Zootaxa 3293: 1–67 (2012)
www.mapress.com/zootaxa/

Monograph

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

ZOOTAXA

3293

The Lower Ordovician (upper Floian) bathyurid trilobite *Aponileus* Hu, with species from Utah, Texas, and Greenland

JONATHAN M. ADRAIN & NEO E. B. McADAMS
Department of Geoscience, 121 Trowbridge Hall, University of Iowa, Iowa City, Iowa 52242, USA; jonathan-adrain@uiowa.edu

Magnolia Press
Auckland, New Zealand

Accepted by G. Edgecombe: 29 Dec. 2011; published: 30 Apr. 2012

JONATHAN M. ADRAIN & NEO E. B. McADAMS

The Lower Ordovician (upper Floian) bathyurid trilobite *Aponileus* Hu, with species from Utah, Texas, and Greenland

(*Zootaxa* 3293)

67 pp.; 30 cm.

30 Apr. 2012

ISBN 978-1-86977-883-5 (paperback)

ISBN 978-1-86977-884-2 (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 previously monotypic bathyurid trilobite *Aponileus* Hu, 1963, was known only from poorly preserved material of its type species, *A. latus*, and was interpreted as a junior subjective synonym of *Psephosthenaspis* Whittington. New species from the upper Floian (Blackhillsian) Fillmore Formation of western Utah belong to *Aponileus* and help demonstrate that the genus is an entirely Lower Ordovician (upper Floian) clade phylogenetically separate from the Middle Ordovician (Dapingian) *Psephosthenaspis*. Species of either group have broadly similar morphology, but the species of *Psephosthenaspis* which most closely resembles those of *Aponileus* is the youngest and most derived member, and the similarities are convergent. *Psephosthenaspis* roots among a group of heavily tuberculate, mostly undescribed, upper Floian species, one of which is briefly illustrated for comparison. The species most resembling some species of *Aponileus*, *P. glabrior*, is illustrated on the basis of new silicified material which extends its range from the upper Juab Formation into the base of the Kanosh Formation. New Blackhillsian species are *A. laikaae* (Fillmore Formation; *Presbynileus ibexensis* Zone), *A. aasei* (Fillmore Formation; probably *Pseudocybele paranasuta* Zone), *A. belkaae*, *A. strelkaae*, and *A. ugolekae* (all Wah Wah Formation; "*Pseudocybele nasuta* Zone"). *Aponileus*? *veterokae* n. sp., from high in the *"Pseudocybele nasuta* Zone" of the Wah Wah Formation, is tentatively assigned. *Bolbocephalus glaber* Poulsen, 1927, from the Nunatami Formation of northwest Greenland, is poorly known but is also a member of *Aponileus*, and is similar in morphology to *A. latus* and *A. aasei*; it is revised on the basis of reillustrated type material. Phylogenetic analysis indicates that *A. laikaae* is the basal species, followed by a sister pair of *A. belkaae* and *A. strelkaae*. These are sister to a pair of subclades, the sister pair of *A. ugolekae* and *A.*? *veterokae*, and an effaced group lacking genal spines including *A. aasei*, *A. latus*, and *A. glaber*.

Key words: Silicified, Utah, Texas, Greenland, taxonomy, cladistics

Introduction

Hu (1963) published a short paper on a small collection of Lower Ordovician trilobites from the El Paso Group of the Franklin Mountains, west Texas. The paper established a new monotypic genus, *Aponileus*, which Hu interpreted as a nileid. The type material of *Aponileus latus* Hu, 1963 (revised below), includes two poorly preserved cranidia, a librigena, and two quite well preserved pygidia. The genus received virtually no mention in the subsequent systematic trilobite literature. An exception is Hughes's (1979, p. 154) accurate opinion that two cranidia assigned by Hintze (1953, p. 137, pl. 26, figs 15, 16) to "*Barrandia*?" represent *Aponileus* (they are assigned herein to *A. belkaae* n. sp.). Adrain (in Jell and Adrain, 2003, pp. 343, 467) first recognized *Aponileus* as a bathyurid and placed it in synonymy of *Psephosthenaspis* Whittington, 1953. *Psephosthenaspis* had been nearly equally obscure until Fortey and Droser (1996) revised it, assigning new species from the Dapingian of Utah.

Separately, Tremblay and Westrop (1991) erected *Ludvigsenella*, which Fortey and Droser (1996) placed in synonymy of *Psephosthenaspis*.

Bathyurid trilobites are common, often dominant, components of shallow water trilobite faunas from the Lower Ordovician of western Laurentia. Most of the bathyurid diversity in the classic sections of Hintze (1951, 1953, 1973) and Ross (1949, 1951), remains undescribed and dozens of new species along with several new genera await treatment. We have begun wholesale revision of the group, dealing with the Tulean (lower Floian) genera *Psalikilopsis* Ross, 1953 (Adrain *et al*., in press) and *Gladiatoria* Hupé, 1955 (Adrain *et al*., in review). In this work, we are concerned with a group of upper Floian (Blackhillsian) species. Initially we considered the possibility that the species should be assigned to *Psephosthenaspis* based on their large palpebral lobes and forwardly expanding glabellae. Discovery of an effaced species belonging to the group (described below as *Aponileus aasei* n. sp.) revealed close similarity with *Aponileus latus* Hu, the type species of *Aponileus*.

Aponileus latus was the only pre-Middle Ordovician species assigned to *Psephosthenaspis*, following Adrain's (in Jell and Adrain, 2003) synonymy. Once we began to document the morphology of the new upper Floian species it became apparent that similarities with the Dapingian species assigned to *Psephosthenaspis* were likely superficial and that a separate, Floian, clade was involved. In addition, sampling has also revealed a great many undescribed new species from the "*Pseudocybele nasuta* Zone" (Adrain *et al*., 2009), which broadly would traditionally be assigned to *Acidiphorus* Raymond, 1925. Among them is a group which is clearly related to *Psephosthenaspis*. Hence, *Psephosthenaspis* is almost certainly an independent clade from *Aponileus* (see extended discussion under *Psephosthenaspis* below).

Recent work has demonstrated that only a fraction of the diversity of most trilobite groups has previously been described from the Great Basin sections, and *Aponileus* is another demonstration of this. Our sampling in the Ibex area of western Utah has yielded six new species, most of which are known from multiple examples of most of their exoskeletal parts, yet only two specimens belonging to a single species appear in open nomenclature in Hintze's classic monograph (1953, pl. 26, figs 15, 16). With the assignment also of a species from Greenland, *Aponileus* is transformed from a monotypic taxon with a poorly preserved type species to a group of probably eight named species, many of which are documented on the basis of silicified sclerites.

The goals of this work are: 1) to revise and reillustrate the type material of *Aponileus latus* Hu, 1963; 2) to describe five new species of *Aponileus* known from silicified material from the Blackhillsian (upper Floian) of the Ibex area, western Utah; 3) to describe a sixth species from Ibex whose affinity is not certain but which is assigned tentatively to *Aponileus*; 4) to revise *Aponileus glaber* (Poulsen, 1927) with new photographs of its type material; 5) to reconstruct the phylogenetic relationships of the eight known species of *Aponileus* via cladistic parsimony analysis; 6) to compare *Aponileus* with the superficially similar *Psephosthenaspis*, to demonstrate that they are separate clades and likely not sister taxa; and 7) to describe new silicified material of *P. glabrior* Fortey and Droser, 1996, which extends the stratigraphic range of this species.

Biostratigraphy

The history of study of the Lower and Middle Ordovician Great Basin faunas along with geographic information, stratigraphic logs, and a new trilobite zonation were given by Adrain *et al*. (2009) and this material is not repeated herein. In that work, we pointed out that the traditional *Pseudocybele nasuta* Zone of Ross *et al*. (1997) ("Zone J" of Ross [1949, 1951] and Hintze [1951, 1953]) was more complex than had been realized and potentially subject to revision and subdivision. Since then, new collections have revealed the presence of six stratigraphically successive assemblages within the "Zone J" interval in the Wah Wah Formation (Fig. 1). The assemblages can be correlated regionally where data exist. The "Zone J" faunas of the Garden City Formation, from Ross's (1949, 1951) localities 8 (Clarkston Mountain) and 13 (Round Hill, Mantua) in northeastern Utah are correlative with the lowest assemblage from the Fillmore Formation. A "Zone J" fauna from Yellow Hill, near Pioche, eastern Nevada, is correlative with the fourth assemblage (in ascending order) in the Wah Wah Formation. The occurrence of species of *Aponileus* is illustrative of the assemblages, as different species occur in isolation at four separate levels within the Wah Wah Formation, with no overlap of stratigraphic ranges. As the faunas become better documented, these levels are likely to be assigned to distinct new zones. Adrain *et al*. (2009) referred to the composite interval as the "*Pseudocybele nasuta* Zone" in quotation marks. Pending formal revision, that convention is followed herein. The

ranges of the new western Utah species, along with that of the species used as the outgroup in the phylogenetic analysis below, are shown in Figure 1.

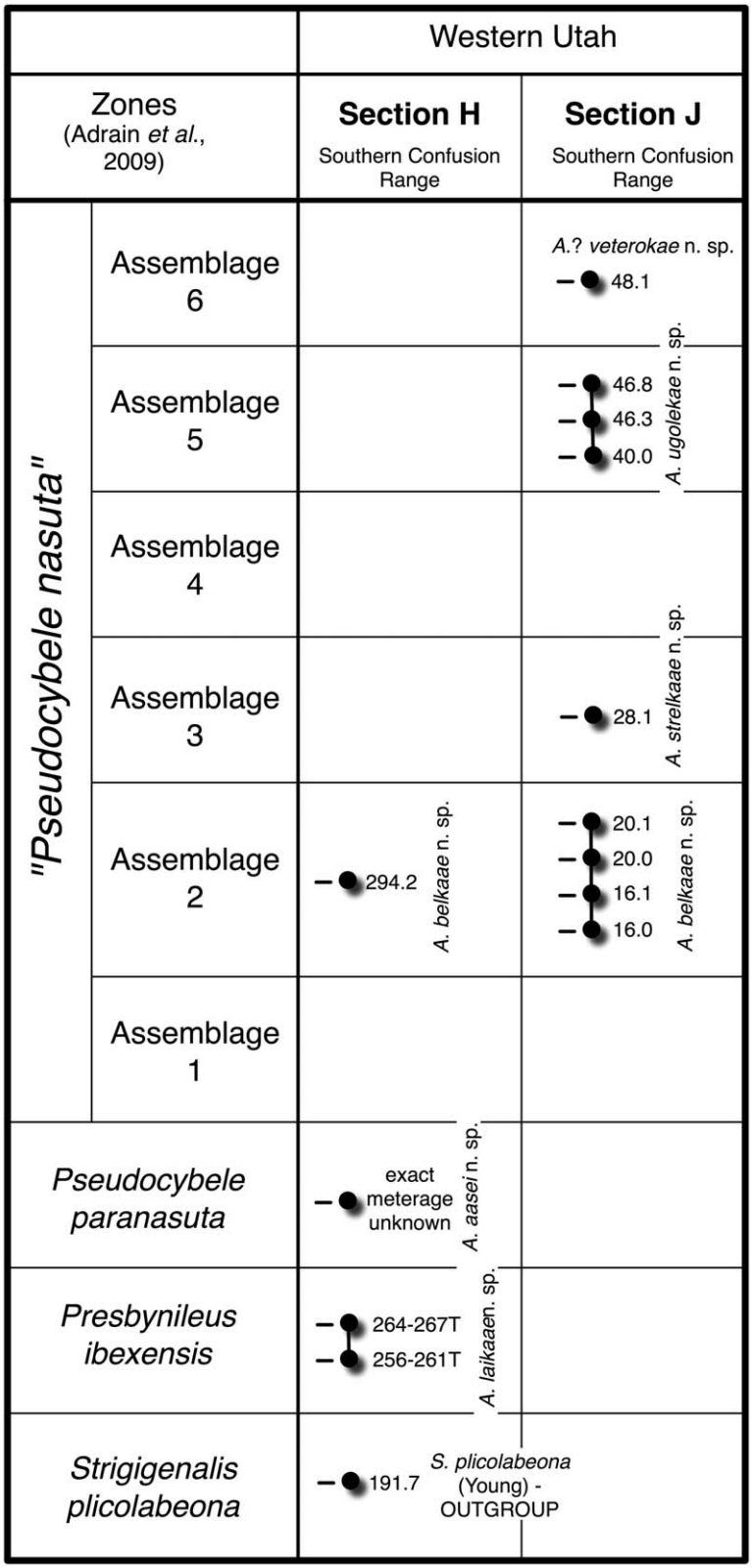

FIGURE 1. Schematic diagram of stratigraphic distribution of species of *Aponileus* and the outgroup species *Strigigenalis plicolabeona* (Young) in Blackhillsian (upper Floian) sections of the Fillmore Formation in western Utah. Measurements are in metres. Meterages are not to scale. Zonation is that established by Adrain *et al*. (2009), with new informal subdivisions of the "*Pseudocybele nasuta* Zone" discussed in text.

Phylogenetic analysis

Taxa. The ingroup comprises all known species of *Aponileus*. In the present state of knowledge, the sister group of *Aponileus* is unclear, but with its thick cuticle, vaulted exoskeleton and strong tuberculation (basally) it seems likely to be related to the "*Acidiphorus* group" *sensu* McAdams and Adrain (2007). This group is centered on *Acidiphorus*, which Brett and Westrop (1996) considered a senior synonym of both *Goniotelus* Ulrich, 1927, and *Goniotelina* Whittington and Ross in Whittington, 1953. A relatively early member of the group, *Strigigenalis plicolabeona* (Young, 1973), was selected as the outgroup taxon. This species is very poorly known in the literature, but we have excellent material of most exoskeletal parts in our collections and will publish a full revision in a forthcoming work. *Strigigenalis plicolabeona* is slightly older than the oldest known species of *Aponileus*, *A. laikaae*, as it occurs in the underlying zone. States in other members of the *Acidiphorus* group are discussed where relevant for each character.

Characters.
The taxon-character matrix used in the analysis is shown in Table 1. All characters are unordered.

TABLE 1.

