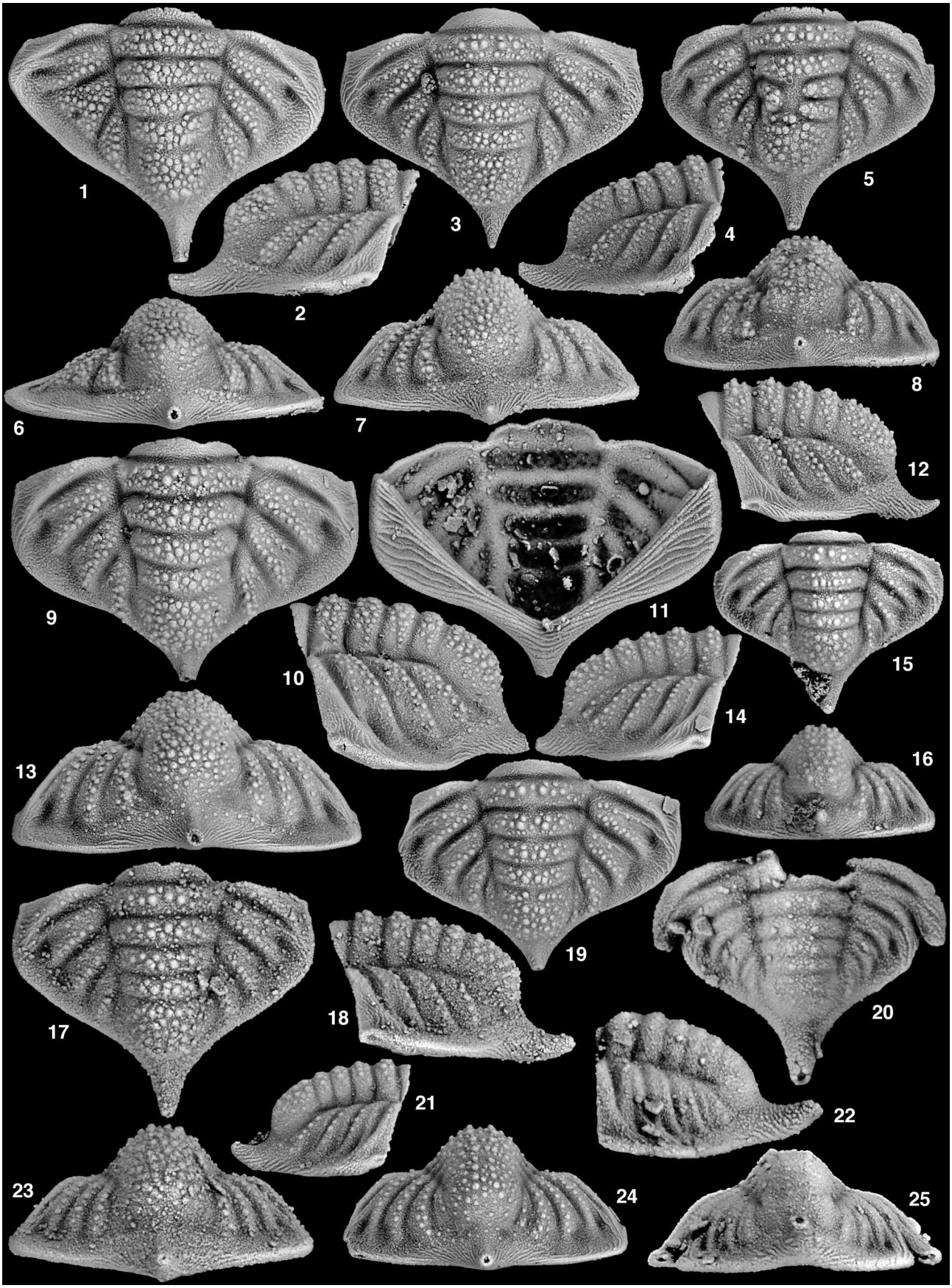

PLATE 7

Pseudoolenoides ludificatus (Hintze, 1953), from Section K-South 1.5T m, Kanosh Formation (Dapingian; *Pseudoolenoides dilectus* Zone), southern Confusion Range, Ibex area Millard County, western Utah, USA.

1, 2, 6. Pygidium, SUI 130013, dorsal, right lateral, and posterior views, x15.
3, 7, 12. Pygidium, SUI 130014, dorsal, posterior, and left lateral views, x15.
4, 5, 8. Pygidium, SUI 130015, right lateral, dorsal, and posterior views, x15.
9–11, 13. Pygidium, SUI 130016, dorsal, left lateral, ventral, and posterior views, x15.
14, 19, 24. Pygidium, SUI 130017, right lateral, dorsal, and posterior views, x17.
15, 16, 21. Pygidium, SUI 130018, dorsal, posterior, and right lateral views, x20.
17, 18, 23. Pygidium, SUI 130019, dorsal, left lateral, and posterior views, x20.
20, 22, 25. Transitory pygidium, SUI 130020, dorsal, left lateral, and posterior views, x30.

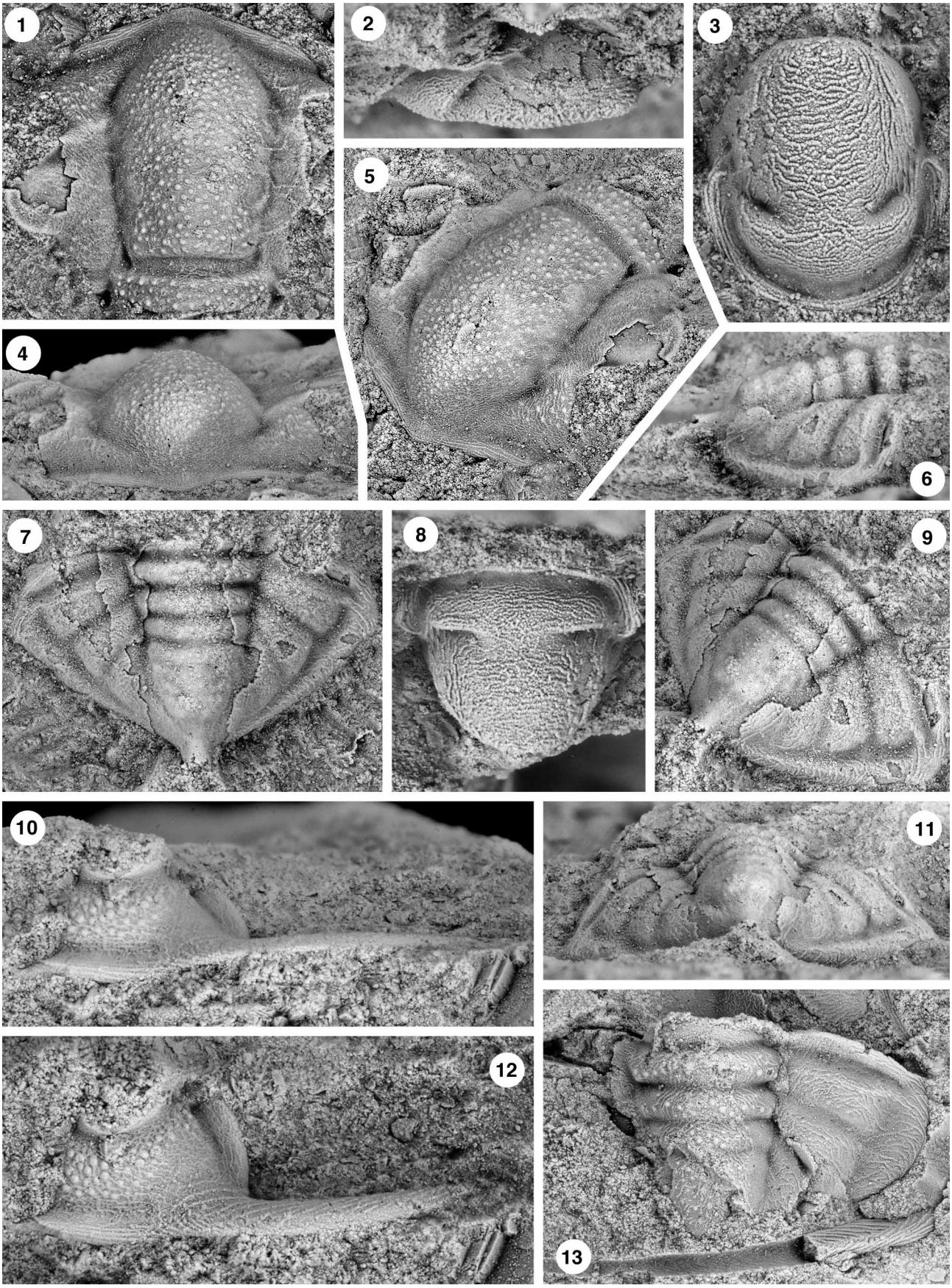

PLATE 8

Pseudoolenoides aspinosus Fortey and Droser, 1996, 36 m above *Hesperonomiella minor* bed ("K"), Juab Formation (Dapingian; *Psephosthenaspis pseudobathyurus* Zone), Thomas Range section, Juab County, western Utah, USA.

1, 4, 5. Cranidium, **holotype**, USNM 481341, dorsal, anterior, and oblique views, x9.
2, 3, 8. Hypostome, USNM 481345, right lateral, ventral, and posterior views, x17.
6, 7, 9, 11. Pygidium, USNM 481346, right lateral, dorsal, oblique, and posterior views, x12.
10, 12. Left librigena, USNM 481344, ventrolateral and external views, x15.
13. Pygidium, unnumbered specimen on same bedding surface, dorsal view, x10.

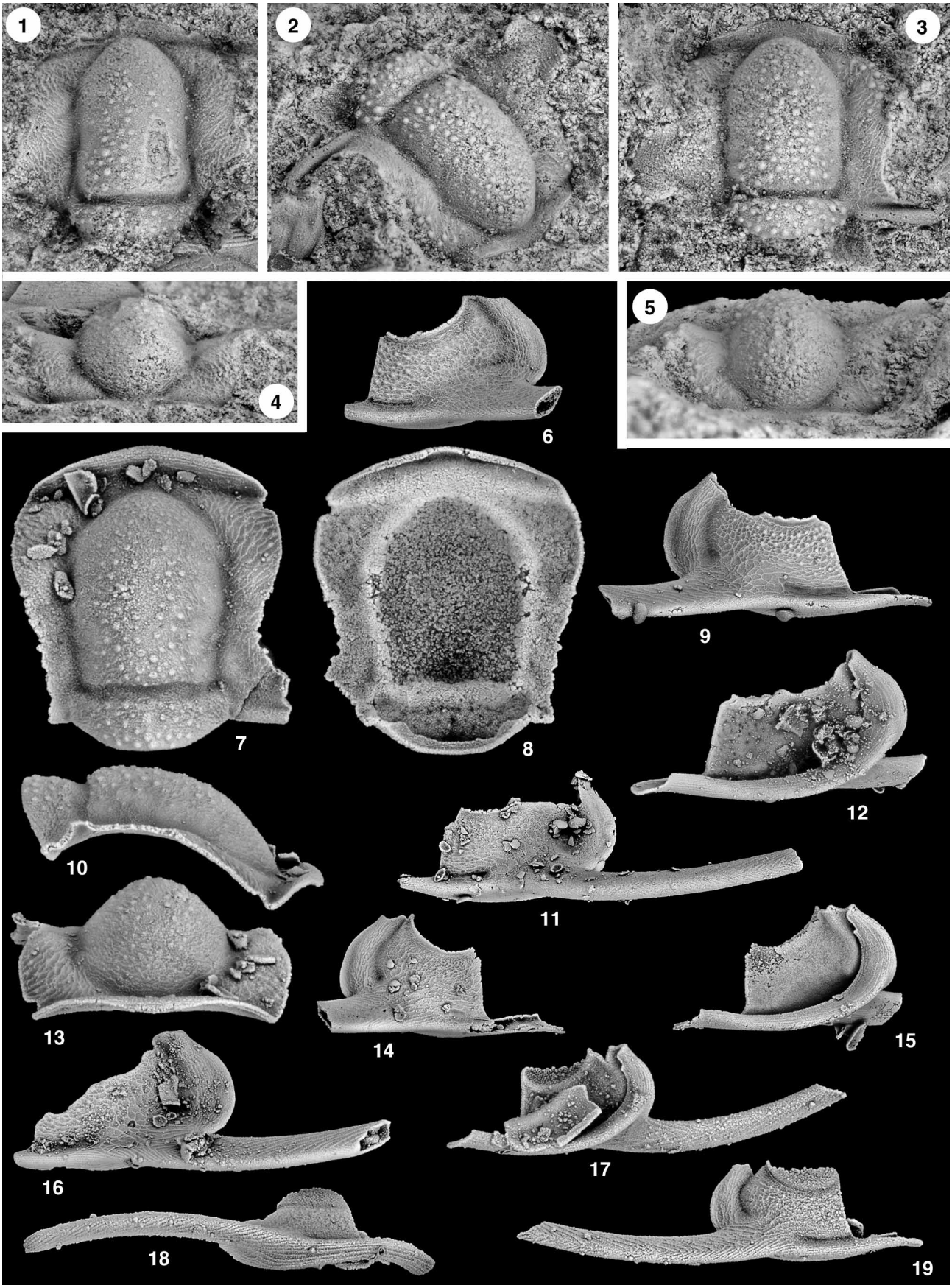

PLATE 9

Pseudoolenoides pogonipensis **n. sp.**?, 36 m above *Hesperonomiella minor* bed ("K"), Juab Formation (Dapingian; *Psephosthenaspis glabrior* Zone), Ibex Section J, southern Confusion Range, Ibex area, Millard County, western Utah, USA.

1, 4. Cranidium, USNM 481343, dorsal and anterior, x14.
2, 3, 5. Cranidium, USNM 481342, oblique, dorsal, and anterior views, x13.

Pseudoolenoides pogonipensis **n. sp.**, from Section K-South 1.5T m, Kanosh Formation (Dapingian; *Pseudoolenoides dilectus* Zone), southern Confusion Range, Ibex area Millard County, western Utah, USA.

6. Left librigena, SUI 130118, external view, x12.
7, 8, 10, 13. Cranidium, SUI 130021, dorsal, ventral, right lateral, and anterior views, x20.
9, 12. Right librigena, SUI 130024, external and internal views, x8.
11. Left librigena, SUI 130023, external view, x12.
14. Right librigena, SUI 130119, external view, x8.
15. Right librigena, SUI 132146, internal view, x8.
16. Left librigena, SUI 130022, external view, x9.
17–19. Right librigena, SUI 130036, internal, ventrolateral, and external views, x14.