Taxa	Characters											
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
Strigigenalis	0	0	0	0	0	0	0	0	0	0	0	0
Aponileus laikaae n.	0	0	0	0	0	0	0	1	0	0	0	1
Aponileus latus (Hu)	?	?	?	1	1	?	1	2	0	1	1	2
Aponileus aasei n. sp.	1	1	0	1	1	?	1	2	0	1	1	2
Aponileus glaber	?	1	?	?	?	?	?	?	0	1	1	2
Aponileus belkaae n.	1	0	0	0	1	0	1	3	1	1	0	1
Aponileus strelkaae n.	1	0	0	0	1	0	1	3	1	1	0	1
Aponileus ugolekae n.	1	1	1	0	1	1	1	3	0	1	1	1
Aponileus? *veterokae*	1	1	1	0	1	1	1	3	0	2	1	1

Cranidium

1. Impression of palpebral furrow: 0, well impressed along length; 1, nearly or completely effaced.

Effacement of the palpebral furrow is rare in tuberculate bathyurids. Almost all members of the *Acidiphorus* group have an inflated rim around the edge of the palpebral lobe with a distinctly impressed and complete furrow immediately adaxial to it. This morphology is retained without effacement in the oldest species of *Aponileus*, *A. laikaae*. *Aponileus belkaae* and *A. strelkaae* have both the rim and the furrow much less well expressed, so they are coded as state 1. All of the remaining species, where the morphology can be observed, almost completely efface both the rim and the furrow, so that the palpebral lobe is dorsally featureless. The furrow can be seen as a very faint depression in some specimens of *A. ugolekae* (e.g., Pl. 13, figs 1, 10) but there is never any expression of the inflated rim.

2. Transverse ridge across midlength of SO: 0, present; 1, absent.

This is a subtle character, so expanded photographic documentation of the states is provided in Figure 2. The length of SO is quite variable among members of the *Acidiphorus* group, but rarely is it a simple furrow with a flat or concave bottom. In most species, there is a sliver-like transverse ridge or swelling occupying the middle part of the furrow, even in cases where SO is very short (sag.; exsag.; e.g., *Strigigenalis plicolabeona*, Fig. 2.2). In *Aponileus laikaae* this structure is retained but is reduced to an ellipsoid median swelling in the furrow (Fig. 2.6), whereas *A. belkaae* (Fig. 2.4) and *A. strelkaae* (Fig. 2.5) display a transverse ridge more like the *Acidiphorus* group condition. The remaining species exhibit a less distinctly impressed SO that in some cases is longer (sag., exsag.) than the plesiomorphic condition. Collectively, they show no sign of a ridge or swelling within SO.

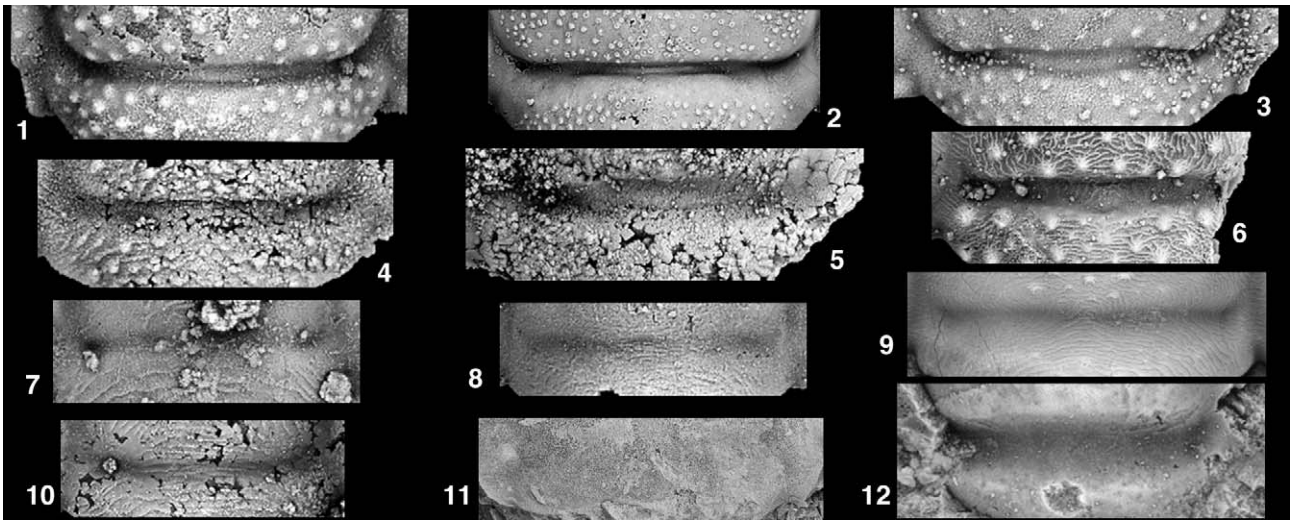

FIGURE 2. Illustrations of states for Character 2, the presence or absence of a fine transverse ridge across the bottom of SO. 1–6, State 0, ridge present. 1. Outgroup state, *Acidiphorus teretus* (Young, 1973), cranidium SUI 131151, Section H 191.7 m, Fillmore Formation (upper Floian; Blackhillsian; *Strigigenalis plicolabeona* Zone), western Utah, x18. 2. Outgroup state, *Strigigenalis plicolabeona* (Young, 1973), cranidium SUI 124830, Section H 191.7 m, Fillmore Formation (upper Floian; Blackhillsian; *Strigigenalis plicolabeona* Zone), western Utah, x7.5. 3. Outgroup state, *Acidiphorus brighti* (Hintze, 1953), cranidium SUI 131152, Section H 290.4 m, Wah Wah Formation (upper Floian; Blackhillsian; "*Pseudocybele nasuta* Zone", Assemblage 1), western Utah, x15. 4. *Aponileus belkaae* **n. sp.**, cranidium SUI 129264, Section H 294.2 m, Fillmore Formation (upper Floian; Blackhillsian; "*Pseudocybele nasuta* Zone"), western Utah, x22.5. 5. *Aponileus strelkaae* **n. sp.**, holotype cranidium SUI 129298, Section J 28.1 m, Wah Wah Formation (upper Floian; Blackhillsian; "*Pseudocybele nasuta* Zone"), western Utah, x15. 6. *Aponileus laikaae* **n. sp.**, holotype cranidium SUI 129234, Section H 256–261T m, Fillmore Formation (upper Floian; Blackhillsian; *Presbynileus ibexensis* Zone), western Utah, x18. 7–12, State 1, ridge absent. 7, 10. *Aponileus ugolekae* **n. sp.**, cranidia SUI 131127 and 131130, Section J 46.3 m, Wah Wah Formation (upper Floian; Blackhillsian; "*Pseudocybele nasuta* Zone"), western Utah, x13.5. 8. *Aponileus*? *veterokae* **n. sp.**, cranidium SUI 129317, Section J 48.1 m, Wah Wah Formation (upper Floian; Blackhillsian; "*Pseudocybele nasuta* Zone"), western Utah, x22.5. 9. *Aponileus aasei* **n. sp.**, dorsal exoskeleton BYU 19975, float high in Section H, Fillmore Formation (upper Floian; Blackhillsian; probably *Pseudocybele paranasuta* Zone), western Utah, x9. 11. *Aponileus latus* Hu, 1963, holotype cranidium USNM 143342, Padre Formation (upper Floian; Blackhillsian), western Texas, x4. 12. *Aponileus glaber* (Poulsen, 1927), cranidium MGUH 2391, Nunatami Formation (upper Floian), gastropod limestone member, northwestern Greenland, x9.

3. Glabellar tubercles: 0, present; 1, completely absent.

Virtually all members of the *Acidiphorus* group have densely and often coarsely tuberculate dorsal sculpture on most sclerites.

Librigena

4. Genal angle: 0, robust spine; 1, rounded angle.

Complete loss of the genal spine in large specimens is rare within the *Acidiphorus* group, though it is achieved in other bathyurids such as derived species of *Benthamaspis* Poulsen, 1946, and the monotypic *Madaraspis* Fortey and Droser, 1996. The most reduced spines within the *Acidiphorus* group are those of species of *Strigigenalis* Whittington and Ross in Whittington, 1953, including the outgroup species. Those species have a distinct spine through most of their ontogeny (Adrain and McAdams, work in progress) and although the genal angle is completely rounded in the largest specimens of some, in *S. plicolabeona* the very largest specimens clearly retain a pointed, though blunt, spine. One would expect the spine to be similarly present and progressively reduced earlier in ontogeny, but this may not be the case in *Aponileus*. First, given the cranidial similarities, one must be careful to rule out ontogenetic change as responsible for the differences. As is typical of silicified faunas, large sample size yields sclerites as large or larger than those typically available in calcareous material. Librigenae of *A. laikaae* (e.g., Pl. 4, fig. 4) and *A. belkaae* (Pl. 8, figs 1, 18) are of similar size to those of *A. aasei* and retain long, robust spines. Hence, simple ontogenetic change cannot account for the difference in morphology. Further, librigenae of species known from silicified material demonstrate that in general and unlike in many other bathyurids, there is no strong ontogenetic trend toward reduction of the spine, and in all species it is of similar relative length in the largest species as in the smallest. This strongly supports the idea that the acquisition of a rounded genal angle is a synapomorphy of the effaced group.

5. Tubercles on librigenal field: 0, present on adaxial part; 1, completely absent.

Even species of the *Acidiphorus* group which have broad and nontuberculate frontal areas and almost smooth librigenal fields still universally retain tubercles posteriorly on the field. *Aponileus laikaae* retains fairly robust tuberculation around the eye, but all other species completely lack tubercles anywhere on the field, even where they remained expressed on the glabella.

6. Length of genal spine: 0, short, exsagittal length clearly less than exsagittal length of main body of librigena; 1, long, exsagittal length well in excess of exsagittal length of main body of librigena.

As noted above (character 4), *Strigigenalis plicolabeona* retains a short genal spine even in the largest specimens. Two (potential) species of *Aponileus*, *A. ugolekae* and *A.*? *veterokae*, share the apparently apomorphic development of an unusually elongate spine. Similarly elongate spines are very common within the *Acidiphorus* group, but the condition seems clearly apomorphic within *Aponileus*. Uncertainty surrounding the affinity of *A.*? *veterokae* is discussed under that species below. This character is inapplicable to *A. aasei* and *A. latus*, and they are coded reductively ("?").

7. Eye socle: 0, weakly inflated socle atop field, beneath furrow below visual surface; 1, socle absent, field runs straight into furrow beneath visual surface.

A very distinct and strongly inflated, though narrow, socle consisting of a single band is characteristic of most species presently assigned to *Acidiphorus*. This band is present in the outgroup species, *S. plicolabeona*, but it is much less distinct and forms a gently swollen rim atop the field, without a distinct abaxial furrow setting it clearly off. This is exactly the condition seen in *Aponileus laikaae*. All other species of *Aponileus* show no sign whatsoever of a socle.

8. Librigenal field raised line sculpture: 0, absent from most of field; 1, anastomosing beneath eye, more or less transverse across field; 2, running strongly posteriorly beneath eye, strongly posteriorly bowed across field; 3, running strongly anteriorly beneath eye, strongly anteriorly bowed across field.

It is rare for the librigenal field to be densely covered with raised line sculpture within the *Acidiphorus* group. Species assigned to *Acidiphorus* usually have a tuberculate sculpture, and raised lines if present tend to be robust and restricted only to the portion immediately in front of the genal spine. *Strigigenalis plicolabeona* librigenae tend to have a few raised lines on the rear of the field which are direct linear continuations of lines on the genal spine and lateral border. All species of *Aponileus* have a pattern of dense anastomosing lines across the entire field. Very large librigenae of *A.*? *veterokae* (e.g., Pl. 16, fig. 1) have the lines effaced, but they are clear on small (Pl. 16, fig. 12) and medium (Pl. 16, fig. 7) sized specimens.

Pygidium

9. Number of pygidial segments: 0, four; 1, three.

Possession of four pygidial segments is a very widely distributed state in Bathyuridae and characterizes most members of the *Acidiphorus* group. Reduction to three as in *A. belkaae* and *A. strelkaae* is very rare. The state in *A. ugolekae* is not immediately clear in dorsal views, as despite the presence of a relatively long axis only three rings are obviously expressed. Ventral views, however (e.g., Pl. 12, fig. 36) unambiguously demonstrate the presence of four rings.

10. Expression of posteromedian spine in large specimens: 0, small nub; 1, completely effaced; 2, long, robust spine.

All species of *Aponileus* have a posteromedian pygidial spine in at least early holaspid ontogeny, but most species apart from *A. laikaae* lose any trace of it in at least the largest known specimens. An exception is *A.*? *veterokae*, which has a long, robust spine. This potential autapomorphy is discussed under the species.

11. Depth of second ring furrow: 0, deep, distinctly impressed; 1, shallow, nearly completely effaced.

The second ring furrow (and often the third) is typically well expressed within the *Acidiphorus* group and this is the plesiomorphic condition in *Aponileus*, shared by *A. laikaae*, *A. belkaae*, and *A. strelkaae*. Other species have the second ring furrow effaced, so that it is only a subtle depression in the largest specimens.

12. Length of post-axial region: 0, extraordinarily long, nearly same length as axis; 1, short, 22% of axial length or less; 2, long, 32% of axial length or more.

The outgroup is highly derived in this feature, as it possesses a very long, posteriorly spatulate pygidium. Hence it does not help polarize the character. Within *Aponileus* there is a clear distinction between species with a very short versus considerably longer post-axial region.

13. Sagittal length (excluding articulating half ring and posterior spine, if present) versus width: 0, over 80%; 1, 43–46%; 2, 53–55%; 3, 36–39%.

Again, *Strigigenalis* is not relevant to this character due to its derived pygidium. Within *Aponileus* there are three morphologically obvious pygidial shapes separated by large discontinuities in length/width ratios. However this is the only character which exhibits homoplasy, as the shortest, widest tail shape (state 3) is unambiguously resolved as occurring twice in parallel (Fig. 3).