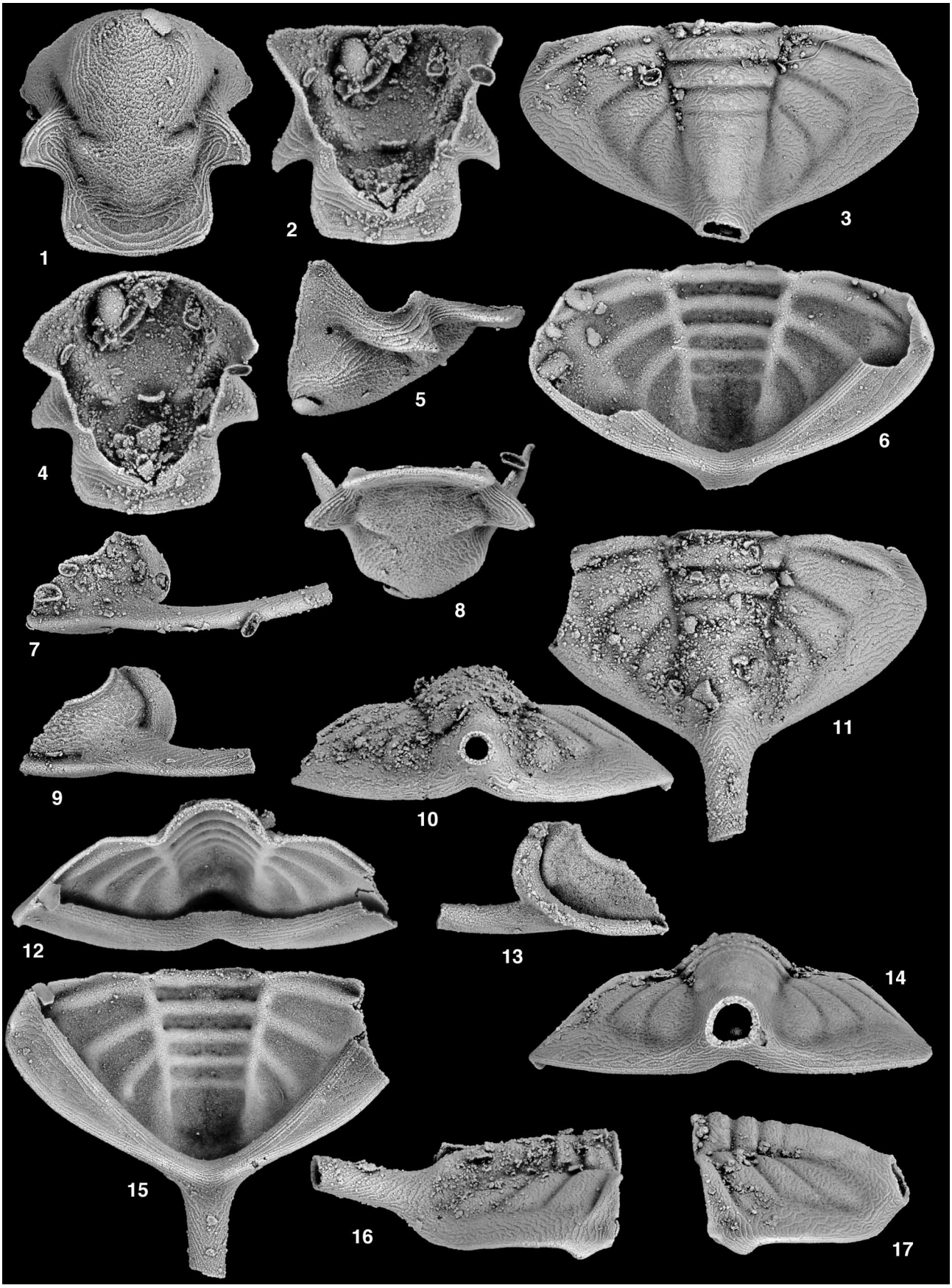

PLATE 10

Pseudoolenoides pogonipensis **n. sp.**, from Section K-South 1.5T m, Kanosh Formation (Dapingian; *Pseudoolenoides dilectus* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

1, 2, 4, 5, 8. Hypostome, SUI 130035, ventral, doublural, dorsal, left lateral, and posterior views, x14.
3, 6, 14, 17. Pygidium, SUI 130117, dorsal, ventral, posterior, and left lateral views, x12.
7. Left librigena, SUI 130037, external view, x10.
9, 13. Left librigena, SUI 130025, external and internal views, x12.
10–12, 15, 16. Pygidium, **holotype**, SUI 130116, posterior, dorsal, anterior, ventral, and right lateral views, x12.

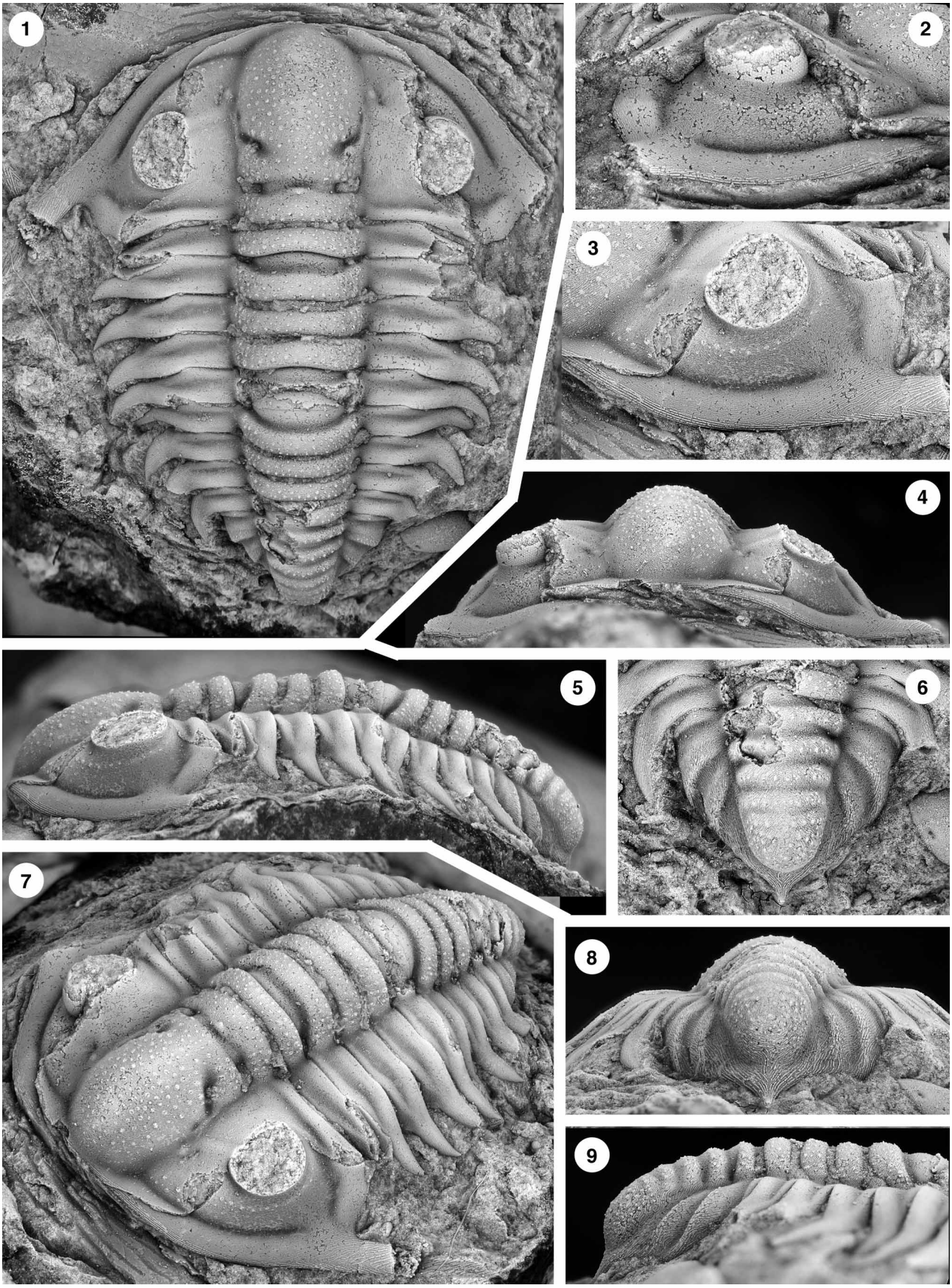

PLATE 11

Pseudoolenoides dilectus Hintze, 1953, from Section J, Locality J-22 of Hintze (1951, 1953), Kanosh Formation (Dapingian; *Pseudoolenoides dilectus* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

1–9. Dorsal exoskeleton, **holotype**, AMNH-FI 26492, dorsal cephalic view (x7.5), external view of right librigena (x10), external view of left librigena (x10), anterior cephalic view (x7.5), left lateral view (x7.5), dorsal view of pygidium (x10), oblique cephalic view (x7.5), posterior view of pygidium (x10), and right lateral view of pygidium (x10).

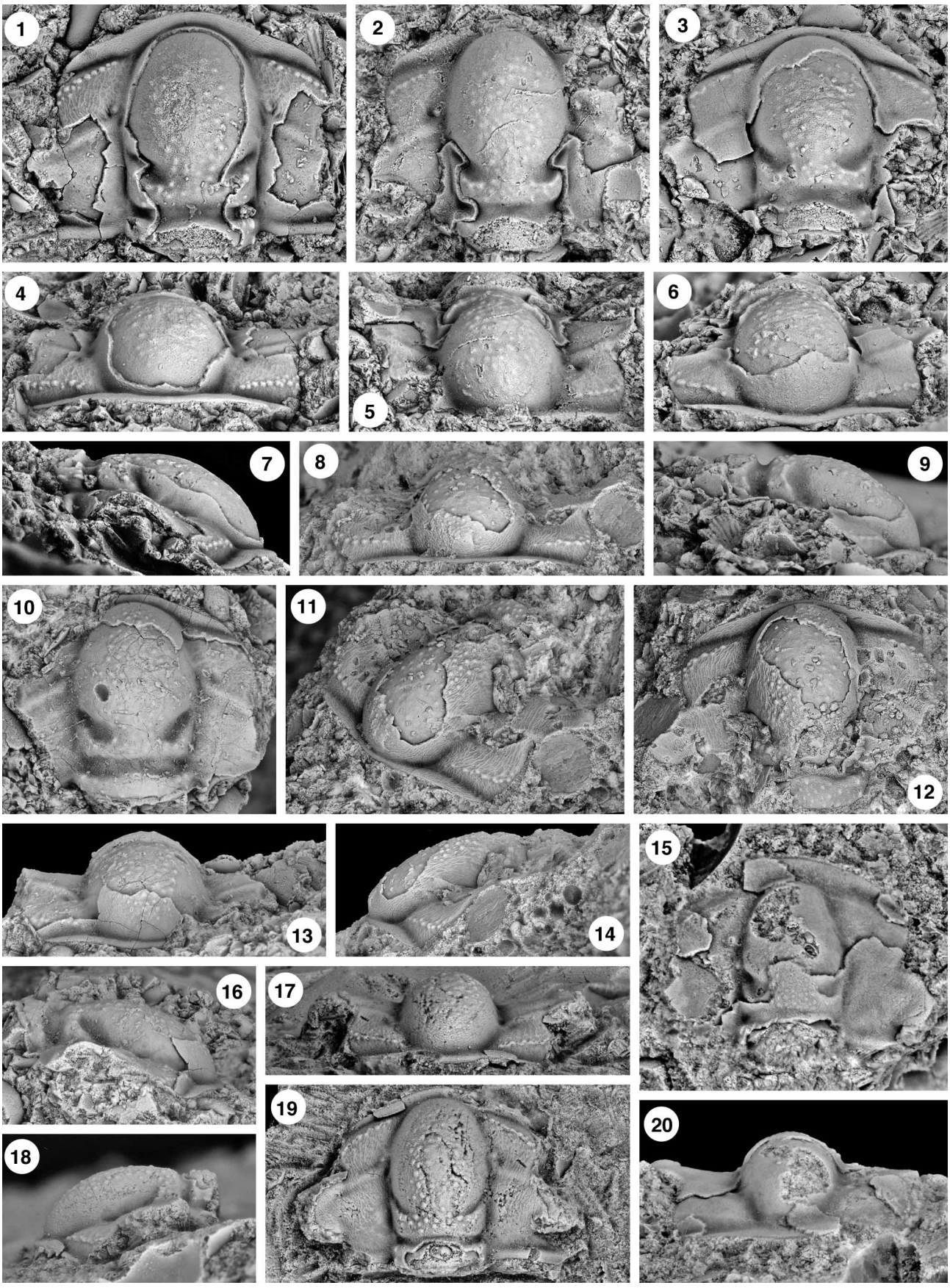

PLATE 12

Pseudoolenoides derbyi Shaw, 1974, from Section N 1 161.5 m, Carter County, and Section WSC 46.3 m, 48.1 m, and 46.3–51.5 m, West Spring Creek, Murray County, all Oil Creek Formation (Darriwilian), Oklahoma, USA.

1, 4, 7. Cranidium, **holotype**, OU 7952, dorsal, anterior, and right lateral views, x8 (WSC 48.1 m).
2, 5. Cranidium, OU 13961, dorsal and anterior views, x8 (WSC 48.1 m).
3, 6, 9. Cranidium, OU 7948, dorsal, anterior, and right lateral views, x8 (WSC 46.3 m).
8, 11, 12, 14. Cranidium, OU 7951, anterior, oblique, dorsal, and left lateral views, x6 (N 161.5 m).
10, 13, 16. Cranidium, OU 7950, dorsal, anterior, and right lateral views, x6 (WSC 46.3 m).
17–19. Cranidium, OU 38914, anterior, left lateral, and dorsal views, x10 (WSC 46.3-51.5 m).

Pseudoolenoides oilcreekensis **n. sp.**, from Section SP 1 104.5 m, Highway 77 section, Oil Creek Formation (Darriwilian), Carter County, Oklahoma, USA.

15, 20. Cranidium, OU 7944, dorsal and anterior views, x10.