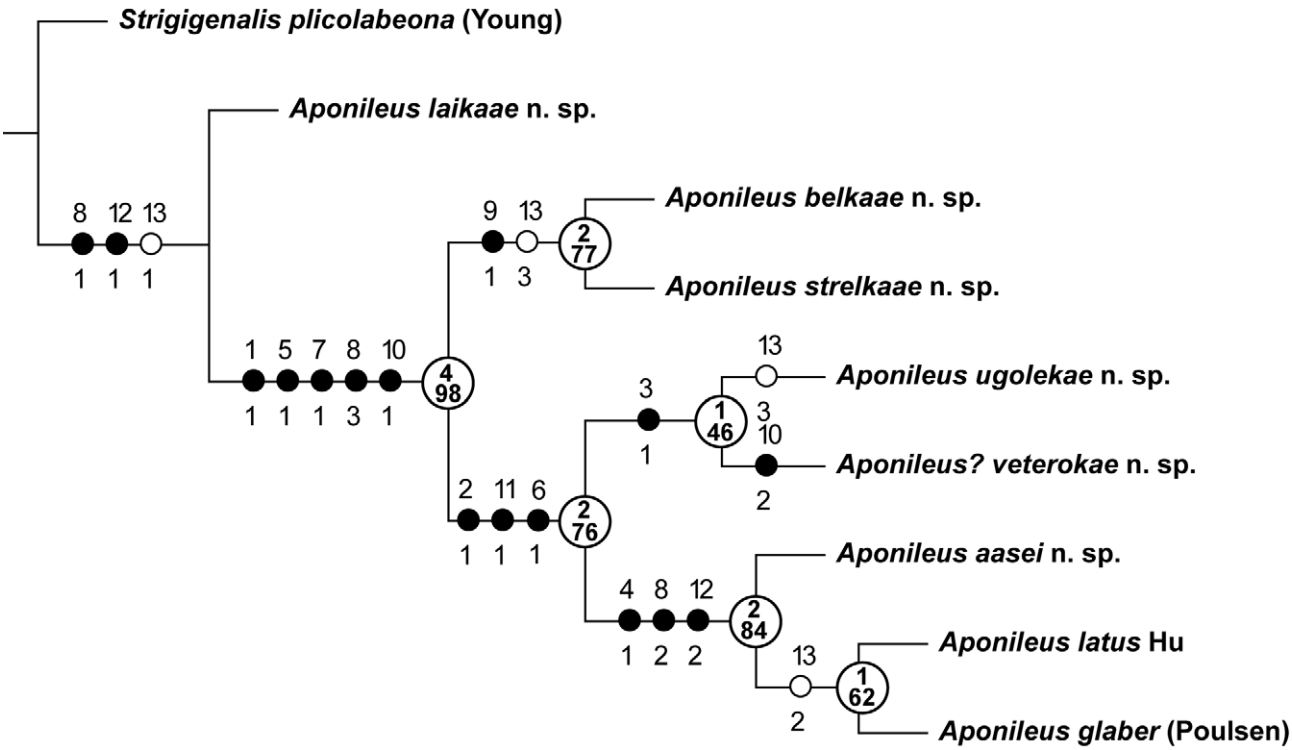

FIGURE 3. Single most parsimonious tree resulting from analysis of the matrix of Table 1. Length = 20; c.i. = 0.95; r.i. = 0.95. Open circles are characters containing homoplasy. Character optimizations are shown carried out under the ACCTRAN assumption. Upper values at nodes are Bremer support values. Lower values at nodes are bootstrapping GC scores.

Results

The matrix is small enough that an exact search was easily employed. The result was a single most parsimonious tree of length 20, with a consistency index of 0.95 and a retention index of 0.95. Characters are shown mapped to the cladogram using the ACCTRAN assumption (Fig. 3). Bremer support is shown as the upper number at each node on Figure 3. Resampling was carried out using standard bootstrapping with 10,000 pseudoreplicates analyzed with exact searches. The resulting GC scores (Goloboff *et al.*, 2003) are shown as the lower numbers at nodes on Figure 3.

The result is broadly congruent with stratigraphic order, though the positions of *Aponileus latus* and *A. glaber* are not precisely known. Only *A. aasei* is incongruent by standard measures of stratigraphic fit, as it is (apparently, see species discussion) the second oldest species yet appears in a derived position on the tree. However, there is virtually no homoplasy in the result — it is limited to a single state of character 13 — so the morphological hypothesis of relationship is at present strongly corroborated.

Aponileus laikaae is the oldest known member of the genus, and is also plainly phylogenetically basal, as it shares many states with the outgroup species. The remaining species form a well supported clade sharing five synapomorphies. This clade has three main components. Sister to the rest is the pair of *A. belkaae* and *A. strelkaae*. This pairing shares only a single non-homoplasious apomorphy, but it is a compelling one: the very rare reduction of pygidial segments to three. The remaining two components are united by loss of the transverse ridge within SO and effacement of the second pygidial ring furrow. A pair of *A. ugolekae* and *A.*? *veterokae* share complete loss of glabellar tuberculate sculpture and a long genal spine. The question remains open whether *A.*? *veterokae* is an ingroup species, though on balance we conclude that it is a highly autapomorphic species sister to *A. ugolekae* (see discussion under *A.*? *veterokae* below). A final component includes *A. latus*, *A. aasei*, and *A. glaber*, which share a smooth genal angle (in the two species with known librigenae), and a long pygidium with a long post-axial region.

Systematics

Repositories. Figured material is housed in the Paleontology Repository, Department of Geoscience, University of Iowa, Iowa City, Iowa, with specimen number prefix SUI; the Museum of Paleontology, Brigham Young University, Provo, Utah, with specimen number prefix BYU; the United States Museum of Natural History, Smithsonian Institution, Washington, D.C., with specimen number prefix USNM; and the Geologisk Museum, Statens Naturhistoriske Museum, Copenhagen, with specimen number prefix MGUH.

Family Bathyuridae Walcott, 1886

Aponileus Hu, 1963

Type species. *Aponileus latus* Hu, 1963, from the Padre Formation (upper Floian; Blackhillsian), El Paso Group, Franklin Mountains, western Texas, USA.

Other species. All are Blackhillsian (upper Floian) in age; *Aponileus aasei* n. sp. (Fillmore Formation; probably *Pseudocybele paranasuta* Zone); *A. belkaae* n. sp. (Wah Wah Formation; "*Pseudocybele nasuta* Zone"); *Bolbocephalus glaber* Poulsen, 1927 (Nunatami Formation, northwest Greenland); *A. laikaae* n sp. (Fillmore Formation; *Presbynileus ibexensis* Zone); *A. strelkaae* n. sp. (Wah Wah Formation; "*Pseudocybele nasuta* Zone"); *A. ugolekae* n. sp. (Wah Wah Formation; "*Pseudocybele nasuta* Zone"); *A.*? *veterokae* n. sp. (Wah Wah Formation; "*Pseudocybele nasuta* Zone").

Diagnosis. Glabella low and large, anteriorly expanded and occupying most of cranidial area; frontal areas small; preglabellar field absent, glabella abutting anterior border medially; palpebral lobes very large; most dorsal surfaces covered with dense raised line sculpture of various morphologies; librigena with large eye, narrow field, and flattened, blade-like genal spine (lost in some species); thorax of ten segments (known from only one species); pygidium wide and short (sag.), with either vestige of posteromedian spine in at least smaller specimens or with robust posteromedian spine.

Discussion. The broad, forwardly expanded glabella, huge palpebral lobes, and blade-like genal spine are an unusual combination for a bathyurid, and *Aponileus* is a distinctive clade. The only closely similar taxon is *Psephosthenaspis* Whittington, 1953, to which, early in the project, we considered assigning the species. Although the genera are possibly related, they appear to be separate clades. The species of *Psephosthenaspis* most similar to those of *Aponileus* is *P. glabrior* Fortey and Droser, 1996. It is revised on the basis of new silicified material below, and facilitates comparison of the genera and evaluation of their relationship (see genus discussion of *Psephosthenaspis* below).

Aponileus latus Hu, 1963

Plate 1

1963 *Aponileus latus* Hu, p. 87, pl. 13, figs 27–31.
1967 *Aponileus latus* Hu; Lochman-Balk and Wilson, p. 905.

1975 *Aponileus latus* Hu; Derby, p. 24.
2003 *Psephosthenaspis lata* (Hu); Adrain in Jell and Adrain, p. 343.

Material. Holotype, cranidium, USNM 143342 (Pl. 1, figs 1, 3, 5), and paratypes USNM 143343a–d, from the Padre Formation (El Paso Group; upper Floian; Blackhillsian), Scenic Drive Section, Franklin Mountains, El Paso County, western Texas, USA.

Diagnosis. Similar to *Aponileus aasei*, but with apparently smaller frontal areas; librigena with much shorter posterior suture and posterolateral region; pygidium and pygidial axis longer relative to width.

Discussion. Hu's (1963) type material is a scarcely adequate basis for a species and is only rendered fully interpretable by new Ibex material belonging to related species. Nevertheless, with the discovery in particular of *Aponileus aasei* n. sp., *A. latus* can be meaningfully compared. Although *A. latus* is known from inadequate material and *A. aasei* from a single specimen, the species, while each other's closest comparison, are definitely distinct. The most obvious difference is the morphology of the librigena. The species share the lack of a genal spine, but the librigena of *A. aasei* is considerably more elongate, particularly in the region behind the eye. Cranidia of *A. latus* are very poorly preserved, but the anterior border and anterior border furrow are less prominent medially and the frontal area seems smaller. The pygidium of the unique specimen of *A. aasei* is partially fragmented, but its general dimensions remain obvious and it is considerably wider relative to its length than those of *A. latus*. One of the pygidia of *A. latus* (Pl. 1, fig. 10) has a definite post-axial ridge (the other has the area where the ridge would be obscured by adhering matrix). There does not seem to be such a ridge in *A. aasei*, and it is definitely absent from other species. In addition to lacking genal spines, the species share a generally effaced morphology, particularly of the pygidial rings, furrows, and pleural regions. The dorsal surfaces of sclerites of both species are covered with a fine, subdued raised line sculpture much less obvious than that of other congenerics. *Aponileus latus* is also similar to the poorly known *A. glaber* from northwestern Greenland. Librigenae of the latter species are not known, but it is clearly another generally effaced species similar to *A. latus* and *A. aasei*. Cranidia of *A. glaber* are not much better preserved than those of *A. latus*, but appear to differ in the possession of straight, obliquely set axial furrows versus strongly anteriorly divergent furrows with the glabella obviously posteriorly waisted, and probably a deeper and longer (sag., exsag.) SO. Pygidia of both species are quite well preserved and that of *A. glaber* differs in being longer relative to its width, so that the posterior margin is nearly semicircular . In addition, the first pleural furrow, though apparent, is not as well impressed as in *A. latus*, and the posterior pleural regions are nearly completely effaced, whereas the pleural regions of the second and third segments are at least faintly expressed on the pygidia of *A. latus*.

***Aponileus aasei* n. sp.**

Plate 2

Material. Holotype, dorsal exoskeleton, BYU 19975 (Pl. 2), from float high in Section H, Fillmore Formation (upper Floian; Blackhillsian; probably *Pseudocybele paranasuta* Zone), southern Confusion Range, Ibex area, Millard County, western Utah.

Etymology. After Arvid Aase, who collected and donated the holotype specimen.

Diagnosis. Dorsal tuberculation restricted to median and rear of glabella; genal spines lost, genal angle rounded, librigena long, especially posteriorly; most dorsal surfaces lacking tubercles but with fine scrobiculate line sculpture; pygidium long, with post-axial region longer than in all tuberculate species but not as long as in *A. latus* or *A. glaber*.

Description. The species is similar enough to *A. belkaae* that extended written description is redundant. This differential description makes note of all observed differences between the species. Cranidium with glabella more strongly waisted posteriorly, axial furrows subparallel posteriorly, then divergent anteriorly, versus more nearly straight along course but obliquely set, and only slightly more strongly divergent anteriorly; scrobiculate raised line sculpture generally finer and more subdued; tuberculate sculpture on glabella more subdued, more finely scattered, and more posteromedially concentrated; frontal areas slightly wider; sculpture on LO much more effaced; librigenae with finer, more closely spaced, and more subdued raised line sculpture, longer posterior facial suture and rear part of field, more subdued lateral border behind midpoint of eye, and completely rounded genal angle versus robust, blade-like spine; pygidium much longer relative to width, with much longer post-axial region, much more

effaced, apparently entirely lacking tuberculate sculpture on axial rings and generally with very subdued and fine raised line sculpture, versus robust and relatively coarse raised lines and strong smattering of small tubercles on axis.

Discussion. The unique holotype of *A. aasei* was collected in the top ¼ of the highest shale unit in Hintze's (1973) informal *Calathium* member, which is the highest member of the Fillmore Formation, at Section H. Although the specimen was collected in 1994, prior to our measurement of the section in metres, this level falls within the narrow *Pseudocybele paranasuta* Zone of Adrain *et al*. (2009). Silicified material from this zone is dominated by only a handful of species, including *Pseudocybele paranasuta* McAdams and Adrain, 2010, and species of *Isoteloides* Raymond, 1910, *Ptyocephalus* Whittington, 1948, and a new genus of asaphid. Very rare sclerites belonging to a species of *Aponileus* occur, but are insufficient to identify (they include a few thoracic segments and a very small pygidium). It is possible these represent *A. aasei*, but more material would be required to be certain. We have thoroughly sampled Section H and there are no other intervals in the vicinity of the level at which the holotype was collected that yield unidentified *Aponileus*.

Aponileus aasei was compared above with *A. latus*. *Aponileus aasei* differs from the Greenland species *A. glaber*, to the extent the latter species can be assessed, in the possession of a more waisted glabella which expands more strongly anteriorly, an apparently shorter SO, and a pygidium which is much wider relative to its length, has a slightly shorter post-axial region, and has less effaced pleural regions.

Aponileus aasei is resolved as the basal species of the effaced group. It has the widest pygidium relative to length, which more closely matches the wide condition seen in most of the tuberculate species. In particular, its cranidium is very close to that of *A. belkaae*. The species share a scattering of small tubercles concentrated on the median and particularly rear parts of the glabella, though they are less well expressed in *A. aasei*. Similarly, there is a background pattern of raised, scrobiculate lines, again somewhat finer in *A. aasei*. In other respects, the cranidia differ only in minor proportions. Hence *A. aasei* is described above via comparison with *A. belkaae*, although the points of close similarity are likely symplesiomorphic as compared with the other effaced species and the younger tuberculate species.

Aponileus glaber (Poulsen, 1927)

Figure 4

	1927	*Bolbocephalus glaber* Poulsen, p. 304, pl. 20, figs 10, 27.
	1927	Genus et sp. ind.; Poulsen, p. 299, pl. 20, fig. 11.
?	1946	*Bolbocephalus glaber* Poulsen; Poulsen, p. 326.
	1953	*Bolbocephalus glaber* Poulsen; Whittington, p. 657.
	1973	*Bolbocephalus*? *glaber* Poulsen; Fortey and Bruton, p. 2238.
	2000	*Illaenus*/*Presbynileus glaber* (Poulsen); Boyce *et al*., p. 123.
	2005	*Bolbocephalus glaber* Poulsen; Adrain and Westrop, p. 1538.

Material. Lectotype (selected here), pygidium, MGUH 2406 (Fig. 4.3, 4.6, 4.8); original of Poulsen (1927, pl. 20, fig. 27), Nunatami Formation (upper Floian), ostracod limestone member, Nunatami, Washington Land, northwestern Greenland.