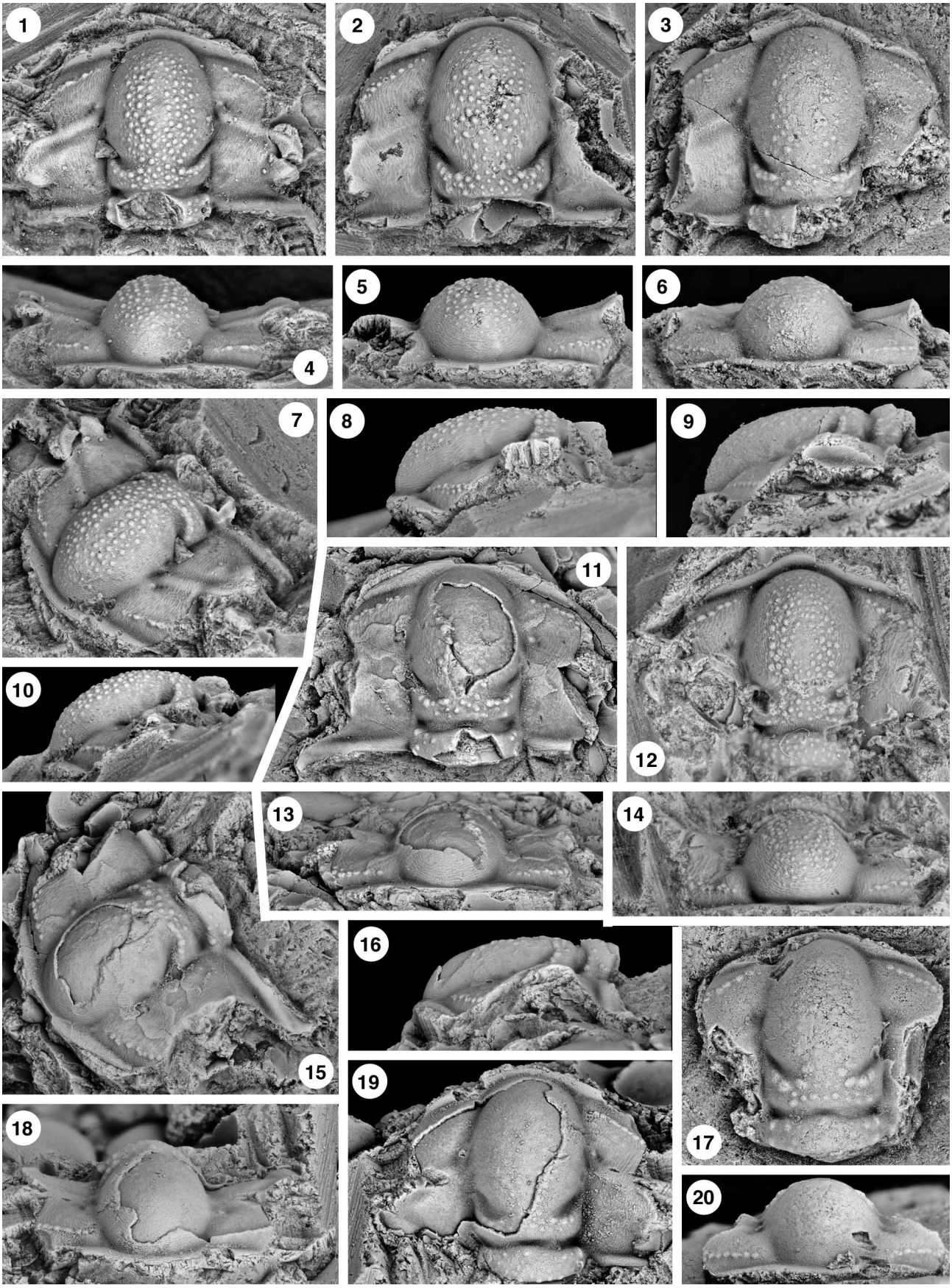

PLATE 13

Pseudoolenoides derbyi Shaw, 1974, from Section WSC 46.3–51.5 m, Oil Creek Formation (Darriwilian), West Spring Creek, Murray County, Oklahoma, USA.

1, 4, 7, 10. Cranidium, OU 38890, dorsal, anterior, oblique, and left lateral views, x8 (WSC 46.3 m).
2, 5, 8. Cranidium, OU 38920, dorsal, anterior, and left lateral views, x8 (WSC 46.3–51.5 m).
3, 6, 9. Cranidium, OU 38889, dorsal, anterior, and left lateral views, x10 (WSC 46.3 m).
11, 13, 15, 16. Cranidium, OU 38917, dorsal, anterior, oblique, and left lateral views, x8 (WSC 46.3–51.5 m).
12, 14. Cranidium, OU 38921, dorsal and anterior views, x10 (WSC 51.5 m).
17, 20. Cranidium, OU 38888, dorsal and anterior views, x10 (WSC 46.3 m).
18, 19. Cranidium, OU 38918, anterior and dorsal views, x10 (WSC 46.3–51.5 m).

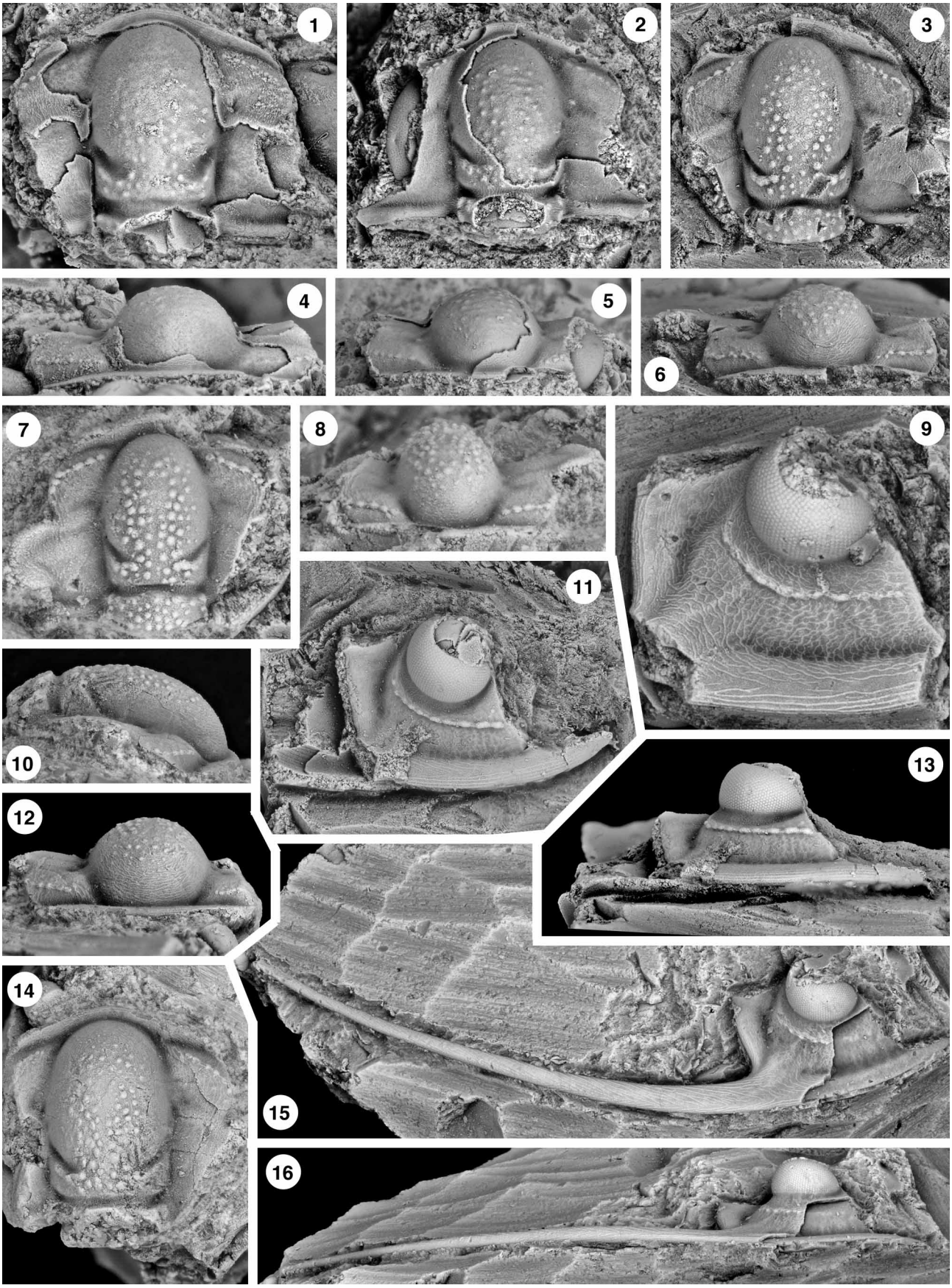

PLATE 14

Pseudoolenoides derbyi Shaw, 1974, from Section WSC 46.3–51.5 m, Oil Creek Formation (Darriwilian), West Spring Creek, Murray County, Oklahoma, USA.

1, 4. Cranidium, OU 38902, dorsal and anterior views, x8 (WSC 46.3 m).
2, 5. Cranidium, OU 38886, dorsal and anterior views, x10 (WSC 51.5 m).
3, 6. Cranidium, OU 38894, dorsal and anterior views, x11 (WSC 46.3 m).
7, 8. Cranidium, OU 38905, dorsal and anterior views, x17 (WSC 46.3 m).
9. Right librigena, OU 38881, external view, x15 (WSC 51.5 m).
10, 12, 14. Cranidium, OU 38919, right lateral, anterior, and dorsal views, x10 (WSC 46.3–51.5 m).
11, 13. Right librigena, OU 38884, external and ventrolateral views, x10 (WSC 46.3 m).
15, 16. Right librigena, OU 38885, external and ventrolateral views, x7.5 (WSC 51.5 m).

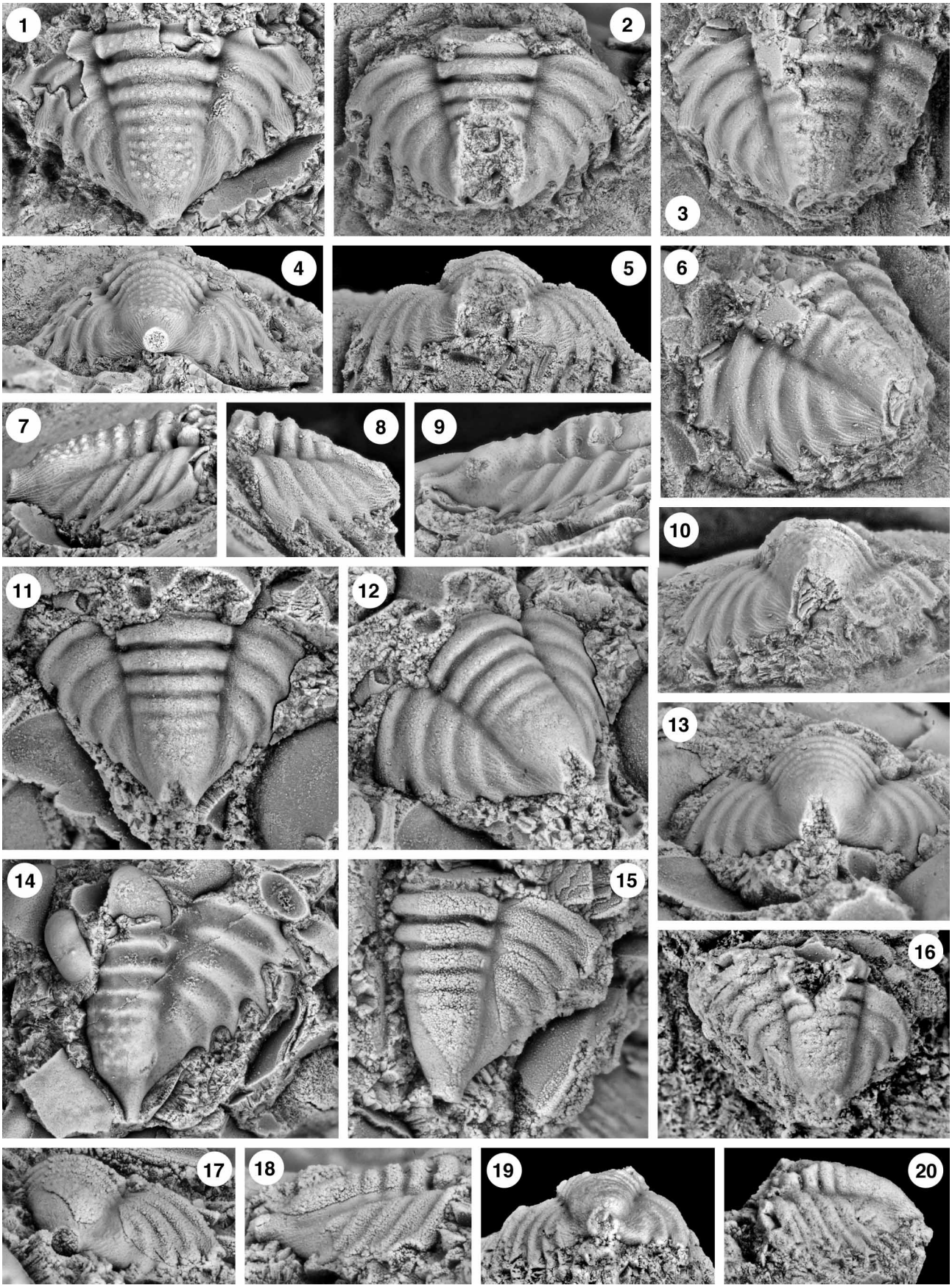

PLATE 15

Pseudoolenoides derbyi Shaw, 1974, from Section WSC 46.3–51.5 m, Oil Creek Formation (Darriwilian), West Spring Creek, Murray County, Oklahoma, USA.

1, 4, 7. Pygidium, OU 7949, dorsal, posterior, and right lateral views, x9 (WSC 48.1 m).
2, 5, 8. Pygidium, OU 38899, dorsal, posterior, and left lateral views, x13 (WSC 46.3 m).
3, 6, 10. Pygidium, OU 38897, dorsal, oblique, and posterior views, x15 (WSC 46.3 m).
9, 14. Pygidium, OU 38904, right lateral and dorsal views, x10 (WSC 46.3 m).
11–13. Pygidium, OU 38912, dorsal, oblique, and posterior views, x17 (WSC 46.3 m).
15, 17, 18. Pygidium, OU 13962, dorsal, posterior, and right lateral views, x17 (WSC 46.3 m).
18–20. Pygidium, OU 13963, dorsal, posterior, and left lateral views, x15 (WSC 46.3–51.5 m).

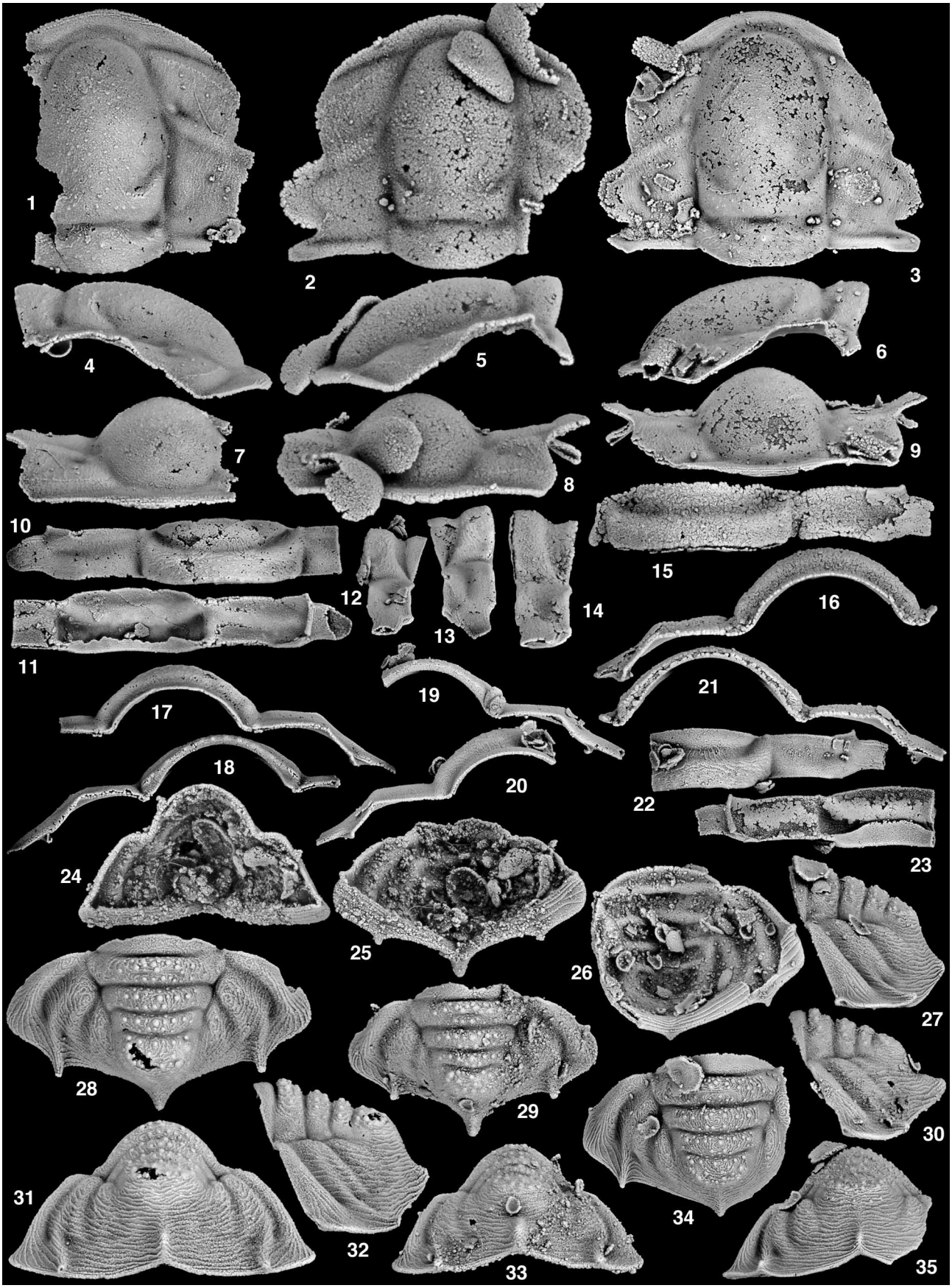

PLATE 16

Pseudoolenoides acicaudus Hintze, 1953, from Section CP 48.8 m, Kanosh Formation (Darriwilian; *Pseudoolenoides acicaudus* Zone), Crystal Peak Hills, Ibex area, Millard County, western Utah, USA.

1, 4, 7. Cranidium, SUI 130029, dorsal, right lateral, and anterior views, x15.
2, 5, 8. Cranidium, SUI 130030, dorsal, left lateral, and anterior views, x20.
3, 6, 9. Cranidium, SUI 130031, dorsal, left lateral, and anterior views, x12.
10, 11, 13, 17, 18. Thoracic segment, SUI 130032, dorsal, ventral, left lateral, anterior, and posterior views, x12.
12, 19, 20, 22, 23. Thoracic segment, SUI 130033, right lateral, posterior, anterior, dorsal, and ventral views, x10.
14–16, 21. Thoracic segment, SUI 130034, right lateral, dorsal, anterior, and posterior views, x12.

Pseudoolenoides cf. *dilectus* Hintze, 1953, from Section K-South 1.5T m, Kanosh Formation (Dapingian; *Pseudoolenoides dilectus* Zone), southern Confusion Range, Ibex area Millard County, western Utah, USA.

24, 25, 29, 30, 33. Pygidium, SUI 130027, anterior, ventral, dorsal, left lateral, and posterior views, x12.
26, 27, 34, 35. Pygidium, SUI 130026, ventral, left lateral, dorsal, and posterior views, x10.
28, 31, 32. Pygidium, SUI 130028, dorsal, posterior, and left lateral views, x15.

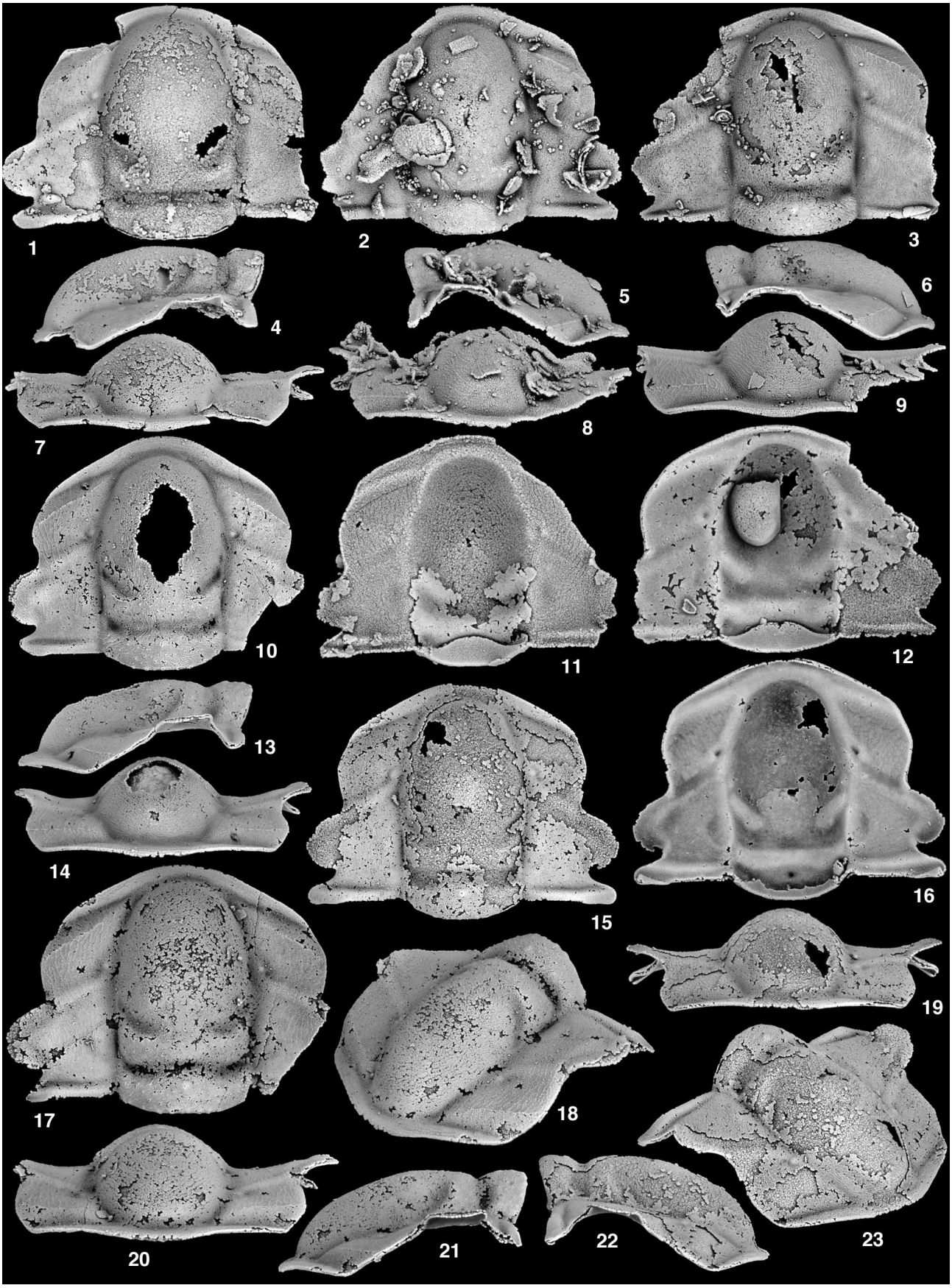

PLATE 17

Pseudoolenoides acicaudus Hintze, 1953, from Section CP 48.8 m, Kanosh Formation (Darriwilian; *Pseudoolenoides acicaudus* Zone), Crystal Peak Hills, Ibex area, Millard County, western Utah, USA.

1, 4, 7. Cranidium, SUI 130038, dorsal, left lateral, and anterior views, x9.
2, 5, 8, 11. Cranidium, SUI 130039, dorsal, right lateral, anterior, and ventral views, x9.
3, 6, 9, 12. Cranidium, SUI 130040, dorsal, right lateral, anterior, and ventral views, x10.
10, 13, 14. Cranidium, SUI 130041, dorsal, left lateral, and anterior views, x10.
15, 16, 19, 22, 23. Cranidium, SUI 130042, dorsal, ventral, anterior, right lateral, and oblique views, x10.
17, 18, 20, 21. Cranidium, SUI 130043, dorsal, oblique, anterior, and left lateral views, x12.

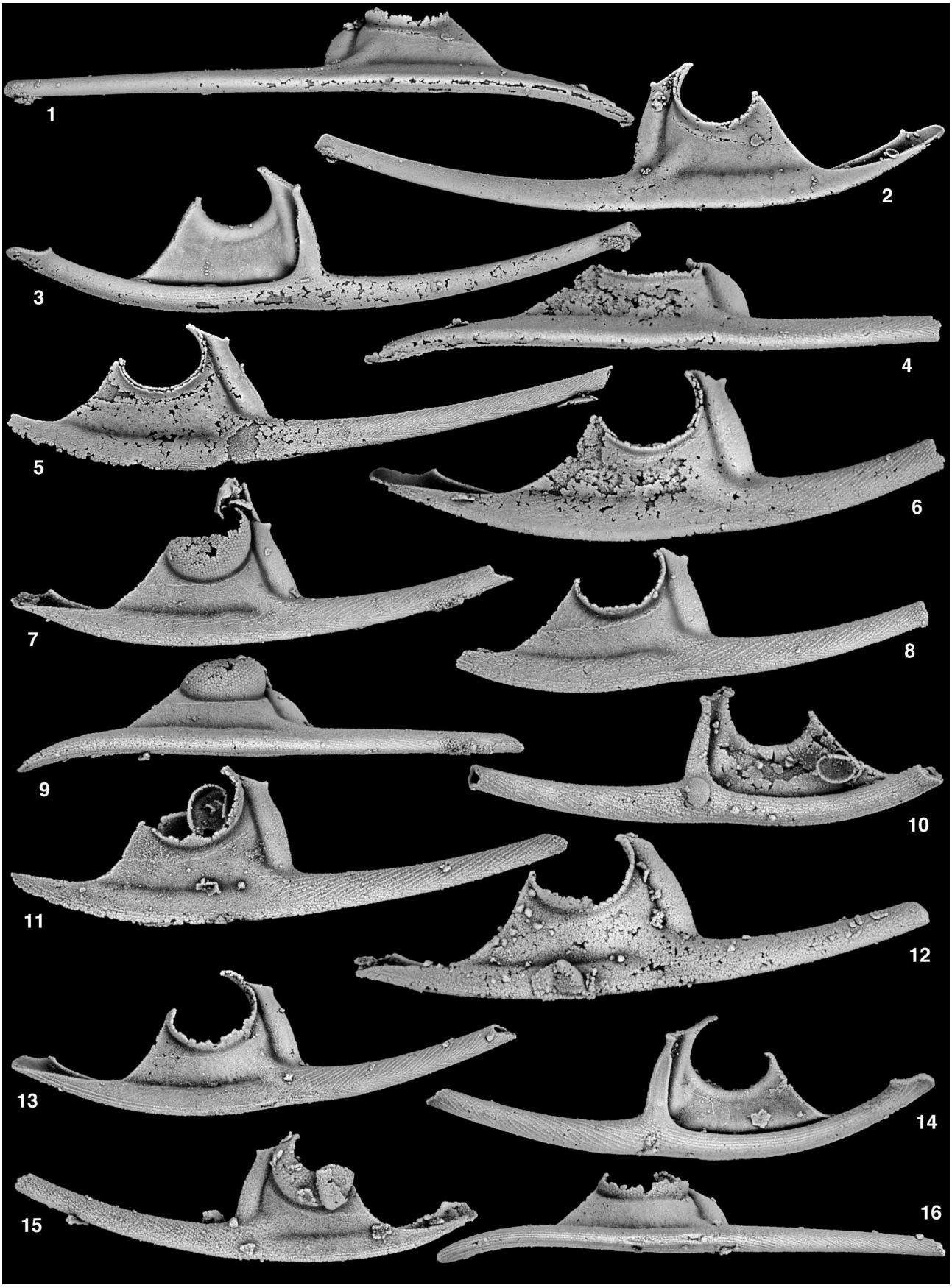

PLATE 18

Pseudoolenoides acicaudus Hintze, 1953, from Section CP 48.8 m, Kanosh Formation (Darriwilian; *Pseudoolenoides acicaudus* Zone), Crystal Peak Hills, Ibex area, Millard County, western Utah, USA.

1–3. Right librigena, SUI 130044, ventrolateral, external, and internal views, x9.
4, 6. Left librigena, SUI 130045, ventrolateral and external views, x15.
5. Left librigena, SUI 130046, external view, x10.
7, 9. Left librigena, SUI 130047, external and ventrolateral views, x12.
8, 10. Left librigena, SUI 130048, external and internal views, x15.
11. Left librigena, SUI 130049, external view, x15.
12. Left librigena, SUI 130050, external view, x15.
13, 14, 16. Left librigena, SUI 130051, external, internal, and ventrolateral views, x15.
15. Right librigena, SUI 130052, external view, x15.