Diagnosis. Effaced species with faint median keel on glabella; pygidium narrow relative to length; posterior pygidial border almost semicircular in outline.

Discussion. This species has been very difficult to interpret owing to the tiny, poorly lit photographs of only two specimens, a cranidium and a pygidium, provided by Poulsen (1927). Poulsen illustrated a second cranidium, but assigned it to "Genus et sp. ind." The material has not previously been revised. Poulsen later (1946, p. 326) assigned a pygidium from Ellesmere Island (Nunavut, Canada) to the species, opining that it was "a little wider than the Greenland pygidia; it is probable that we have before us a sex dimorphism...." As he did not illustrate the specimen, its affinity is impossible to evaluate. Whittington (1953, p. 657) interpreted the species as an effaced member of *Bolbocephalus*, but Fortey and Bruton (1973) noted that it lacks the inflated glabella of *Bolbocephalus*, and thought that it "may be more correctly referred to the Scutelluidae." Boyce *et al*. (2000, p. 123) did not discuss the species, but their listing of its genus assignment as "*Illaenus*/*Ptyocephalus*" demonstrates similar doubt about Poulsen's assignment.

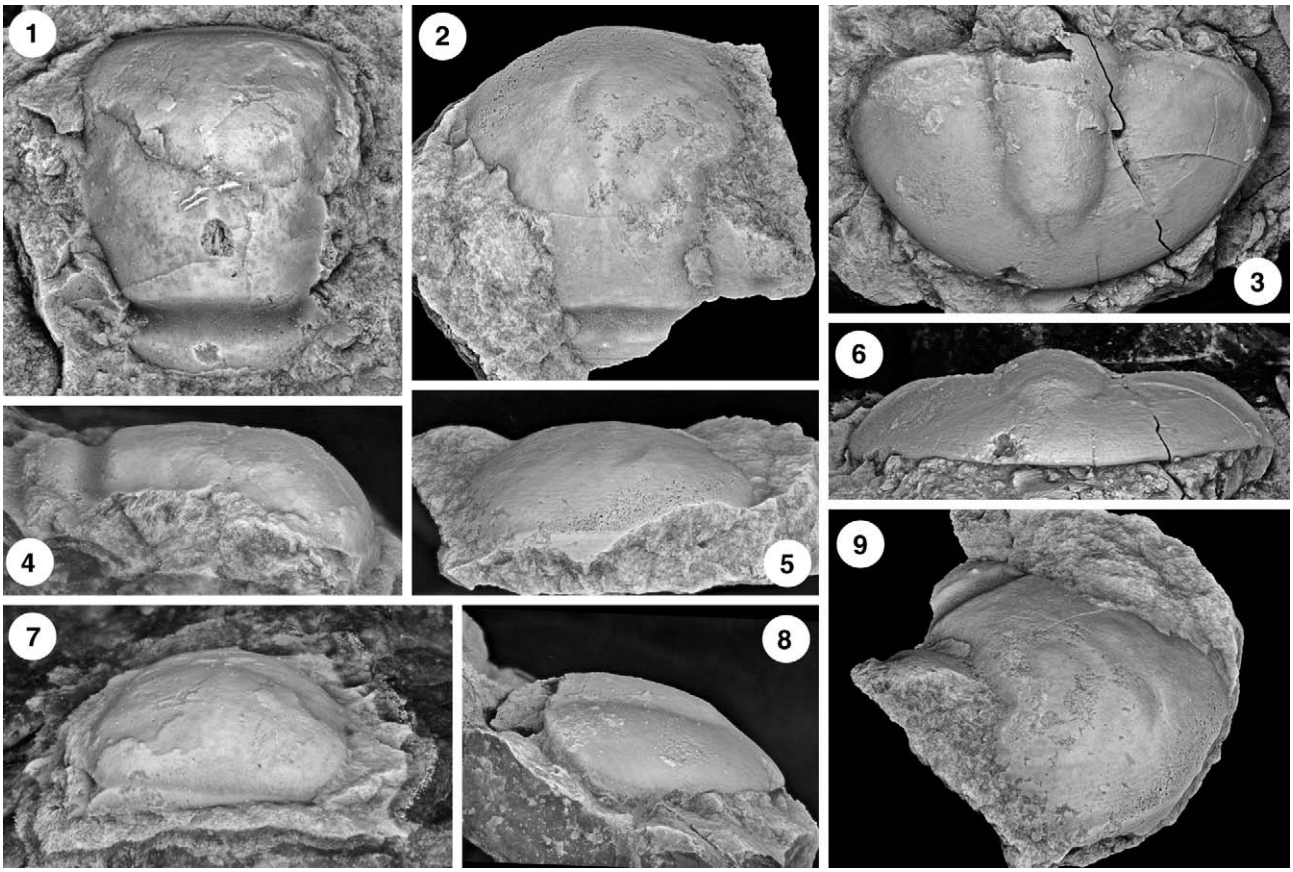

FIGURE 4. *Aponileus glaber* (Poulsen, 1927), from the Nunatami Formation (upper Floian), gastropod limestone member (figs 1, 4, 7) and ostracod limestone member (figs 2, 3, 5, 6, 8, 9), Nunatami, Washington Land, northwestern Greenland. 1, 4, 7. Cranidium, MGUH 2391, dorsal, right lateral, and anterior views, x6 (original of Poulsen, 1927, pl. 20, fig. 11). 2, 5, 9. Cranidium, MGUH 2390, dorsal, anterior, and oblique views, x3 (original of Poulsen, 1927, pl. 20, fig. 10). 3, 6, 8. Pygidium, **lectotype**, MGUH 2406, dorsal, posterior, and left lateral views, x3 (original of Poulsen, 1927, pl. 20, fig. 27).

New photographs of the available three specimens show that while they are generally poorly preserved, there is little doubt that an effaced member of *Aponileus* similar to the type species is represented. The cranidium illustrated in open nomenclature by Poulsen (1927, pl. 20, fig. 11; Fig. 4.1, 4.4, 4.7 herein) agrees in all available detail with the cranidium assigned to the species by Poulsen (1927, pl. 20, fig. 10; Fig. 4.2, 4.5, 4.9 herein), including the faint median glabellar keel, upturned anterior border, broad, forwardly expanding glabella, and long SO, and there is no reason to doubt that it belongs to the species.

Aponileus glaber was compared with the most similar species, *A. latus* and *A. aasei*, under discussion of those species above. While poorly known, the median glabellar keel has not been observed in any other species, and the narrow, long pygidium with nearly semicircular outline also clearly distinguishes the taxon.

***Aponileus laikaae* n. sp.**

Figure 5, Plates 3, 4, Plate 5, figs 1–15

2009 Bathyuridae gen. nov. 6 sp. nov. 1; Adrain *et al*., p. 574.

Material. Holotype, cranidium, SUI 129234 (Pl. 3, figs 1, 4, 8, 10), from Section H 256–261T m, and assigned specimens SUI 129235–129254 from H 256-261T m and H 264–267T m, Fillmore Formation (upper Floian; Blackhillsian; *Presbynileus ibexensis* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. The species also occurs at Section H 251.4 m, in the same zone.

Etymology. After Laika.

Diagnosis. Dorsal surfaces of cranidia, librigenae, thoracic segments, and pygidia with sculpture of dense anastomosing lines and star-shaped tubercles, the ridges of which connect with the lines; eye socle retained in large

librigenae; librigenal field with tubercles grouped on adaxial part only; pygidium with long, deep pleural and ring furrows and well inflated pleural bands; four pygidial segments present; faint posteromedian spine retained as small node even in large pygidia.

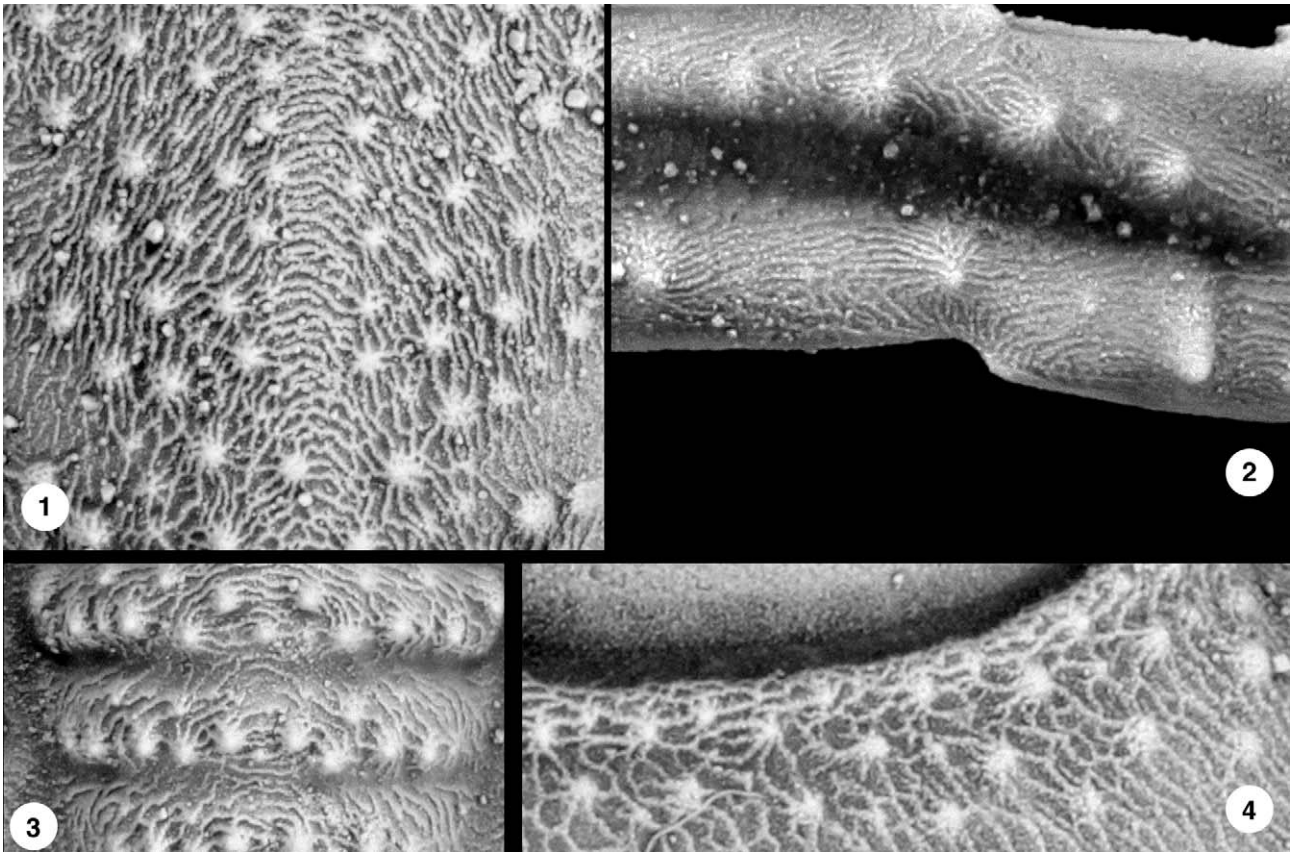

FIGURE 5. Detail views of star-shaped tubercles and anastomosing line sculpture of *Aponileus laikaae* **n. sp.** 1. Medial part of glabella of holotype, SUI 129234 (see Pl. 3, figs 1, 4, 8, 10), x40. 2. Pleural region of thoracic segment, SUI 129246 (see Pl. 4, figs 10–13), x30. 3. Pygidial axis, SUI 129252 (see Pl. 5, figs 2, 3, 5, 7, 8), x40. 4. Librigenal field, SUI 129244 (see Pl. 4, fig. 8), x40.

Description. Cranidial measurements based on most intact specimen of Pl. 3, fig. 2. Cranidium low and wide, with only gentle dorsal vaulting; maximum width across posterior projections, but comparison of width to sagittal cranidial length is not preserved intact on any specimen; anterior border short, similar in length sagittally and exsagittally, anterior margin forwardly concave laterally, bulged forward and forwardly convex medially; border raised into strong rim, with sculpture of dense, fine raised lines running slightly obliquely to anterior margin; anterior face of border tall, with transverse ventral margin, cut laterally by long, obliquely set connective sutures, with sculpture of fine raised lines slightly larger than those on dorsal part, set subparallel to one another and bowed laterally, describing shallow inverted "U" shape in anterior view; anterior border furrow deep, short, partially obscured medially by overhanging glabella; preglabellar field absent, glabella abutting rear of anterior border medially; frontal areas small and triangular with fine anastomosing line sculpture; anterior sections of facial suture strongly laterally bowed; distance across β 93.0% cranidial sagittal length and distance across γ 86.1% cranidial sagittal length; palpebral lobe very large, exsagittal length 46.4% cranidial sagittal length; distance across palpebral lobes 136.5% cranidial sagittal length; lobes drooped posteriorly, maximum of curvature well behind midlength; edge of palpebral lobe inflated into rim; palpebral furrow with complex morphology; true furrow is set some distance adaxially from rim (best seen in ventral view, Pl. 3, fig. 4), narrow and curved around rear margin of lobe, broader anteriorly, progressively shallower anteriorly and shallowed out posterior to anterior edge of lobe, with stronger lateral curvature than lateral margin of lobe; furrow is separated from margin by a narrow, flat, crescentic area which is separated from the rim by a shallow secondary furrow; part of lobe adaxial to true palpebral furrow is weakly dorsally inflated; palpebral lobe held at moderate angle to general plane of glabella, abaxial parts turned to lie flat and subparallel with general plane of glabella; lobe with dorsal sculpture of dense anastomosing lines and a few tiny, faint tubercles; inflated rim of lobe continued anteriorly around γ and onto frontal area almost to β as

sutural ridge; rear of palpebral lobe with ε reentrant, posterior margin of lobe overhanging anterior edge of posterior projection; eye ridge not obvious, anterior edge of palpebral lobe nearly abutting axial furrow; posterior edge of lobe well separated from glabella; distance across ε almost identical to that across γ; posterior fixigena with very fine anastomosing line sculpture, more subdued than on other parts of cranidium, fixigena running along projection as very short (exsag.) strip with transverse row of median tubercles; posterior border furrow deep, running to contact with posterior facial suture where it is met by a slight sutural ridge; posterior border very short, shortest just proximal to fulcrum, wider distally, with sculpture of two or three transverse tubercles proximally and seven or eight tubercles on lobate distal part; glabella evenly forwardly expanding, minimum width posteriorly 72.2% maximum anterior width, which is developed opposite β; maximum glabellar width 91.6% sagittal glabellar length (excluding LO); sagittal length (excluding LO) 74.9% cranidial sagittal length; axial furrows fairly narrow and quite shallow, deflected slightly around faint lateral swellings of glabella, turned sharply into preglabellar furrow at maximum width of glabella; preglabellar furrow slightly narrower than axial furrow, most of course obscured beneath overhanging frontal lobe of glabella and tall anterior border, essentially merged in this region with anterior border furrow; glabella with sculpture of anastomosing lines more prominent than that on fixigena, and with moderate sized star-shaped tubercles connecting with intersecting lines (Fig. 5.1), tubercles slightly smaller anteriorly; glabella with distinct but slight lateral inflation behind anterior edge of palpebral lobe, some specimens (e.g., Pl. 3, fig. 12) with several faint swellings and furrows, but relationship to glabellar lobation uncertain; glabella only weakly to moderately inflated in transverse and sagittal profiles; SO long (sag., exsag.) and quite deep, running almost exactly transversely but for median posterior embayment in front of LO; distance across LO 56.3% sagittal length of cranidium; sagittal length of LO 15.2% that of cranidium; LO longer medially than laterally, with line and tubercle sculpture similar to that of glabella, except tubercles slightly larger and posterior tubercles arranged in some specimens in an approximate transverse row in front of posterior margin (e.g., Pl. 3, figs 1, 2, but not Pl. 3, fig. 12); median node not obviously expressed; axial furrow bowed posterolaterally opposite LO and shallower; doublure forming large articulating surface beneath LO with sculpture of very fine, transverse raised lines; forming groove beneath proximal part of posterior border for articulation with anterior edge of first thoracic segment; fossulae not apparent.

Librigena with large, long eye set on weakly differentiated eye platform; eye platform separated from field by deep furrow, arcuate anteriorly and posteriorly but slightly straighter in midlength of course; eye socle partially merged into field, narrow inflated rim with very subtle bounding furrow, but sculpture of field is continued over socle; field narrow anteriorly, broader posteriorly, weakly inflated adaxially, dorsally concave abaxially, with sculpture of fine anastomosing lines across entire surface and two or three more or less longitudinal rows of small star-shaped tubercles (Fig. 5.4) restricted to adaxial half; lateral border furrow very broad and shallow; lateral border inflated and large, with dense subparallel raised lines independent of anastomosing sculpture on field (intersecting and overriding the field sculpture along border furrow) set obliquely to margin on posterior part of border and subparallel with margin on anterior part; border with dorsal part more ridge-like anteriorly to match tall anterior border, more semi-circular in section posteriorly; posterior border short, scarcely differentiated from rear of field by weak posterior border furrow, with sculpture of a few tubercles; genal spine long and robust, blade-like with sharp dorsolateral edge arising from rear part of lateral border; dorsal aspect flattened and with anastomosing sculpture; lateral aspect with subparallel raised lines continued without interruption from lateral border; spine slightly shorter than field (exsag.), tapered to sharp distal point; anterior projection relatively short; doublure underlying lateral border forming sharp angle with ventrolateral edge of sculptured border, with a few raised lines on lateral part but progressively effaced adaxially, slightly concave, slightly narrower anteriorly, forming broad shelf; only a small portion of doublure underlying restricted course of posterior border, intruded on by Panderian notch; Panderian notch very large, bounded by small raised rim; underside of genal spine with subdued, chevron-like raised lines.

Rostral plate not identified.

Hypostome (tentatively assigned; see discussion) subquadrate, with strong, scrobiculate raised line sculpture; anterior margin turned slightly dorsally, slightly anteriorly bowed but more or less transverse; anterior wing large, expanded distally, running at about 45° angle dorsolaterally; lateral margins widest at shoulder, moderately posteriorly convergent posterior to shoulder, turned into posterior margin at distinct posterolateral corner; posterior margin posteriorly bowed, very slightly irregular in very shallow "W" shape; lateral border only weakly differentiated, marked mainly by several raised lines subparallel with margin; posterior border with more independent inflation;

both lateral and posterior border well inflated laterally and dorsolaterally, with prominent raised lines; lateral border furrow hardly expressed, lateral border almost contiguous with middle body; posterior border furrow distinct but long (sag.; exsag.) and shallow, appearing as concave sculptureless region; anterior part of middle body strongly ventrally inflated, with irregular, scalloped line sculpture; middle furrow set about three quarters distance posteriorly, expressed as pair of deep lateral slots oriented slightly obliquely; posterior part of middle body weakly inflated, with transverse raised line sculpture; doublure running from anterior wing to small posterior wing, forming small shelf above posterior border, broader at posterior corners; lateral notch shallow.

Thoracic segments with axial lobe slightly wider (tr.) than (Pl. 4, figs 10, 17) to slightly narrower than (Pl. 4, fig. 26) pleural lobe, depending on position in thorax; axial ring with rear margin describing shallow "W" (Pl. 4, figs 10, 16) to nearly transverse (Pl. 4, fig. 26); anterior margin similar in course, but with shallower inflections; ring with about 16 prominent, star-shaped tubercles arranged approximately in two transverse rows, with background sculpture of connecting raised lines similar to that on dorsal surfaces of other sclerites (Fig. 5.2); ring with very shallow transverse depression at about half length (sag; exsag) and between transverse tubercle rows; ring furrow long (sag.; exsag.), pinched distally, with distinct breaks in slope at anterior and posterior margins, flat-bottomed with very faint, anteriorly bowed, crescentic swelling set within furrow; articulating half-ring large, transversely ellipsoid, with gentle sagittal convexity, lacking sculpture; axial furrow shallow, defined as exsagittally aligned furrow posteriorly, where it cuts across posterior pleural band, but obscure anteriorly; peg-like articulating process directed anteriorly at anterior extent of axial furrow; socket directed posteriorly at rear of axial furrow (Pl. 4, figs 23, 27); pleura with sharp break in slope at fulcrum, set just over half distance distally (Pl 4, figs 10, 16) to far distally (Pl. 4, fig. 26) depending on position in thorax; segment of pleura proximal to fulcrum with very prominent anterior articulating ridge along anterior margin and posterior articulating groove along posterior margin; anterior margin with subtriangular forward projection at fulcrum, posterior margin with corresponding posterior notch; anterior pleural band strongly exsagittally convex, almost ridge-like, very short (exsag.) proximally, progressively wider distally, with sculpture of approximately four prominent tubercles and one or two much smaller tubercles, arranged in approximate transverse row beginning about half distance along portion proximal to fulcrum and continued distally behind articulating facet; posterior pleural band similar in morphology to anterior band, except of similar length (exsag.) proximally and distally and longer than anterior band across most of width, with tubercle row started immediately adjacent to axial furrow and continued distally onto surface of pleural spine; pleural furrow very prominent, long, and deep, with flat bottom, pinched and shortened (exsag.) distally, pinched out near base of pleural spine; anterior and posterior pleural bands merged around termination of pleural furrow; articulating facet with distinct different plane than remaining distal region of segment but otherwise not large and prominent, subtriangular and sliver-like, with large anterolaterally directed socket set at anterior point of triangle; short, subtriangular pleural spine directed slightly posterolaterally to nearly directly posteriorly, depending on position, short and stubby (Pl. 4, fig. 16) to more elongate (Pl. 4, fig. 26), depending on position; dorsal sculpture of anastomosing raised lines on pleural bands coalesced into loose, posteriorly-directed chevron pattern on spine; doublure consisting of crescentic articulating surface beneath posterior part of ring, slightly ventrally concave, lacking sculpture; thin shelf underlying part of posterior pleural band distal to fulcrum, longer distally; pleural tip underlain by broad doublural shelf with loosely organized, sinuous raised lines, anterolateral socket near front, small ventrally directed swelling or peg-like process developed behind and in most specimens slightly abaxial to socket, rear with prominent notch and adaxially directed process for articulation with anterolateral socket of next most posterior segment (or pygidium).

Pygidial measurements are based on the specimens of Pl. 5, figs 1, 3, 12. Pygidium with sagittal length 51.3% (50.8–51.9) maximum width; axis with maximum anterior width 87.1% (85.7–89.5) sagittal length and 37.7% (36.4–38.4) pygidial maximum width, and sagittal length 84.4% (83.1–86.1) pygidial sagittal length; axis consists of four rings and a terminal piece; entire dorsal surface with prominent background sculpture of anastomosing raised lines, expressed even in ring furrows and pleural furrows, and connected to large, star-shaped tubercles; articulating half ring large, transverse in middle part, pinched abruptly laterally, with anastomosing line sculpture expressed on posteromedian region; first ring furrow long (sag. exsag.), slightly longer laterally than medially, flat bottomed, with anastomosing line sculpture expressed on median half (tr.); first through third rings of similar length, fourth shorter; all four rings with distinct pair of large tubercles near midline and several slightly smaller but still large tubercles arranged in irregular transverse row near posterior margin, still more irregular row of smaller tubercles set anteriorly; second, third, and fourth ring furrows progressively shorter and shallower than

first, but still prominently impressed; furrow between fourth ring and terminal piece much less impressed and more transverse; pseudoarticulating half ring expressed in front of second ring furrow, occupying crescentic median portion of rear of first ring, but bearing sculpture contiguous with that of first ring; pseudoarticulating half rings posterior to second segment not obviously expressed; axial furrow shallow anteriorly, beginning behind anterior articulating peg set immediately beside axis, deflected around first two axial rings, more linear in course posterior to second ring; axial furrows gently posteriorly convergent, bowed around rear of axis to meet medially and fully circumscribe axis; no post-axial ridge developed; pleurae of first segment with morphology closely similar to that of thoracic segments, anterior pleural band longer than posterior band, pleural furrow very long and deep; two or three tubercles on anterior band of first segment, mainly distal to fulcrum, posterior band with three or four tubercles arranged transversely along entire width; first interpleural furrow shallow, not a lineation but a broad trough, second interpleural furrow visible but faint, no posterior interpleural furrows expressed; second segment with anterior and posterior bands subequal in length, each bearing tubercles across width; second pleural furrow narrower than first, but only slightly shorter and shallower; anterior pleural band of third segment expressed with two or three tubercles; third pleural furrow visible but faint; posterior pleural band of third segment barely swollen, with a single tubercle expressed; pleural bands and furrows of fourth segment not differentiated; rear margin of pygidium broadly arcuate, border not independently swollen but marked by termination of pleural bands and furrows, broad, broader laterally than medially, with raised line sculpture organized into prominent evenly spaced lines set subparallel with margin; small spine base positioned medially just above border, spine itself consisting of small raised nubbin; margin with very shallow posteromedian inflection in posterior transverse profile, lateral portions broadly ventrally bowed, median portion gently dorsally flexed; doublure broad, exactly underlying dorsally expressed border with inner margin aligned with distal expression of pleural bands and furrows, strongly ventrally convex over most of course with very prominent raised line sculpture, slightly flatter with shallow concave region laterally behind articulating facet and anterolateral articulating socket.

Ontogeny. Although well preserved, the available sample size of *A. laikaae* is relatively small, so knowledge of holaspid ontogeny is correspondingly limited. In the cranidium, there does seem to be a trend toward stronger expression of the glabellar lobes and furrows. The smallest specimen (Pl. 3, fig. 2) has them barely differentiated whereas the largest (Pl. 3, fig. 12) has very well expressed furrows and subtly independently inflated lobes, and the second largest (Pl. 3, fig. 3) also shows stronger development of these features. The axial furrows also appear to become more strongly anteriorly divergent, and the frontal lobe of the glabella somewhat broader, in the largest specimens.

Changes in the librigena involve gradual effacement of the fine tubercles on the adaxial half of the field, though they remain expressed even in the largest specimens. There is a trend towards slight expansion of the width of the field, particularly earlier in ontogeny. There are no obvious ontogenetic changes among the available pygidia, but they are all fairly close to one another in size.

Discussion. Assignment of a hypostome to *Aponileus laikaae* is somewhat tentative, and is based on exclusion and the morphological correspondence between the robust raised line sculpture and the dorsal raised line sculpture of other sclerites. Several other bathyurids occur with *A. laikaae*, including undescribed species of *Acidiphorus*, *Strigigenalis*, *Benthamaspis*, and a species which appears to represent early *Bathyurus* Billings, 1859. Bathyurid hypostomes are generally not well known, but the morphology of the present example is markedly different from those we have definitely associated with *Acidiphorus* group taxa, such as *Acidiphorus* and *Strigigenalis*, in our collections. *Benthamaspis* is small and very rare in the collection and the hypostome corresponds poorly with its effaced morphology. Of the available options, the only significant alternative is the apparent *Bathyurus*, as the hypostome compares closely with that assigned by Tremblay and Westrop (1991, fig. 9.35, 9.46) to *B. angustus* Ross, 1970. Despite the similarity in general proportions, however, we consider our hypostome more likely to belong to *A. laikaae*. The hypostome is clearly conterminant, with a suture along its anterior edge. This is true also of those assigned by Tremblay and Westrop. *Bathyurus angustus*, like most species of *Bathyurus*, lacks a preglabellar field in mature specimens. The early species of *Bathyurus* occurring with *A. laikaae*, however, retains a fairly long preglabellar field in mature holaspides. This is in conflict with a secondarily docked hypostome, whereas *A. laikaae* completely lacks a preglabellar field and would be expected to have a conterminant hypostome. Secondarily conterminant bathyurid hypostomes may share a generally similar morphology, as that assigned by Tremblay and Westrop (1991, fig. 15.11, 15.12) to *Psephosthenaspis ellipsepyga* (Tremblay and Westrop) is also very similar to that of species of *Bathyurus* and the specimen assigned here to *A. laikaae*.

Aponileus laikaae is the oldest known species of the genus, and has the most spectacularly developed sculpture. Much of the external surface of the cranidium (Fig. 5.1), librigena (Fig. 5.4), thoracic segments (Fig. 5.2), and pygidium (Fig. 5.3) is covered with strongly raised, scrobiculate lines. The lines run together from multiple directions to form raised tubercles, which seen in magnification are star-shaped. The well expressed tuberculate sculpture and lack of effacement distinguish the species from all other members of the genus. Most potential sister taxa of *Aponileus* are strongly tuberculate and non-effaced, and *A. laikaae* is retrieved as the basal-most known species of the genus (Fig. 3). It differs from the effaced group including the type species further in the possession of a genal spine. It differs from *A. belkaae* in the possession of a somewhat shorter genal spine, tubercles on the adaxial part of the librigenal field, finer scrobiculate lines on the librigenal field, anteriorly shallower librigenal lateral border furrow, longer, narrower, pygidium with a small posteromedian spine retained as a nub in largest specimens versus totally effaced through ontogeny, four versus three pygidial axial rings, and well impressed versus posteriorly effaced pygidial pleural regions.