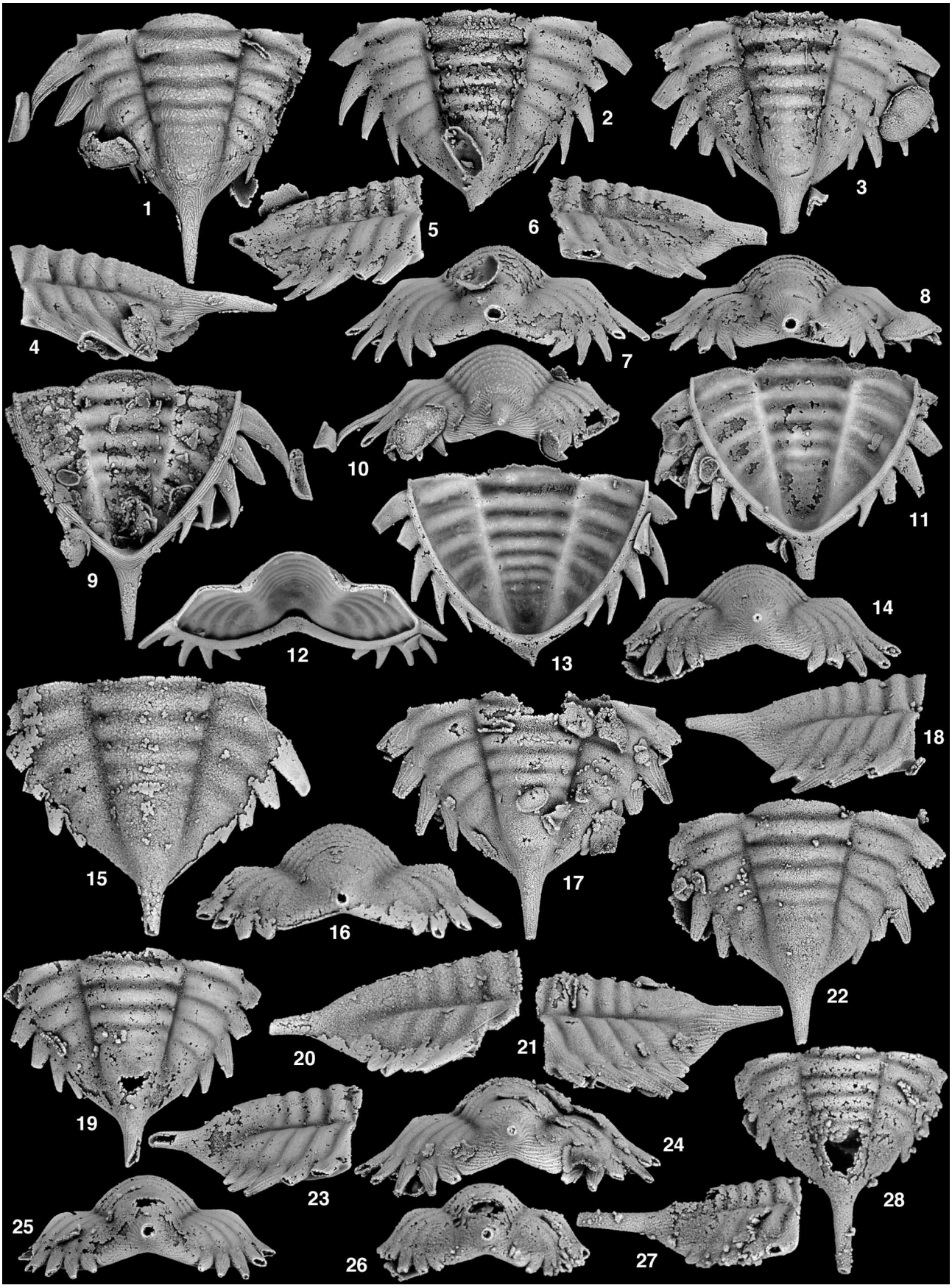

PLATE 19

Pseudoolenoides acicaudus Hintze, 1953, from Section CP 48.8 m, Kanosh Formation (Darriwilian; *Pseudoolenoides acicaudus* Zone), Crystal Peak Hills, Ibex area, Millard County, western Utah, USA.

1, 4, 9, 10. Pygidium, SUI 130053, dorsal, left lateral, ventral, and posterior views, x9.
2, 5, 7, 12, 13. Pygidium, SUI 130054, dorsal, right lateral, posterior, anterior, and ventral views, x9.
3, 6, 8, 11. Pygidium, SUI 130055, dorsal, left lateral, posterior, and ventral views, x9.
14, 18, 22. Pygidium, SUI 130056, posterior, right lateral, and dorsal views, x12.
15, 16, 20. Pygidium, SUI 130057, dorsal, posterior, and right lateral views, x12.
17, 21, 24. Pygidium, SUI 130058, dorsal, left lateral, and posterior views, x12.
19, 23, 25. Pygidium, SUI 130059, dorsal, right lateral, and posterior views, x12.
26–28. Pygidium, SUI 130060, posterior, right lateral, and dorsal views, x15.

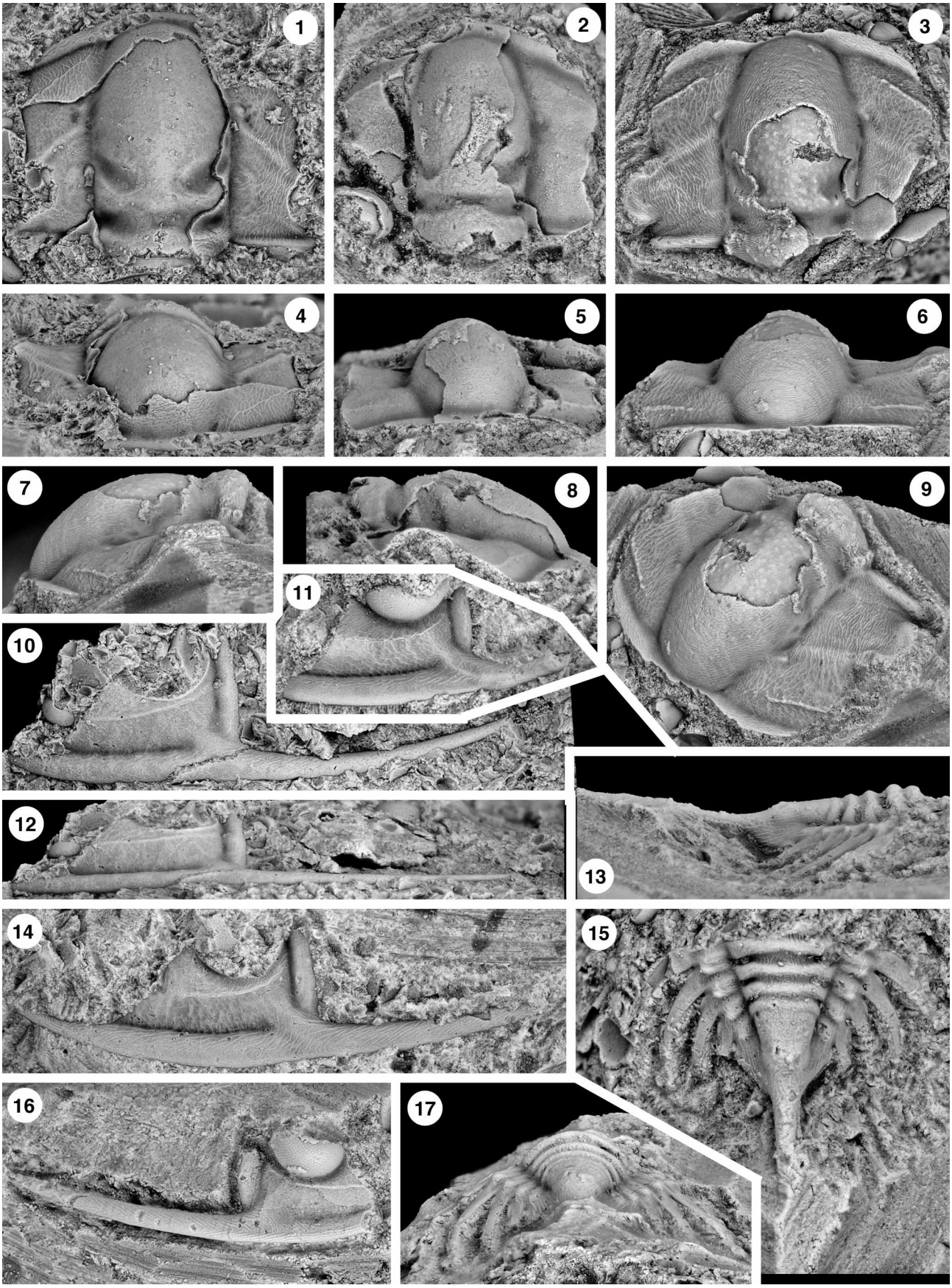

PLATE 20

Pseudoolenoides oilcreekensis **n. sp.**, from Section SP 1 104.5 m and 126.8 m, Highway 77 section, Oil Creek Formation (Darriwilian), Carter County, Oklahoma, USA.

1, 4. Cranidium, **holotype**, OU 7939, dorsal and anterior views, x8 (126.8 m).
2, 5, 8. Cranidium, OU 7940, dorsal, anterior, and right lateral views, x9 (104.5 m).
3, 6, 7, 9. Cranidium, OU 7943, dorsal, anterior, left lateral, and oblique views, x7.5 (104.5 m).
10, 12. Left librigena, OU 7941, external and ventrolateral views, x10 (126.8 m).
11. Left librigena, OU 7946, external view, x12 (126.8 m).
13, 15, 17. Pygidium, OU 7942, right lateral, dorsal, and posterior views, x12 (126.8 m).
14. Left librigena, OU 7947, external view, x10 (126.8 m).
16. Right librigena, OU 7945, external view, x12 (104.5 m).

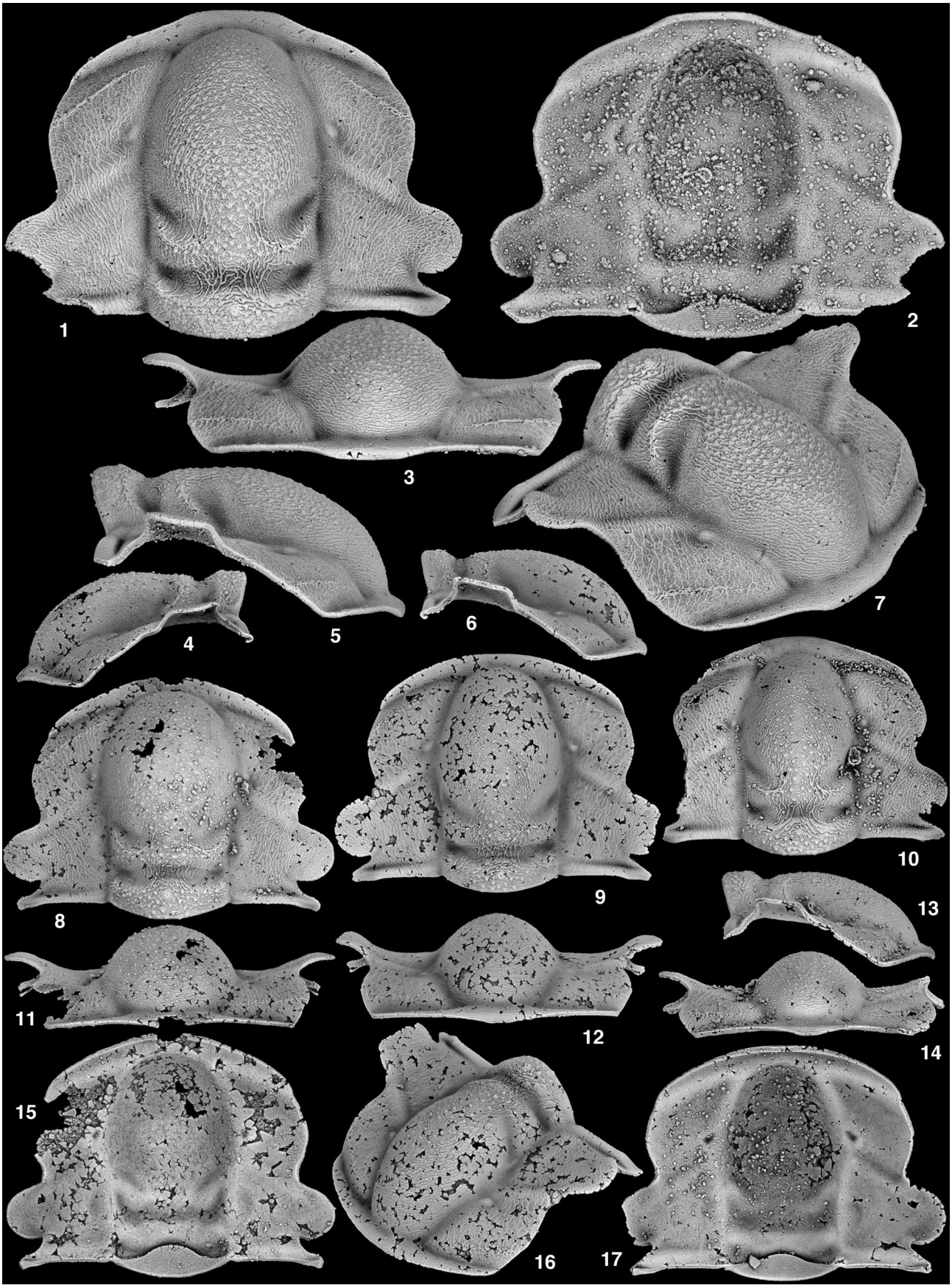

PLATE 21

Pseudoolenoides fossilmountainensis **n. sp.**, from Section K-South 152.4T m and 159.7T m, Kanosh Formation (Darriwilian; *Pseudoolenoides fossilmountainensis* Zone), southern Confusion Range, Ibex area Millard County, western Utah, USA.

1-3, 5, 7. Cranidium, **holotype**, SUI 130061, dorsal, ventral, anterior, right lateral, and oblique views, x9 (K-South 152.4T m).
4, 8, 11, 15. Cranidium, SUI 130062, left lateral, dorsal, anterior, and ventral views, x8 (K-South 152.4T m).
6, 9, 12, 16, 17. Cranidium, SUI 130063, right lateral, dorsal, anterior, oblique, and ventral views, x9 (K-South 159.7T m).
10, 13, 14. Cranidium, SUI 130064, dorsal, right lateral, and anterior views, x8 (K-South 152.4T m).