***Aponileus belkaae* n. sp.**
Plate 5, figs 16–25, Plates 6-10

? 1884 *Barrandia* ? sp. ?; Walcott, p. 96, pl. 12, fig. 6.
1953 "*Barrandia* ? sp."; Hintze, p. 137, pl. 26, figs 15, 16.
2000 *Theamataspis* sp.; Boyce *et al*., p. 125.
2009 Bathyuridae gen. nov. 6 sp. nov. 2; Adrain *et al*., p. 575, fig. 21I, M.

Material. Holotype, cranidium, SUI 129258 (Pl. 6, figs 1, 6, 9, 12), from Section J 16.1 m, and assigned specimens SUI 115403, 115404, 129255–129257, 129259–129261, 129267–129274, 129278, 129282, 129283, 129286, 129287–129297 from Section J 16.0 m, J 16.1 m, J 20.0 m, and J 20.1 m, all Wah Wah Formation; assigned specimens SUI 129262–129266, 129274–129277, 129279, 129281, 129284, 129285 from Section H 294.2 m, Fillmore Formation; all from the upper Floian (Blackhillsian; "*Pseudocybele nasuta* Zone"), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

Etymology. After Belka.

Diagnosis. Cranidium with prominent tuberculate sculpture restricted to posteromedian region of glabella and LO in large specimens; raised line sculpture on most dorsal surfaces coarse and relatively widely spaced; flattened dorsal face of genal spine broad; pygidium very wide relative to length; three pygidial segments present, with third ring prominent; posteromedian pygidial spine completely lost in large specimens.

Description. Cranidial measurements were made (where relevant features are preserved) on the large specimens of Pl. 6, figs 1, 3, 10 and Pl. 7, figs 1, 4. Cranidium with sagittal length 76.1% (73.1–79.2) width across palpebral lobes; width across intersection of anterior border furrow and facial suture 62.1% (60.6–64.1) width across palpebral lobes; width across β 72.0% (71.0–73.8) width across palpebral lobes; width across γ 67.1% (63.0–68.5) width across palpebral lobes and 94.8% (92.6–95.9) width across ε; width across rear of LO 58.8% (55.8–63.8) sagittal length; anterior margin of anterior border bowed forward medially, ranging from more or less arcuate (Pl. 6, fig. 10) to more obliquely straight (Pl. 7, fig. 1); anterior border very short in dorsal view, shorter medially, but with broad anteriorly-facing area; dorsal rim-like portion of border with five or six fine, subparallel raised lines, forward-facing region with coarser, much more widely spaced subparallel raised lines; connective sutures cutting obliquely across forward face at low angle, ventral margin of forward face occupying approximately median three-fifths of width, with slight ventral convexity; anterior margin of forward face describing shallow inverted "W"; anterior border furrow about same length (exsag.) as dorsal rim of border laterally, shorter and obscured by glabella medially, shallow but distinct; anterior section of facial sutures bowed strongly laterally; frontal area with prominent raised lines set obliquely to suture; palpebral lobes very large, slung posteriorly so that posterior half of margin has much stronger curvature than anterior half; palpebral furrow very faint, creating subtle raised rim near margin of lobe; interocular fixigena rising with gradual change in slope to palpebral lobes, areas not clearly distinguished, with sculpture of subdued scrobiculate raised lines; posterior projections not well preserved on available species, proximal part crowded against rear of palpebral lobe; posterior fixigena with only small area in front of posterior projection, and occupying only very short (exsag.) strip on projection; posterior border lacking sculpture, with strong dorsal convexity; posterior border furrow very deep; glabella with maximum width across

frontal lobe 96.9% (93.1–103.7) sagittal length (excluding LO) and posterior width across L1 58.8% (55.8–63.8) sagittal length; axial furrow anteriorly convergent opposite LO and very rear of L1, anteriorly divergent in front of L1 to maximum divergence opposite frontal lobe, gently deflected around subtle swellings of lateral glabellar lobes, shallow but distinctly impressed, similar to lateral definition of anterior border furrow; preglabellar furrow running without interruption from axial furrows, shallower, running into anterior border furrow as anterior part of glabella overhangs anterior border; glabella with sculpture of fingerprint-like prominent raised lines, with arcs directed anteriorly, much more prominent on frontal lobe and partially to wholly effaced posteriorly, and large tubercles, gathered more prominently posteriorly and posteromedially, smaller and much more subdued and more widely scattered anteriorly and laterally; glabellar furrows expressed as very shallow depressed areas and indentations in lateral margin of glabella; L1–L3 expressed as subtly differentiated independent swollen regions; anteromedian part of glabella completely overhanging anterior border furrow; SO long (sag., exsag.), with sharper break in slope to main part of glabella anteriorly than to LO posteriorly; LO with sagittal length 16.9% (15.9–17.8) that of cranidium, somewhat shorter laterally, with sculpture of prominent tubercles similar to that on posteromedian portion of glabella; doublure consisting of large articulating surface beneath LO, with sculpture of fine subparallel raised lines, anterior margin describing "W" shape, and articulating transverse groove beneath proximal part of posterior border (distal portion of doublure not preserved on any available specimen); fossulae not obvious.

Librigena with eye long and tall, visual surface with strong outward convexity; anterior facial suture strongly bowed; posterior facial suture with short course; eye socle not expressed, visual surface separated from field by moderately deep, narrow furrow; field long, widest behind eye, surface with moderate convexity, with sculpture of prominent raised lines, describing anteriorly directed arcs on adaxial half of field, aligned subparallel with lateral margin on abaxial half of anterior region, and mostly effaced on abaxial half of posterior region of field; posterior border furrow nearly effaced, field separated from posterior border mainly by change in slope, raised lines contiguous across both surfaces; lateral border shallow and nearly effaced posteriorly, progressively deeper anteriorly, deep and trench-like near anterior facial suture; anterior portion of lateral border with morphology similar to that of anterior border of cranidium, with dorsal rim-like portion and flattened ventrolateral face; rim-like portion with fine, crowded raised lines, ventrolateral face with coarser, more widely spaced lines; change of slope between rim-like portion and ventrolateral face continued posteriorly and onto lateral aspect of long genal spine, but more subdued on posterior part of lateral border; genal spine with dorsal surface flattened, so that lateral rim is blade-like; dorsal aspect of spine with raised line sculpture continued from rear of field and posterior border; genal spine about as long as remainder of librigena, robust, tapered to sharp point; ventral aspect of spine more inflated than dorsal aspect, with sculpture of densely spaced raised lines running subparallel to margins; ventrolateral aspect of lateral border grading into ventral aspect of genal spine; doublure turned sharply in from ventrolateral face of border, forming sharp rim; doublure lacking sculpture, slightly concave anteriorly to markedly so posteriorly, forming depressed area between base of genal spine and large Panderian notch; Panderian notch with fine raised rim; doublure broader posteriorly than anteriorly; anterior projection (not well preserved in most available specimens) relatively small and narrow.

Rostral plate, hypostome, and thorax not identified.

Pygidial measurements are based on the large, intact specimens of Pl. 9, figs 1, 2, 7, 14. Pygidium with sagittal length 42.6% (39.4–44.0) maximum width; anterior width of axis 98.5% (91.3–109.4) sagittal length of axis and 35.4% (34.2–36.4) maximum pygidial width; sagittal length of axis 84.6% (82.9–86.3) that of pygidium; articulating half ring relatively short, lacking sculpture; ring furrows all transverse, progressively shallower posteriorly; axis with three rings and terminal piece; very small lineation not connected laterally with axial furrow separating third ring from terminal piece; rings with sculpture of prominent scrobiculate raised lines overlain by medium tubercles ranging from prominently expressed on all rings (Pl. 9, fig. 7, Pl. 10, fig. 18) to largely subdued (Pl. 9, fig. 1, Pl. 10, fig. 10); pseudoarticulating half ring expressed on second segment of some specimens as thin sliver in ring furrow (Pl. 10, fig. 10), not expressed in others, pseudoarticulating half ring not expressed on third segment; terminal piece large, about as long (sag.) as first ring; axial furrows well impressed, moderately posteriorly convergent, bowed medially to meet and fully define axis posteriorly, no post-axial ridge developed; pleural field relatively narrow, particularly behind first segment; pleural region with prominent, coarse, scrobiculate raised line sculpture over entire surface, some specimens with a few very small scattered tubercles on posterior parts (Pl. 10, figs 1, 18); anterior pleural band of first segment slightly longer than posterior band, developed into large, triangular articulating facet distal to fulcrum, with anterolateral, forwardly directed point housing an articulating socket;

first pleural furrow well impressed and deep, narrowed and pinched out distally, pleural bands uniting behind articulating facet; interpleural furrows barely expressed; second pleural furrow only about half the width of first and less well expressed, pleural bands of second segment not completely expressed; pleural region of third segment not differentiated from generalized pleural field; posterior margin of pygidium describing continuous, medially transversely elongate, arc; border broad, broader laterally, with sculpture on posterior rim of subparallel raised lines somewhat finer than those on dorsal pleural surface; pygidium with gentle median flexure in posterior view and median embayment; largest specimens lacking any hint of a posteromedian spine, but small nubbin present in medium sized specimens; doublure broad, with sculpture of subparallel raised lines, more closely spaced medially than laterally, ventrally convex medially but with concave lateral regions behind articulating sockets.

Ontogeny. Of the available material, ontogenetic change can be observed in the cranidia and pygidia, but the morphology of the librigenae seems more stable through the available size range. Cranidial changes in holaspid ontogeny include a relative widening of the glabella, an increasing median anterior overhang of the frontal glabellar lobe, a relative shallowing of the axial furrows, and a reduction in the prominence of the scrobiculate raised line sculpture on the glabella, particularly posteriorly.

The pygidium is much narrower relative to length in smallest specimens (Pl. 9, fig. 19); relative width increased with size. Smaller specimens have more prominent tuberculate sculpture and less prominent raised line sculpture. Tubercles generally decrease in density with size, though some large specimens retain dense axial tuberculation. The posteromedian spine is thorn-like and upturned in smallest specimens, progressively reduced to small nubbin in medium sized specimens, and lost entirely in largest specimens. The posteromedial profile of postaxial region changes from strongly upturned with spine (Pl. 9, fig. 24), to still strongly upturned after the spine is nearly lost (Pl. 10, fig. 25), to not upturned at all in large specimens (Pl. 9, fig. 4).

Discussion. As discussed above, *A. belkaae* is sister to *A. strelkaae*, sharing the distinctive apomorphy of a short, wide pygidium which is reduced from four to three segments. *Aponileus belkaae* was compared with *A. aasei* and *A. laikaae* above. It is compared with *A. strelkaae* and *A. ugolekae* under discussion of those species below.

Aponileus strelkaae n. sp.

Plate 11, Plate 12, figs 1–20, 22–24

2009 Bathyuridae gen. nov. 6 sp. nov. 3; Adrain *et al*., p. 575.

Material. Holotype, cranidium, SUI 129298 (Pl. 11, figs 1, 2, 4, 6, 9), and assigned specimens SUI 129299–129311, from Section J 28.1 m, Wah Wah Formation (upper Floian; Blackhillsian; "*Pseudocybele nasuta* Zone"), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

Etymology. After Strelka.

Diagnosis. Frontal glabellar lobe not as broadly expanded as in other species; dorsal surfaces with very dense, fine, and crowded raised line sculpture, tubercles faint on rear of glabella in large specimens, best expressed on LO; genal spine relatively short, with narrow dorsal flattened surface; pygidium small and narrow, with three rings but third ring tiny and visible mainly ventrally, completely lacking expression of posteromedian spine even in smaller specimens.

Description. *Aponileus strelkaae* is similar enough to the slightly older *A. belkaae* that extended written description would be redundant; all differences between the species are noted in the following differential description. Cranidium with anterior sections of facial sutures of large specimens anteriorly convergent, versus laterally bowed; cranidium considerably narrower across anterior border; glabella much narrower anteriorly, not strongly waisted, and considerably more dorsally vaulted; axial furrows essentially straight and oblique, versus bowed laterally anteriorly; librigenae with shorter genal spine (comparison is hampered by the fact that the spine is incomplete in many specimens, but compare the intact and similarly sized specimens of Pl. 8, fig. 1 and Pl. 12, fig. 1); librigenal field slightly narrower, with denser and more closely spaced anastomosing line sculpture; pygidium relatively smaller, narrower relative to length, with third segment poorly versus obviously expressed dorsally, and with much finer and denser raised lined sculpture on all surfaces; although there is some overlap, the second pleural furrow is very weakly expressed on all specimens of *A. strelkaae* whereas it is well expressed on many specimens of *A. belkaae*.

Discussion. Apart from the differences noted in the differential description, *A. strelkaae* is very similar to the slightly older *A. belkaae*. As noted several times above, reduction to three pygidial segments is a very unusual feature. *Aponileus strelkaae* extends this trend by greatly reducing the third segment. In dorsal view, it is not clearly differentiated from the terminal piece, but ventral views (Pl. 12, figs 15, 18) show that the third segment is definitely present.

***Aponileus ugolekae* n. sp.**
Plate 12, figs 21, 25–36, Plates 13–15, Plate 16, figs 15–19

Material. Holotype, cranidium, SUI 131127 (Pl. 13, figs 1, 3, 5, 9), and assigned specimens SUI 131128–131150, from Section J 46.3 m, assigned specimen SUI 129331 from Section J 40.0 m and assigned specimens SUI 129312–129215 from J 46.8 m, Wah Wah Formation (upper Floian; Blackhillsian; "*Pseudocybele nasuta* Zone"), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

Etymology. After Ugolëk.

Diagnosis. Cranidium entirely lacking tuberculate sculpture; cranidial fixigenae broader than in any other species; genal spine huge and scythe-like, very broad at base; librigenal field greatly reduced in area and narrow.

Description. Although *Aponileus ugolekae* has some striking autapomorphies, particularly on the librigena, it remains fundamentally similar to *A. belkaae*, and as with *A. strelkaae* description is best accomplished via an extended comparison with that species, cataloguing all differences. Cranidium with width across frontal areas relative to sagittal length approximately similar, but glabella relatively smaller, so that frontal areas and interocular fixigenae are considerably broader; axial furrows straight and oblique versus flared laterally anteriorly; glabella not waisted; glabella completely lacking tuberculate sculpture versus clearly retained sculpture on median and posterior areas; SO shallow and lacking any transverse ridge; LO narrower, longer, and lacking tubercles versus densely tuberculate; palpebral lobe somewhat larger, and much more anteriorly set.

Librigena with eye slightly narrower relative to length; field much narrower, both anteriorly and posteriorly; posterior border merged with genal spine in larger specimens versus clearly distinct; lateral border much more shallow anteriorly; genal spine huge, with base as wide as entire body of librigena, long, flattened, broad for most of length, and scythe-like, versus narrow, rapidly tapering, and only moderately long; anterior edge of genal spine base extended forward to connect with lateral border opposite midlength of eye versus behind rear of eye.

Pygidium of four versus three segments, though fourth only obvious in ventral view; raised line sculpture much finer and denser; tubercles completely absent from versus crowded on axis; pygidium wider relative to sagittal length; axis slightly longer and more V-shaped versus U-shaped posteriorly; axial furrows shallowed prior to posteromedian union, hint of a faint post-axial ridge in some specimens, versus confluent medially to fully circumscribe the axis posteriorly; axial rings poorly versus well expressed; pleural furrows shallow to obscure versus well expressed.

Discussion. The phylogenetic position of *Aponileus ulgolekae* was discussed under results of the analysis above. A key question is whether *A.*? *veterokae*, which is resolved as its sister species, is genuinely an ingroup *Aponileus*. This is dealt with under discussion of that species below.

***Aponileus*? *veterokae* n. sp.**
Plate 16, figs 1–14, Plates 17, 18

Material. Holotype, cranidium, SUI 129316 (Pl. 13, figs 1, 5, 8, 11, 14), and assigned specimens SUI 129317–129330, 129332–129337, from Section J 48.1 m, Wah Wah Formation (upper Floian; Blackhillsian; "*Pseudocybele nasuta* Zone"), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

Etymology. After Veterok.

Diagnosis. Glabella much narrower than any other species and anteriorly pointed; anterior border flat and long, not turned up as in all other species; sculpture on all sclerites more reduced than in any other species, but fine anastomosing lines present on most surfaces through most of ontogeny; librigenal lateral border furrow almost completely effaced in larger specimens; pygidium with large, long posteromedian spine.

Description. Cranidial measurements were made on the large, best preserved, holotype specimen of Pl. 17, fig. 1. Although the specimen of Pl. 17, fig. 15 is also well-preserved, it is much smaller and features such as the proportions of the glabella change during ontogeny, making it unsuitable for comparative measurement. Cranidium moderately vaulted (sag., tr.), broad, very broad across palpebral lobes (width across δ 114.8% sagittal length) and anteriorly expanded (width across γ 78.7% sagittal length and width across β 86.9% sagittal length), narrower posterior to palpebral lobes, with width across ε 81.2% sagittal length, cranidium effaced but for line sculpture, larger specimens increasingly effaced; anterior border moderately short, 8.2% sagittal cranidial length, tapered far exsagittally by cut of facial suture, otherwise of even length (very slightly shorter medially in front of glabella), broadly anteriorly bowed, somewhat pointed medially, dorsal surface horizontal to slightly anteroventrally sloped (lateral view), also gently dorsally bowed (anterior view), with lateral edges lower than middle section, and with sculpture of fine, closely spaced subparallel ridges following curvature of border on anterior third, posterior section effaced (in large specimens; small specimen of Pl. 17, fig. 2 with ridges on entire border); doublure mainly expressed as anterior face of border, very slightly ventroposteriorly curved to make a ventral rim, narrower than width of border and narrower yet ventrally, with ventromedially angled lateral margins from cut of facial suture, about half length of dorsally visible border, with sculpture of 6–7 subparallel ridges slightly coarser than those on dorsal border; anterior border furrow short and shallow (increasingly shallow in larger specimens), broadly anteriorly bowed, with median section around anterior margin of glabella more strongly bowed and deeper than lateral sections, tangent to preglabellar furrow medially; preglabellar furrow short, moderately deep, very strongly anteriorly bowed; frontal areas small, wedge-shaped, very short adaxially and only a little longer than anterior border at maximum abaxial length, fairly steeply anteroventrally sloped, about 35–40º below horizontal; anterior branch of facial suture long, very strongly laterally bowed around frontal areas; glabella large, long and broad, anteriorly expanded from SO to maximum width approximately even with β (except very slight waisting about halfway between SO and S1), then tapered along very strongly anteriorly bowed anterior margin, with sagittal length 76.6% cranidial length, maximum width 83.2% sagittal length, and minimum width across L1 75.8% maximum width, gently vaulted (sag., tr.), convexity less posteriorly, LF slopes down to anterior border at about 50–60º below horizontal, glabella with fine anastomosing line sculpture following curve of LF (Pl. 17, figs 2, 10) or effaced (larger specimens); lateral lobes and furrows poorly defined dorsally on large specimens, but better visible ventrally and on small specimens, all furrows moderately long and shallow, S1 occurs approximately even with half-length of palpebral lobe, posteromedially directed and widest, reaches almost to 1/3 glabellar width, S2 and S3 anteromedially directed, S3 occurs even with γ, very narrow, barely extends beyond axial furrow, S2 slightly closer to S3 than S1, about half width of S1; glabellar lobes not independently inflated, lateral lobes ill-defined by furrows, but L1 very long, L2 longer medially and shorter laterally due to opposite directions of S1 and S2, L3 a little shorter than maximum length of L2, LF very large, sub-semi-circular, median lobe very wide; SO moderately long and fairly shallow, shallower in larger specimens, very shallow near axial furrows (Pl. 17, fig. 2), course mainly transverse, far abaxial portions slightly anteriorly curved, with line sculpture like that of LO at least in small specimens (Pl. 17, figs 2, 15); LO moderately long, longest medially and tapered laterally, somewhat longer than anterior border, 16.3% sagittal length of cranidium, broad, with width across intersection of axial furrows and cranidial posterior margin 47.0% sagittal length of cranidium, LO only very slightly independently inflated, effaced (large specimens) or with fine anastomosing line sculpture and small median node located at mid-length (small specimens); doublure not well preserved except on single small specimen (Pl. 17, fig. 19), lens-shaped, long medially and pinched out laterally; axial furrows narrow, very shallow posteriorly, somewhat deeper from approximately S1 forward, deeper at lateral glabellar furrows, separated from preglabellar furrow by small, short, lightly swollen, oblique ridge located just in front of S3 (best seen on Pl. 17, figs 2, 10), course anteriorly divergent; fixigena almost all interocular, posterior fixigena just a short strip behind palpebral lobe and extending along posterior border, interocular fixigena narrow anteriorly, expanded posteriorly due to set of palpebral lobes and expansion of glabella, roughly horizontal opposite lobes, ends gently antero- or posteroventrally sloped; palpebral lobes gently anteroventrally sloped (exsag.), slightly elevated from horizontal (tr.), very large, long, with exsagittal length 33.1% cranidial sagittal length, irregularly sub-semi-circular in shape, wide, with maximum width occurring at about 1/3 length, tapered anteriorly and posteriorly, lobe with slightly more inflated lateral rim, bordered adaxially by slightly depressed, moderately narrow, laterally crescentic region bordering slightly raised, adaxial, semilunate area; palpebral furrows almost totally effaced dorsally, somewhat better visible ventrally, furrow located between raised semilunate area and crescentic depressed area, very narrow and very shallow, moderately laterally bowed; posterior

border furrow, posterior border, and its doublure extremely poorly known, border furrow moderately long and deep, shallow near glabella; posterior border short, very slightly inflated, higher posteriorly; preserved doublure only rim-like.

Rostral plate, hypostome, and thorax not identified.

Librigenae of *Aponileus? veterokae* are not well known from large specimens, and none are suitable for full measurements. Anterior branch of facial suture poorly preserved, particularly along anterior projection of border, much (over two times) longer than posterior branch, steeply sloped along field, broadly curved at lateral border, cuts border at shallow angle exposing large, triangular swath of inner face of doublure; posterior branch of facial suture short, slopes steeply down field from eye, less steeply sloped across posterior border; eye with visual surface made of tiny, closely packed lenses, long and narrow, crescentic–reniform, strongly raised, with steeply sloped lateral side almost perpendicular to librigenal field; eye rimmed at base by extremely fine raised ridge (Pl. 16, fig. 14); separated from librigenal field by narrow, moderately shallow circumocular furrow; librigenal field long and fairly narrow, with width from midlength of eye to lateral border furrow approximately (based on specimen of Pl. 16, fig. 3) 25.7% exsagittal length, field slightly narrower posteriorly, weakly laterally convex (tr.), effaced except for fine caecal pitting (Pl. 16, figs 1, 6); lateral border furrow better seen internally, highly effaced, broad and shallow, weakly laterally bowed; lateral border (including indistinct furrow) wide relative to field, approximately (based on Pl. 16, fig. 3) 60.0% as wide, gently laterally bowed, moderately inflated, with sculpture of subparallel, occasionally intersecting terrace lines following curvature of border and continuing onto genal spine; spine long, full extent unknown, but at least a little longer than librigenal field (Pl. 16, fig. 11), broad-based, gradually tapered, dorsoventrally flattened, blade-like, but moderately inflated, shallowly curved, with sculpture like that of border; posterior border furrow effaced dorsally, visible internally (Pl. 16, fig. 10); posterior border short, about half as long as width of lateral border, with terrace lines only on posterior margin; lateral doublure broad, nearly reaches border furrow, posterior section of doublure short, but also nearly reaches posterior furrow, doublure with slightly raised outer rim extending not quite to facial suture anteriorly, doublure sloped dorsolaterally toward field, with sculpture of fine terrace lines more widely spaced than those on external aspect, and with small Panderian notch near cut of posterior branch of facial suture.

Pygidial measurements were made on the well-preserved specimens of Pl. 18, figs 1, 12. Pygidium broad and shallowly vaulted (sag., tr.), with maximum width across posterior band of first segment (even with rear of articulating facet) 220.7% (216.5, 224.8%) sagittal length excluding articulating half ring and posterior median spine, with semilunate main body and long posterior spine, and with curvilinear sculpture of fine ridges over entire surface; articulating half ring short, 7.7% (6.5, 8.8%) sagittal length of pygidium, shorter laterally, sculptured with terrace lines; articulating furrow short, fairly shallow, transverse; axis of four rings and terminal piece, strongly vaulted, gradually less vaulted posteriorly, with steep slope from top of terminal piece to base of spine, broad, with width across first ring 33.5% (32.8, 34.2%) pygidial width, gradually posteriorly tapered, with third ring 77.5% (76.3, 78.7%) width of first ring, relatively long, with sagittal length 80.5% (79.2, 81.8%) sagittal pygidial length; axial rings poorly defined by furrows, only very slightly independently inflated, rings of nearly equal length, only slightly shorter posteriorly, second ring (possibly also third) with short, crescentic pseudo-articulating half ring; terminal piece fairly short and wide, ill-defined, with sloped posterior margin; inter-ring furrows moderately short, progressively shorter posteriorly, very shallow, better viewed ventrally (Pl. 18, fig. 4), fourth furrow basically effaced, all furrows transverse; axial furrows narrow, moderately deep, steadily anteriorly divergent; post-axial furrow long, moderately deep, effaced medially in most, but not all (Pl. 18, figs 12, 17) specimens; posterior spine very long, at least 150% (Pl. 18, fig. 12) longer than main part of pygidium (although spines of larger specimens may be relatively shorter; the spine of Pl. 12, fig. 14 is about equal in length to the pygidium), conical, strongly posteriorly tapered, posterodorsally angled about 15º above horizontal, with sculpture of discontinuous (although many wrap around to ventral face), anastomosing, generally slightly posteriorly curved ridges, somewhat resembling overlapping scales, slightly more regularly curved, more like a chevron pattern ventrally, spine protrudes from posterior border, but dorsal base possibly connected to rear of axis by narrow and faint post-axial ridge in some specimens (e.g., Pl. 18, figs 1, 5); pleurae mostly ill-defined by furrows, pleural bands slightly independently inflated, pleural bands all short, posterior bands and anterior bands of subsequent segments (starting with first segment) merged due to indistinct interpleural furrows to appearance of single long band, pleurae increasingly posteriorly angled; inner pleurae wide anteriorly, about half width of pleurae (anterior view), progressively narrower posteriorly as tail tapers, separated by fulcral angle of about 143º (anteriorly); anterior pleural band of first segment

short adaxially, lengthened abaxially into large articulating facet; pleural furrows very long, longer exsagittally, moderately shallow, first furrow gently posterolaterally directed, posterior furrows increasingly posterolaterally angled, fourth furrow steep; interpleural furrows effaced, without even a ventral presence; pygidial border moderately wide, poorly independently inflated, separated from pleural bands by wide, shallow, indistinct furrow, sculpture (best seen in lateral and posterior views) of sideways "V"s, with vertices pointed anterolaterally, and with ventral line of "V" extended into subparallel ridges continuing onto doublure; doublure moderately wide/long, of equal extent (ventral view), anterolateral parts dorsomedially angled while posteromedial parts are tucked up inside posterior of tail, so that doublure appears to taper in anterior view, doublure with sculpture of subparallel ridges a little coarser than those of dorsal sculpture.

Ontogeny. Cranidia of *A.*? *veterokae* are not very well preserved, but ontogenetic changes can still be observed. The cranidium becomes broader overall; the anterior border shortens; the palpebral lobes become relatively smaller; the glabella broadens anteriorly, changing from bullet-shaped to anteriorly expanded; and all the cranidial furrows become slightly longer/wider and shallower.

Librigenae are generally poorly preserved, but the librigenal field becomes slightly wider relative to the length; the lateral border furrow becomes completely effaced; and the lateral border inflates.

Pygidia broaden overall; all furrows shallow; the lateral border furrow becomes completely effaced and the border inflates to match the pleurae; the axis broadens and loses some convexity; the posterior median spine shortens; and the anastomosing line sculpture becomes more effaced, except on border and spine.

Discussion. *Aponileus*? *veterokae* is obviously very different from all other species included in the genus, so much so that although we consider on balance that it belongs we have opted to assign it with question. It has a "normal" flattened anterior border, a glabella that is not greatly expanded anteriorly and which comes to a blunt point anteromedially, it displays a faint oblique ridge crossing the axial furrow opposite the frontal glabellar lobe, it has smaller palpebral lobes than any other species, and most obviously it has a pygidium with a large posteromedian spine. All of these features are common within *Acidiphorus* and superficially it might appear this is the taxon to which the species should be assigned. However, despite these similarities, the species does not closely resemble any species of *Acidiphorus* known from the literature, nor the many new species awaiting description in our collections. Species of *Acidiphorus* almost all have a nasute anterior border, which *A.*? *veterokae* lacks, they have cylindrical or subcylindrical genal spines (where not strongly reduced) whereas those of *A.*? *veterokae* are flattened and blade-like, and they almost all have strong tuberculate sculpture on most surfaces, whereas *A.*? *veterokae* has a sculpture of very fine, subdued, anastomosing lines on most surfaces. It is hard to make any detailed case for a relationship with any species of *Acidiphorus*.