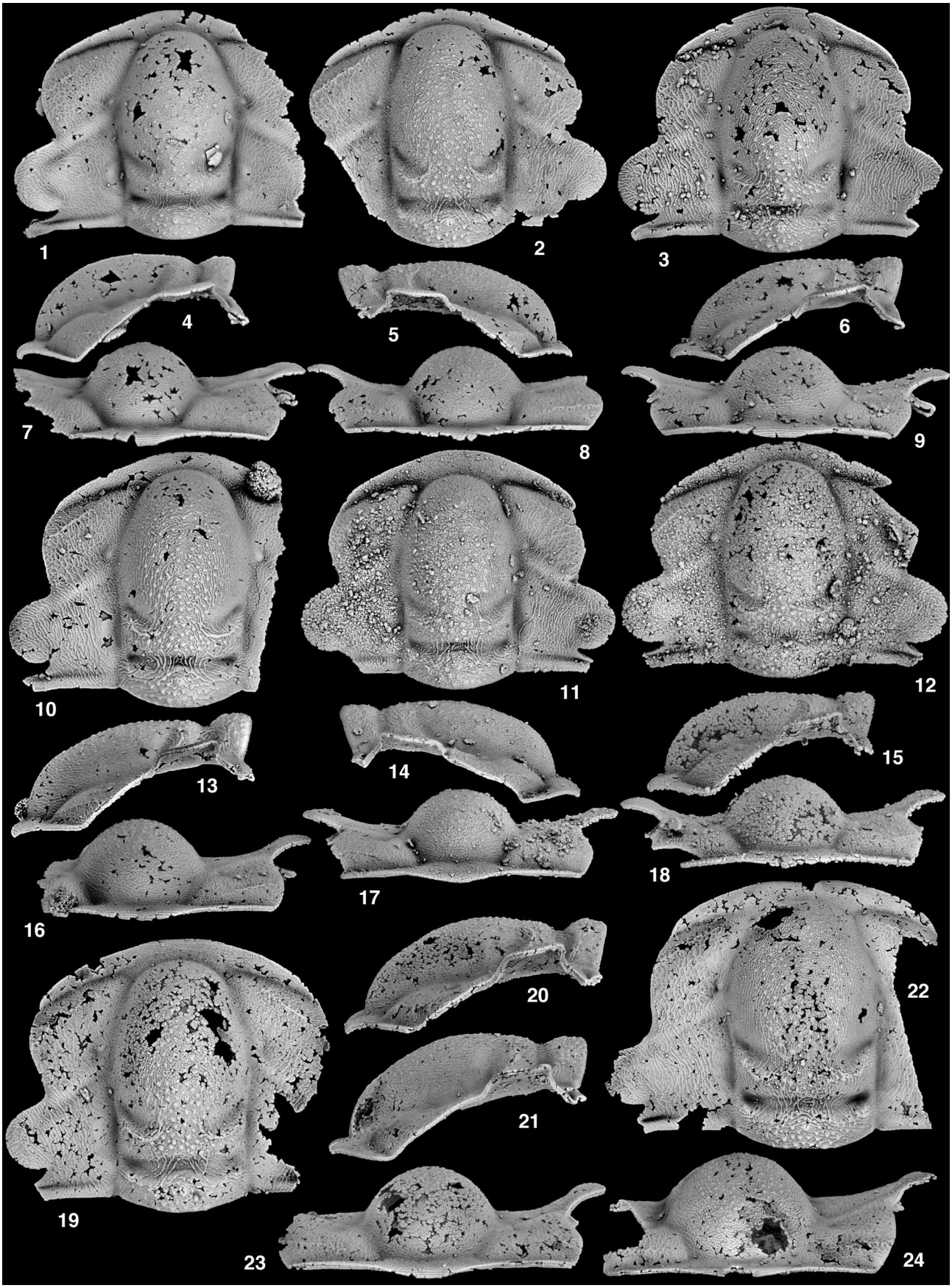

PLATE 22

Pseudoolenoides fossilmountainensis **n. sp.**, from Section K-South 152.4T m, Kanosh Formation (Darriwilian; *Pseudoolenoides fossilmountainensis* Zone), southern Confusion Range, Ibex area Millard County, western Utah, USA.

1, 4, 7. Cranidium, SUI 130065, dorsal, left lateral, and anterior views, x13.
2, 5, 8. Cranidium, SUI 130066, dorsal, right lateral, and anterior views, x10.
3, 6, 9. Cranidium, SUI 130067, dorsal, left lateral, and anterior views, x13.
10, 13, 16. Cranidium, SUI 130068, dorsal, left lateral, and anterior views, x12.
11, 14, 17. Cranidium, SUI 130069, dorsal, right lateral, and anterior views, x12.
12, 15, 18. Cranidium, SUI 130070, dorsal, left lateral, and anterior views, x12.
19, 20, 23. Cranidium, SUI 130071, dorsal, left lateral, and anterior views, x11.
21, 22, 24. Cranidium, SUI 130072, left lateral, dorsal, and anterior views, x8.

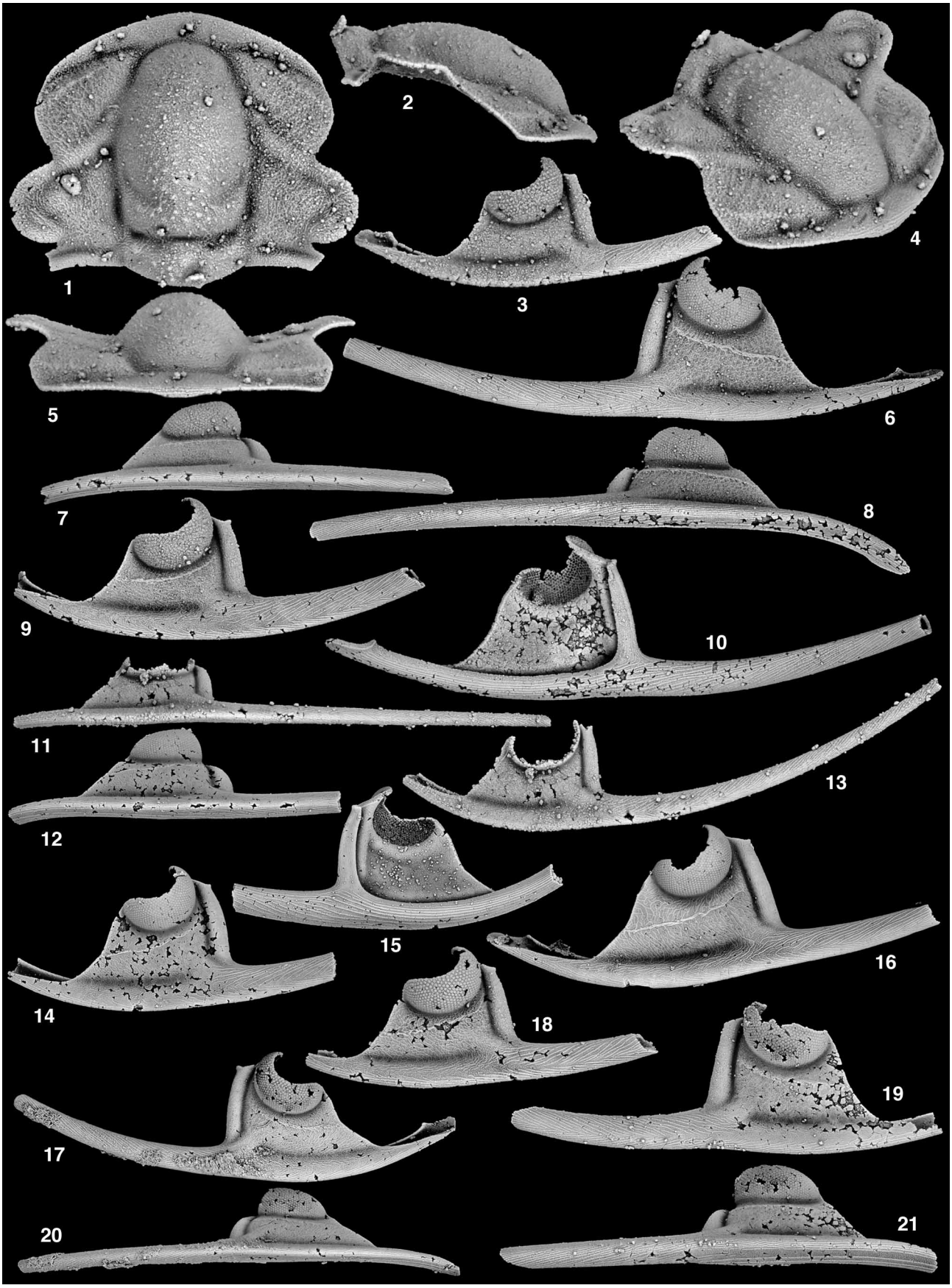

PLATE 23

Pseudoolenoides fossilmountainensis **n. sp.**, from Section K-South 152.4T m and 159.7T m, Kanosh Formation (Darriwilian; *Pseudoolenoides fossilmountainensis* Zone), southern Confusion Range, Ibex area Millard County, western Utah, USA.

1, 2, 4, 5. Cranidium, SUI 130073, dorsal, right lateral, oblique, and anterior views, x20 (K-South 159.7T m).
3. Left librigena, SUI 130074, external view, x15 (K-South 152.4T m).
6, 8, 10. Right librigena, SUI 130075, external, ventrolateral, and internal views, x9 (K-South 152.4T m).
7, 9. Left librigena, SUI 130076, ventrolateral and external views, x12 (K-South 152.4T m).
11, 13. Left librigena, SUI 130077, ventrolateral and external views, x12 (K-South 152.4T m).
12, 14, 15. Left librigena, SUI 130078, ventrolateral, external, and internal views, x8 (K-South 159.7T m).
16. Left librigena, SUI 130079, external view, x7.5 (K-South 152.4T m).
17, 20. Right librigena, SUI 130080, external and ventrolateral views, x9 (K-South 152.4T m).
18. Left librigena, SUI 130081, external view, x12 (K-South 152.4T m).
19, 21. Right librigena, SUI 130082, external and ventrolateral views, x9 (K-South 159.7 m).

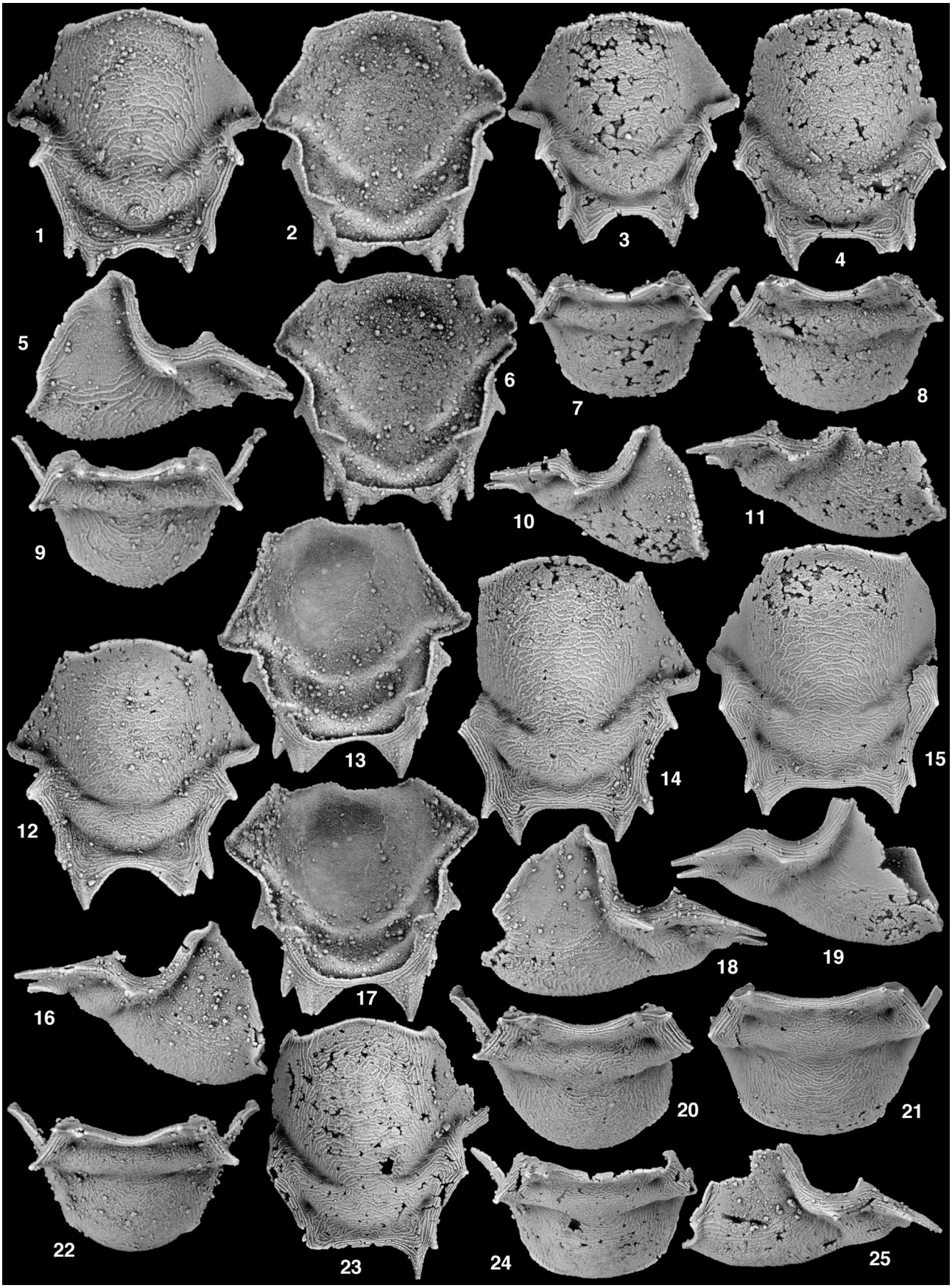

PLATE 24

Pseudoolenoides fossilmountainensis **n. sp.**, from Section K-South 152.4T m and 159.7T m, Kanosh Formation (Darriwilian; *Pseudoolenoides fossilmountainensis* Zone), southern Confusion Range, Ibex area Millard County, western Utah, USA.

1, 2, 5, 6, 9. Hypostome, SUI 130083, ventral, dorsal, left lateral, doublural, and posterior views, x20 (K-South 159.7T m).
2, 7, 10. Hypostome, SUI 130084, ventral, posterior, and right lateral views, x17 (K-South 159.7T m).
4, 8, 11. Hypostome, SUI 130085, ventral, posterior, and right lateral views, x17 (K-South 159.7T m).
12, 13, 16, 17, 22. Hypostome, SUI 130086, ventral, dorsal, right lateral, doublural, and posterior views, x17 (K-South 159.7T m).
14, 18, 20. Hypostome, SUI 130087, ventral, left lateral, and posterior views, x15 (K-South 159.7T m).
15, 19, 21. Hypostome, SUI 130088, ventral, right lateral, and posterior views, x12 (K-South 159.7T m).
23–25. Hypostome, SUI 130089, ventral, posterior, and left lateral views, x12 (K-South 152.4T m).

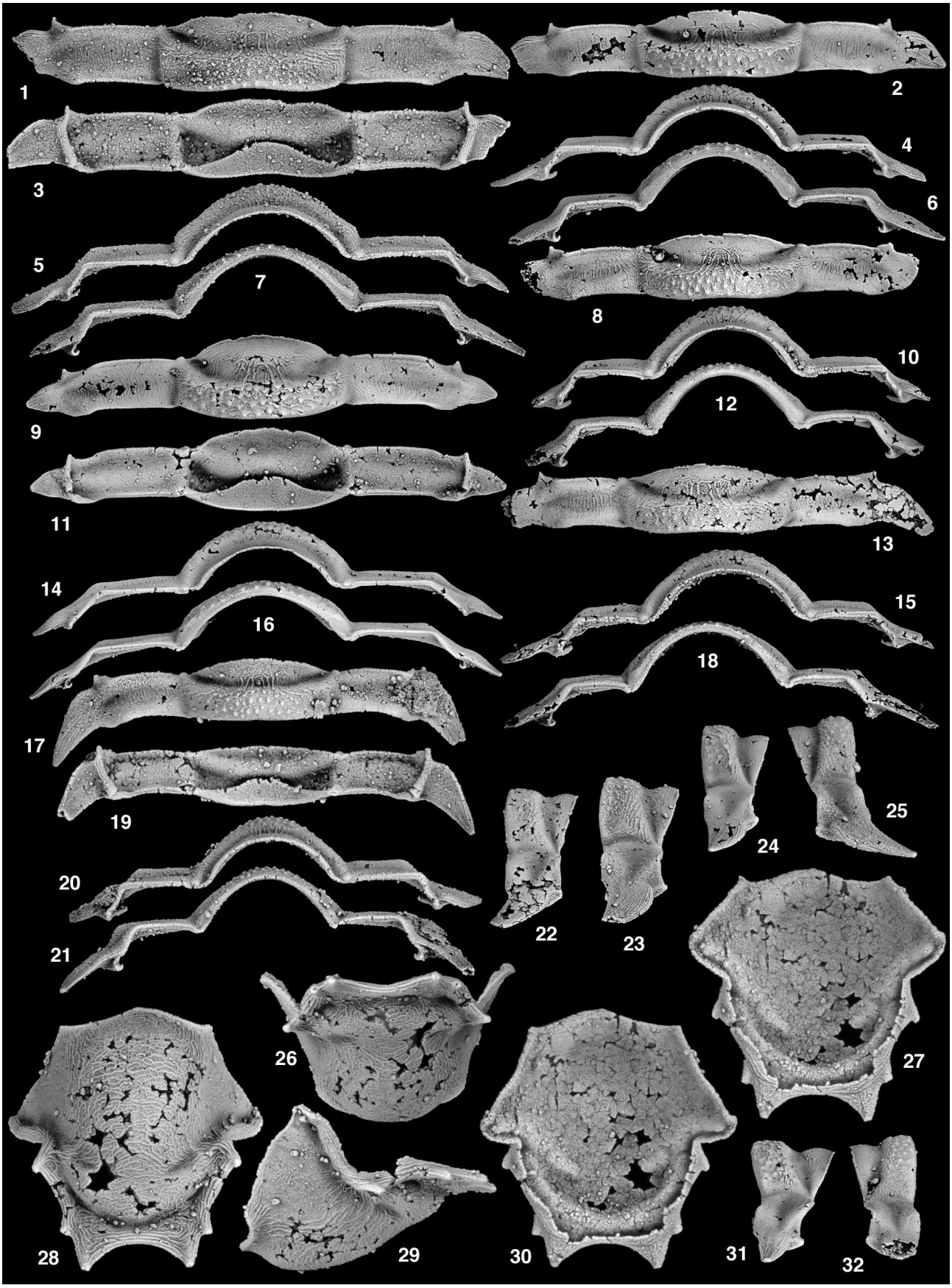

PLATE 25

Pseudoolenoides fossilmountainensis **n. sp.**, from Section K-South 152.4T m and 159.7T m, Kanosh Formation (Darriwilian; *Pseudoolenoides fossilmountainensis* Zone), southern Confusion Range, Ibex area Millard County, western Utah, USA.

1, 3, 5, 7, 23. Thoracic segment, SUI 130090, dorsal, ventral, anterior, posterior, and right lateral views, x12 (K-South 159.7T m).
2, 4, 6, 24. Thoracic segment, SUI 130091, dorsal, anterior, posterior, and right lateral views, x12 (K-South 159.7T m).
8, 10, 12, 32. Thoracic segment, SUI 130092, dorsal, anterior, posterior, and left lateral views, x10 (K-South 152.4T m).
9, 11, 14, 16, 31. Thoracic segment, SUI 130093, dorsal, ventral, anterior, posterior, and right lateral views, x12 (K-South 152.4T m).
13, 15, 18, 22. Thoracic segment, SUI 130094, dorsal, anterior, posterior, and right lateral views, x10 (K-South 152.4T m).
17, 19, 20, 21, 25. Thoracic segment, SUI 130095, dorsal, ventral, anterior, posterior, and left lateral views, x15 (K-South 152.4T m).
26–30. Hypostome, SUI 130096, posterior, doublural, ventral, left lateral, and dorsal views, x17 (K-South 152.4T m).

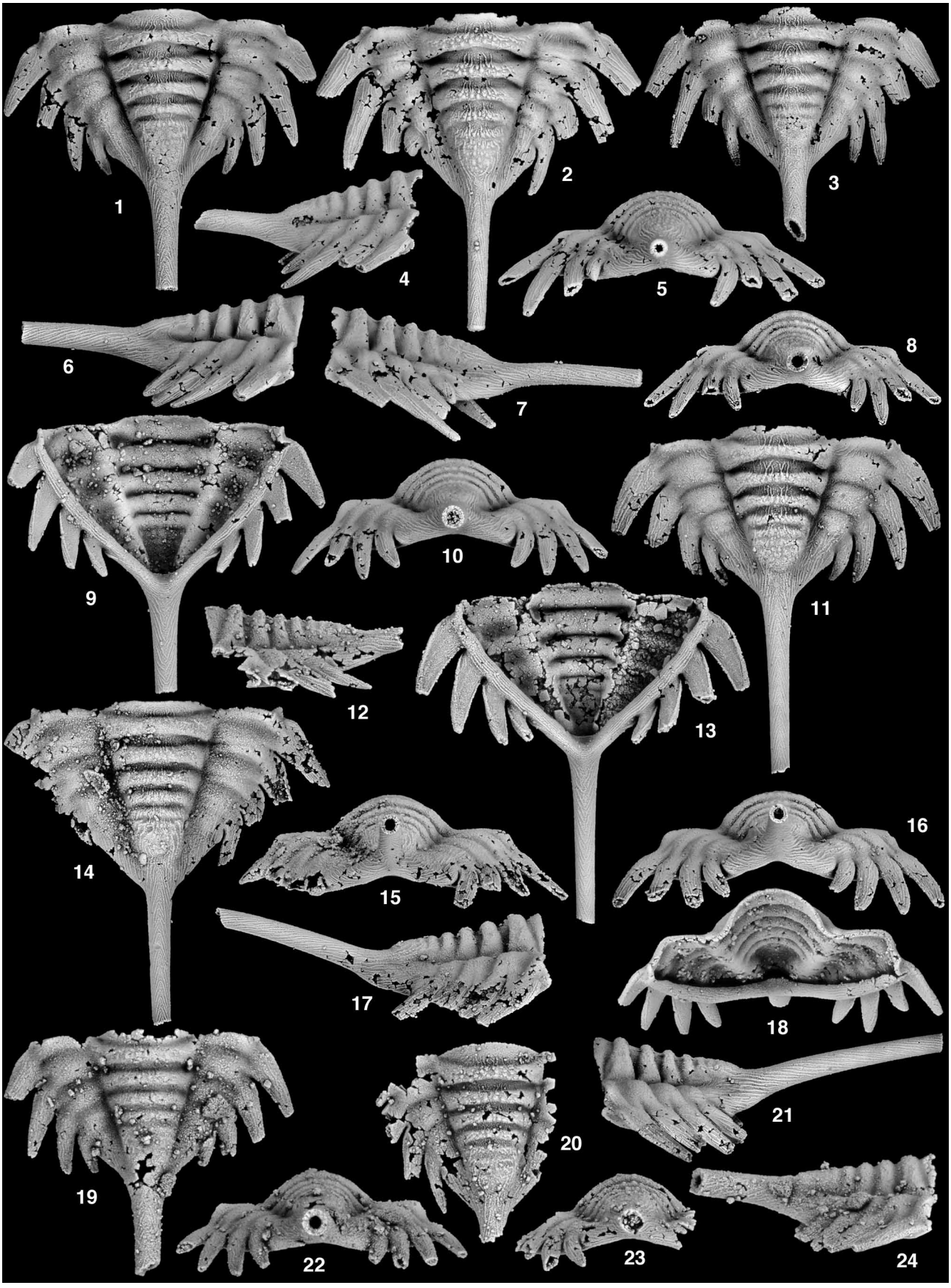

PLATE 26

Pseudoolenoides fossilmountainensis **n. sp.**, from Section K-South 152.4T m and 159.7T m, Kanosh Formation (Darriwilian; *Pseudoolenoides fossilmountainensis* Zone), southern Confusion Range, Ibex area Millard County, western Utah, USA.

1, 6, 9, 10. Pygidium, SUI 130097, dorsal, right lateral, ventral, and posterior views, x11 (K-South 152.4T m).
2, 5, 7. Pygidium, SUI 130098, dorsal, posterior, and left lateral views, x11 (K-South 152.4T m).
3, 4, 8. Pygidium, SUI 130099, dorsal, right lateral, and posterior views, x11 (K-South 152.4T m).
11, 13, 16, 18, 21. Pygidium, SUI 130100, dorsal, ventral, posterior, anterior, and left lateral views, x11 (K-South 152.4T m).
12, 20, 23. Pygidium, SUI 130101, left lateral, dorsal, and posterior views, x15 (K-South 159.7T m).
14, 15, 17. Pygidium, SUI 130102, dorsal, posterior, and right lateral views, x10 (K-South 152.4T m).
19, 22, 24. Pygidium, SUI 130103, dorsal, posterior, and right lateral views, x17 (K-South 152.4T m).

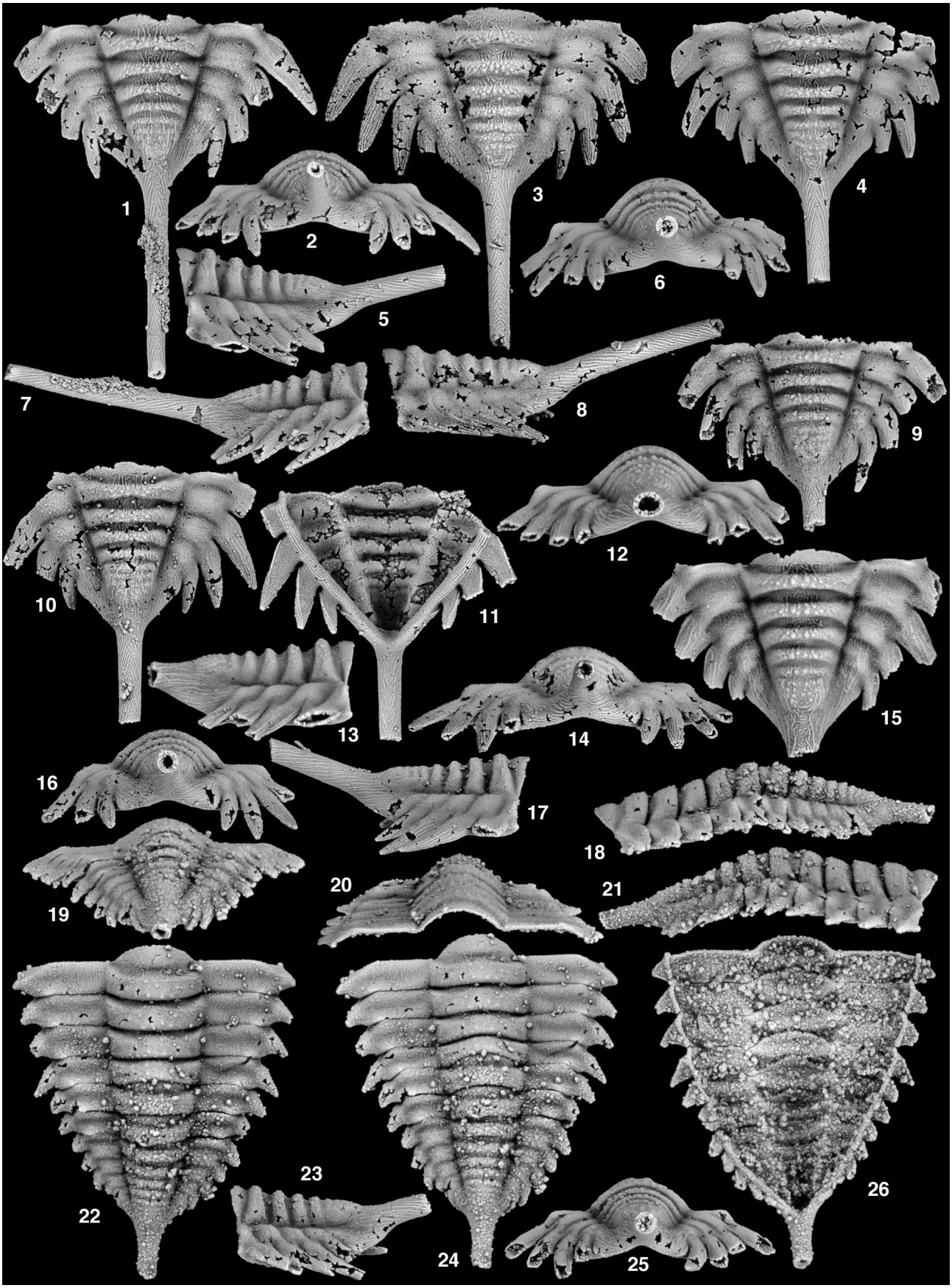

PLATE 27

Pseudoolenoides fossilmountainensis **n. sp.**, from Section K-South 152.4T m and 159.7T m, Kanosh Formation (Darriwilian; *Pseudoolenoides fossilmountainensis* Zone), southern Confusion Range, Ibex area Millard County, western Utah, USA.

1, 2, 7. Pygidium, SUI 130104, dorsal, posterior, and right lateral views, x13 (K-South 152.4T m).
3, 8, 14. Pygidium, SUI 130105, dorsal, left lateral, and posterior views, x13 (K-South 152.4T m).
4-6. Pygidium, SUI 130106, dorsal, left lateral, and posterior views, x13 (K-South 152.4T m).
9, 23, 25. Pygidium, SUI 130107, dorsal, left lateral, and posterior views, x15 (K-South 159.7T m).
10, 11, 16, 17. Pygidium, SUI 130108, dorsal, ventral, posterior, and right lateral views, x12 (K-South 159.7T m).
12, 13, 15. Pygidium, SUI 130109, posterior, right lateral, and dorsal views, x20 (K-South 159.7T m).
18-22, 24, 26. Thoracopygidium, SUI 130110, left lateral, posterior, anterior, right lateral, dorsal thoracic, dorsal pygidial, and ventral views, x20 (K-South 159.7T m).

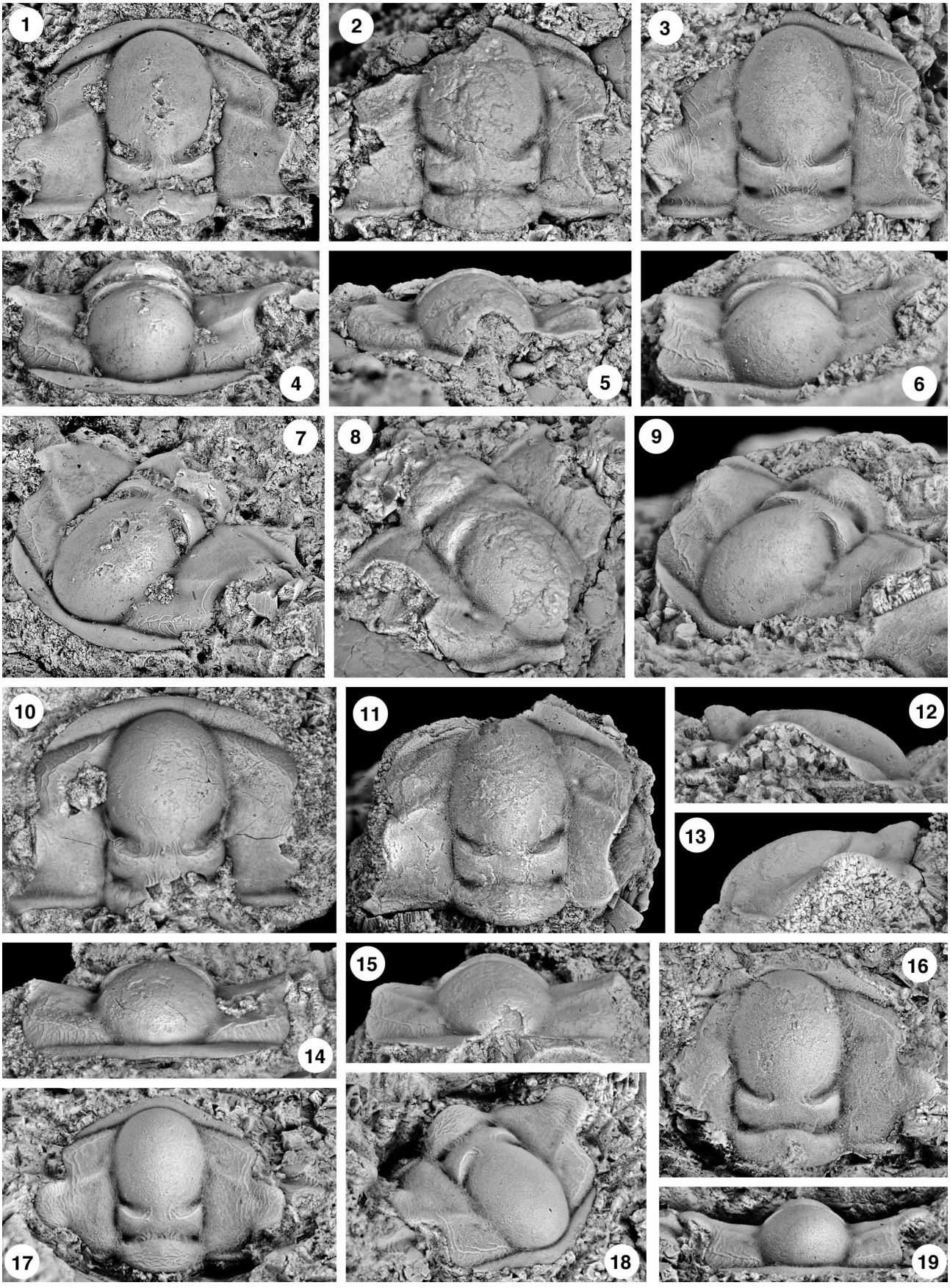

PLATE 28

Pseudoolenoides carterensis Shaw, 1974, from Section SP 1 175.6 m, Highway 77 section, Section AW 1 approximately 122 m, north end of Criner Hills, and Section N 1 161.5 m, Carter County, and Section WSC 107.6 m, West Spring Creek, Murray County, all Oil Creek Formation (Darriwilian), Oklahoma, USA.

1, 4, 7. Cranidium, OU 7929, dorsal, anterior, and oblique views, x7.5 (N 1 161.5 m)
2, 5, 8. Cranidium, OU 7935, dorsal, anterior, and oblique views, x7.5 (AW 1 approx. 122 m).
3, 6, 9, 12. Cranidium, **holotype**, OU 7932, dorsal, anterior, oblique, and right lateral views, x15 (SP 1 175.6 m).
10, 14. Cranidium, OU 30139, dorsal and anterior views, x9 (SP 1 175.6 m).
11, 13, 15. Cranidium, OU 38930, dorsal, left lateral, and anterior views, x10 (WSC 107.6 m).
16. Cranidium, OU 38926, dorsal view, x12 (WSC 107.6 m).
17–19. Cranidium, OU 38927, dorsal, oblique, and anterior views, x12 (WSC 107.6 m).

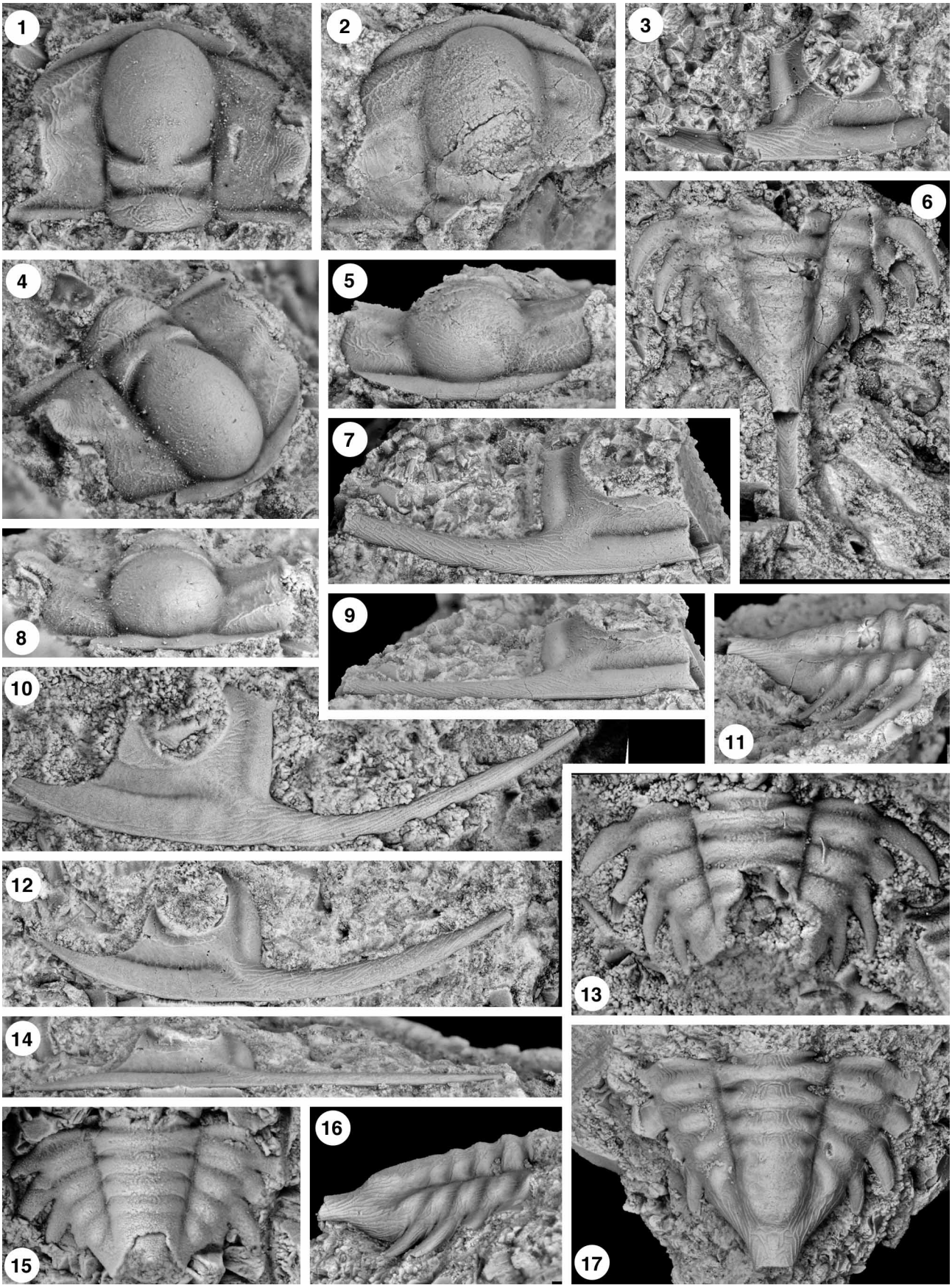

PLATE 29

Pseudoolenoides carterensis Shaw, 1974, from Section SP 1 175.6 m, Highway 77 section, and Section N 1 161.5 m, Carter County, and Section WSC 107.6 m, West Spring Creek, Murray County, all Oil Creek Formation (Darriwilian), Oklahoma, USA.

1, 4, 8. Cranidium, OU 30128, dorsal, oblique, and anterior views, x15 (SP 1 175.6 m).
2, 5. Cranidium, OU 30124, dorsal and anterior views, x12 (SP 1 175.6 m).
3. Right librigena, OU 30123, external view, x12 (SP 1 175.6 m).
6, 11. Pygidium, OU 30122, dorsal and right lateral views, x9 (SP 1 175.6 m).
7, 9. Right librigena, OU 7934, external and ventrolateral views, x12 (SP 1 175.6 m).
10. Left librigena, OU 7933, external view, x12 (N 1 161.5 m).
12, 14. Left librigena, OU 7938, external and ventrolateral views, x12 (SP 1 175.6 m).
13. Pygidium, OU 7937, dorsal view, x15 (SP 1 175.6 m).
15. Pygidium, OU 38928, dorsal view, x15 (WSC 107.6 m).
16, 17. Pygidium, OU 30125, right lateral and dorsal views, x10 (SP 1 175.6 m).

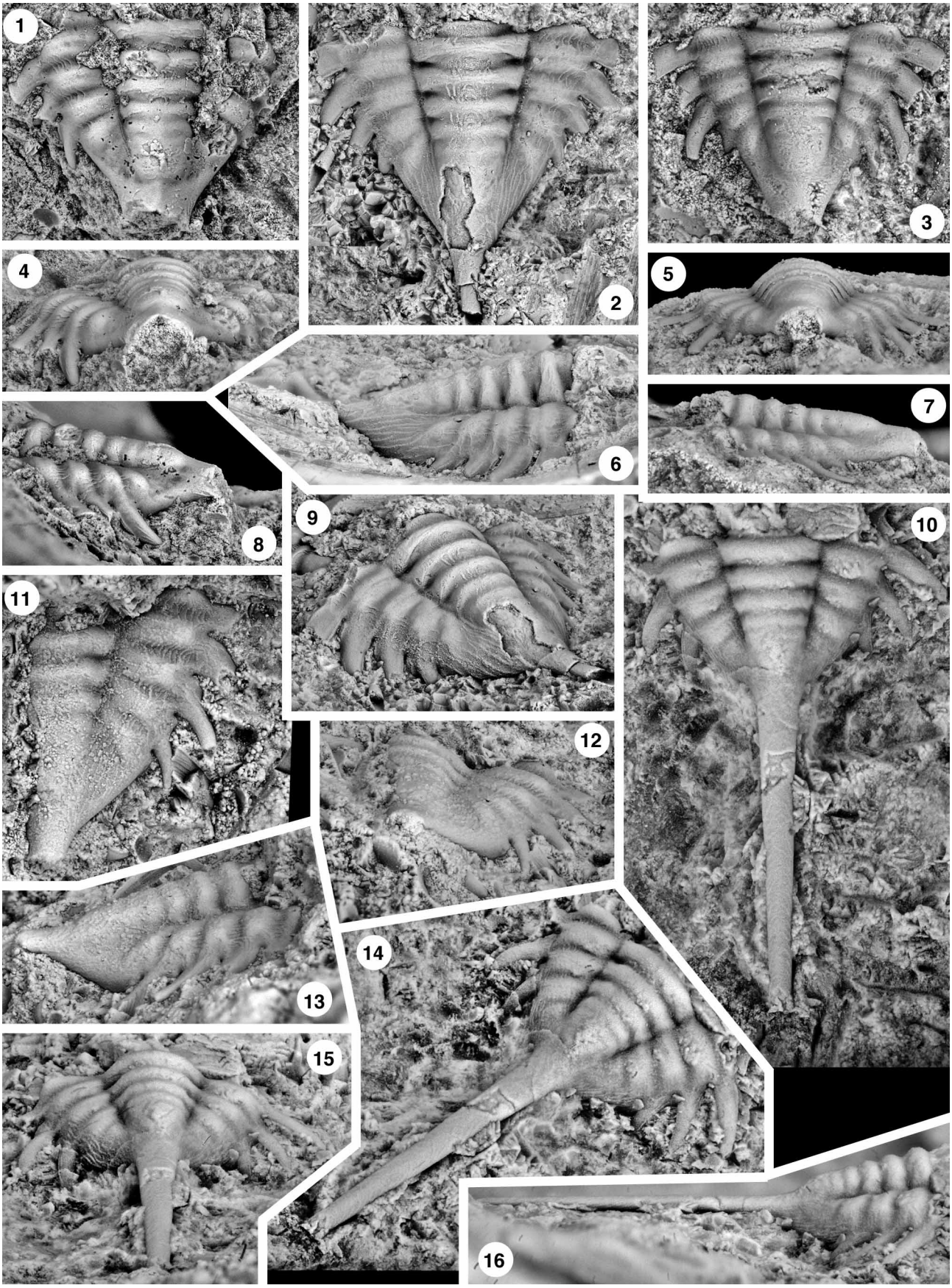

PLATE 30

Pseudoolenoides carterensis Shaw, 1974, from Section SP 1 171.0 and 175.6 m, Highway 77 section, and Section N 1 161.5 m, Carter County, and Section WSC 107.6 m, West Spring Creek, Murray County, all Oil Creek Formation (Darriwilian), Oklahoma, USA.

1, 4, 8. Pygidium, OU 7927, dorsal, posterior, and left lateral views, x10 (N 1 161.5 m).
2, 6, 9. Pygidium, OU 7928, dorsal, right lateral, and oblique views, x9 (SP 1 175.6 m).
3, 5, 7. Pygidium, OU 7931, dorsal, posterior, and left lateral views, x15 (SP 1 171.0 m).
10, 14–16. Pygidium, OU 7936, dorsal, oblique, posterior, and right lateral views, x15 (SP 1 175.6 m).
11–13. Pygidium, OU 7930, dorsal, posterior, and right lateral views, x10 (SP 1 175.6 m).