Despite the autapomorphic features, *A.*? *veterokae* seems to share more characters with *Aponileus*, and in particular the slightly older *A. ugolekae*. Although the glabella is narrower and the palpebral lobes are smaller, they are still generally similar in plan and *A.*? *veterokae* remains a very large-eyed species. The sculpture of most surfaces is a direct match, save for its progressive effacement in *A.*? *veterokae*. The structure of the librigena is particularly compelling, as *A.*? *veterokae* retains the same basic dimensions and particularly the blade-like genal spine characteristic of *Aponileus*. It particularly resembles *A. ugolekae* in the fashion in which the base of the genal spine is flattened and merged with the posterior border furrow into a single continuous face. Pygidia of the two species are virtually identical with the (prominent) exception of the huge spine developed in *A.*? *veterokae*, with nearly indistinguishable sculpture and expression of pleural and ring furrows.

The shared features are convincing enough, especially given the absence of any other known species with which *A.*? *veterokae* compares in detail, that we consider the best supported current hypothesis to be that it is a highly autapomorphic species of *Aponileus*, sister to *A. ugolekae*. The autapomorphies are so striking, however, that we acknowledge the issue should remain open, and assign the species only with question.

Psephosthenaspis Whittington, 1953

= *Ludvigsenella* Tremblay and Westrop, 1991

Type species. *Bathyurellus strenuus* Billings, 1865, from a boulder at St. Antoine de Tilly, Quebec, Canada.

Other species. *Ludvigsenella ellipsepyga* Tremblay and Westrop, 1991, Sunblood Formation (Dapingian), Northwest Territories, Canada; *Psephosthenaspis glabrior* Fortey and Droser, 1996, Juab Formation (Dapingian),

Utah, USA; *P. microspinosa* Fortey and Droser, 1996, Juab Formation (Dapingian), Utah, USA; *Acidiphorus*? *pseudobathyurus* Ross, 1967, Garden City Formation (Dapingian), Utah, USA.

Diagnosis. See Fortey and Droser (1996, p. 82).

Discussion. *Psephosthenaspis*, prior to the work of Fortey and Droser (1996), was a taxon comparable to *Aponileus*: monotypic, little discussed, and with an incompletely known type species. Fortey and Droser (1996) recognized *Acidiphorus*? *pseudobathyurus* Ross, 1967, and *Ludvigsenella ellipsepyga* Tremblay and Westrop, 1991, as members of the genus, and described two new species from the Dapingian of western Utah.

As noted above, Adrain (in Jell and Adrain, 2003) placed *Aponileus* in subjective synonymy of *Psephosthenaspis*. At the time *Aponileus* was known only from Hu's (1963) illustrations of its unique type species. There are certainly several points of similarity. Both genera feature species with an upturned anterior border, a forwardly expanding glabella which occupies most of the area of the cranidium anteriorly and often exhibits waisting, anastomosing raised line sculpture (often mixed to greater or lesser extent with tuberculate sculpture), very large palpebral lobes, librigenae with a blade-like genal spine, and pygidia of similar dimensions which often exhibit a very small posteromedian spine in large specimens.

These similarities, however, are strongest when comparing the youngest known species of *Psephosthenaspis*, *P. glabrior*, with younger species of *Aponileus*. Fortey and Droser (1996) demonstrated that three species of *Psephosthenaspis* occur in stratigraphic succession in the Juab Formation at Ibex. We will present a detailed phylogenetic analysis of the overall group in a later work, but we agree with Fortey and Droser that stratigraphic order correlates with phylogenetic order in these species and that *Psephosthenaspis microspinosa* Fortey and Droser, the oldest known species, is phylogenetically basal to the genus. There are many aspects of morphology, discussed by Fortey and Droser (1996) in which *P. pseudobathyurus* (Ross, 1967) shows transition in states from the older *P. microspinosa* to the younger *P. glabrior*. This suggests that the morphology of *P. glabrior* is a poor comparison for *Aponileus*, as much of it is derived within *Psephosthenaspis*. The affinity of *Psephosthenaspis* is best considered with reference to the morphology of *P. microspinosa*.

Fortey and Droser (1996, p. 83) entertained the idea that *Psephosthenaspis* was related to species currently assigned to *Jeffersonia* Poulsen, 1927, but instead favoured the hypothesis that *Acidiphorus brevus* (Hintze, 1953) was closely related to, and possibly a member of, *Psephosthenaspis*. *Acidiphorus brevus* is presently not well known. We will revise it on the basis of rich new collections in a forthcoming work. We have also discovered several new species from the "*Pseudocybele nasuta* Zone" that are closely related to it. All will be described in detail later, but we briefly figure one of them here as Figure 6 for purposes of comparison. This species, from high in the "zone" (Assemblage 5 of Figure 1) is extremely morphologically similar to *P. microspinosa*, differing mainly in minor proportions. The undescribed species retains a slightly nasute border which is lost in *Psephosthenaspis*, but the border is very short as in *P. microspinosa*. The librigena of *P. microspinosa* shows a distinct dorsal ridge on the genal spine which foreshadows the blade-like structure developed in *P. glabrior*. That of *"Acidiphorus"* n. sp. does not have a distinct ridge, but is dorsally swollen in the same area. Pygidia differ only in the relatively better impressed border furrow in *P. microspinosa*.

Hence we agree with Fortey and Droser (1996) and consider that the sister taxon of the Dapingian *Psephosthenaspis* is among this upper Floian group which includes *"A." brevus* and *"A."* n. sp. (Fig. 6). Detailed systematics of this group, including genus assignments, must await description of many undescribed species and comprehensive phylogenetic analysis of the *Acidiphorus* group. Recognition of the affinities of *Psephosthenaspis* nevertheless strongly indicates that it is a separate clade, not particularly closely related to *Aponileus*.

Psephosthenaspis glabrior **Fortey and Droser, 1996**

Plates 19, 20

1996 *Psephosthenaspis glabrior* Fortey and Droser, p. 87, fig. 11.1–11.11.

Material. Assigned specimens SUI 129338–129357, from Locality K-1, Kanosh Formation (Dapingian), base of Section K-South, Fossil Mountain, Confusion Range, Ibex area, Millard County, western Utah, USA.

Discussion. Fortey and Droser (1996) described *P. glabrior* on the basis of two cranidia, a librigena, and three pygidia from a single horizon high in the Juab Formation at Ibex Section J. They indicated (Fortey and Droser,

1996, fig. 2, left part) that it occurred at three higher horizons but did not illustrate material from these. The highest occurrence was about five metres below the contact with the overlying Kanosh Formation. At Section K-South (see Hintze, 1973) a silicified fauna occurs immediately above this contact. This is Hintze's (1953, p. 41) sample K-1 which he listed as occurring at five feet (1.5 m) above the contact. We have made new collections from this level. There is no outcrop of the bed containing the silicified fossils, but fossiliferous talus occurs as small lumps clearly arranged along strike, so there is little question the fossils are essentially in situ. The fauna is dominated by species of the bathyurid *Pseudoolenoides* Hintze, 1953, but rare sclerites belonging to *Psephosthenaspis* also occur. Following extensive sampling, enough are available to adequately treat the taxon.

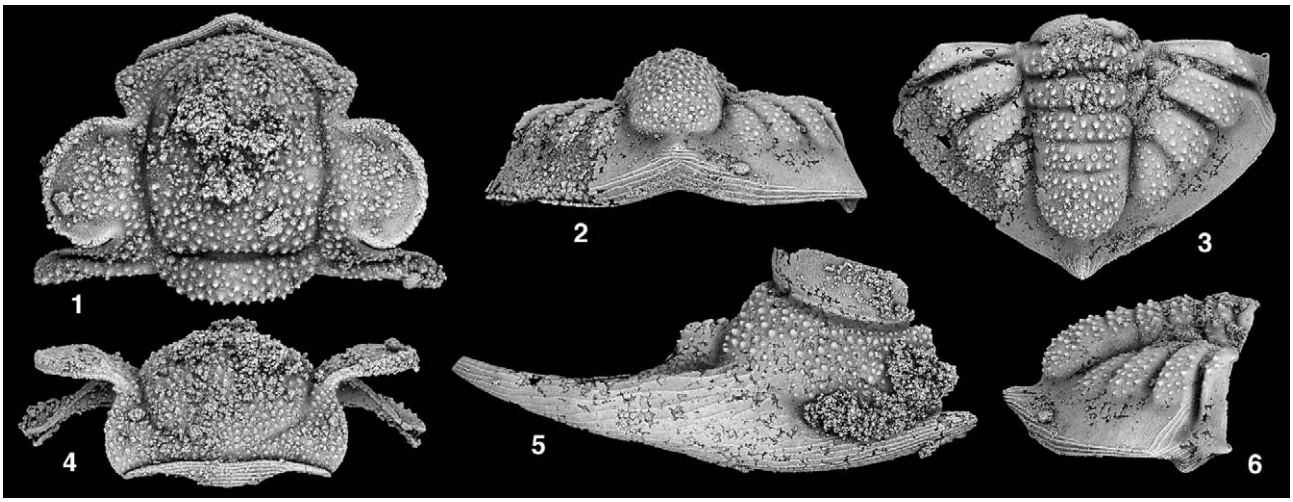

FIGURE 6. *"Acidiphorus"* n. sp., from Section J 40.0 m, Wah Wah Formation (upper Floian; Blackhillsian; "*Pseudocybele nasuta* Zone"), southern Confusion Range, Ibex area, Millard County, western Utah, USA. This species and other undescribed species from the "*Pseudocybele nasuta* Zone" are closely related to the younger *Psephosthenaspis* Whittington, 1953. It is illustrated to facilitate comparison and will be described in detail in a forthcoming work. See text for discussion. 1, 4. Cranidium, SUI 131853, dorsal and anterior views, x7.5. 2, 3, 6. Pygidium, SUI 131854, posterior, dorsal, and right lateral views, x6. 5. Right librigena, SUI 131855, external view, x5.

The sclerites appear to represent *P. glabrior*, and the material is important in supplementing knowledge of the species, in particular showing ventral and internal surfaces and providing insight into earlier holaspid ontogeny. The silicified pygidia are shorter (sag.) relative to their length than the holotype, but the holotype is very large, more than double the size of any other known specimen. When the largest silicified pygidium (Pl. 20, fig. 23) is compared with the second largest calcareous pygidium (Fortey and Droser, 1996, fig. 11. 7), which is only slightly larger, the proportions are almost the same. Smaller silicified pygidia (e.g., Pl. 20, fig. 31) suggest that the pygidium becomes increasingly longer with respect to its width through ontogeny. Differences that are less easy to dismiss involve the expression of furrows on the pygidium. The first pleural furrow is incised in the smaller silicified pygidia (Pl. 20, figs 16, 22) but it is weak on the largest (Pl. 20, fig. 23). The second pleural furrow is not deeply impressed on any specimens. Further, only the first and, more weakly, the second ring furrows are well expressed on the silicified specimens, and only abaxially. The type material shows a very deeply impressed first pleural furrow, a similarly deep second pleural furrow, and all of the ring furrows deep and well impressed. These differences cannot be due to either preservation (both sets of material are very well preserved) or ontogeny (as the pygidium of Fortey and Droser, 1996, fig. 11.7 is similar in size to that of Pl. 20, fig. 23). Hence an argument could be made that the Kanosh species is diagnosibly distinct from *P. glabrior* and should be named as a separate taxon. Although information is somewhat limited, there are no apparent differences between the cranidia and librigenae in either sample. We prefer to assign all of the material to one species, but the question could be further investigated were a more extensive sample of cranidial and librigenal material of the Juab *P. glabrior* available.

Cranidia appear to change very little, despite the fact that the largest available specimen (Pl. 19, fig. 3) is nearly three times the size of the smallest (Pl. 19, fig. 1). Dense but relatively subdued tuberculate sculpture covers the glabella (the large specimen of Pl. 19, fig. 3 has clearly been effaced, with the tubercles cut across their bases). The relative size of the palpebral lobe also seems stable through ontogeny. Neither of the two calcareous cranidia

have the posterior projections exposed or preserved. The largest silicified cranidium (Pl. 19, fig. 3) shows that it was very slender.

Librigenae reveal that the Panderian notch is small and located near the posterior facial suture (Pl. 20, figs 5, 7). Across the size range represented, there is no obvious trend in the length of the genal spine. However, the librigenal field is markedly broader anteriorly in the largest specimens (Pl. 20, fig. 15) versus the smallest (Pl. 20, fig. 3). The silicified librigenae show that the genal spine, including its swollen base, is densely covered with subparallel raised lines (the single calcareous specimen is exfoliated in this region).

The silicified librigenal material also confirms that *Psephosthenaspis*, despite the superficial similarity, is morphologically very different in detail to *Aponileus*. The librigena of *P. glabrior* retains a strong and complete socle, as does that of *P. microspinosa*. This feature is only faintly retained in the phylogenetically basal species of *Aponileus* and lost in all later species. The Panderian notch of *P. glabrior* is small and crowded near the posterior facial suture. That of species of *Aponileus* (e.g., Pl. 4, figs 2, 3, Pl. 8, figs 16, 20) is much larger and set further forward. The librigenal doublure of *P. glabrior* is very wide posteriorly, more than double its anterior width. That of species of *Aponileus* is of similar width along the cheek, expanded only slightly posteriorly. The librigenal lateral and posterior border furrows of *P. glabrior* are complete and connected in front of the genal spine. These furrows are effaced posteriorly in most species of *Aponileus*.

Acknowledgements

Research was supported by National Science Foundation grant DEB 0716065. Tiffany Adrain provided assistance with SUI numbers, loans, and curation. We are grateful to Arvid Aase for donating his specimen for study, to the staff of the United States Museum of Natural History, Smithsonian Institution, for loan of the type material of *Aponileus latus*, and to David Harper, Geologisk Museum, Copenhagen, for loan of the type material of *Aponileus glaber*. The *Aponileus aasei* holotype specimen was prepared by Gerry Kloc. We are grateful to Lucy McCobb and an anonymous referee for helpful comments on the manuscript.

Literature cited

Adrain, J.M. & Westrop, S.R. (2005) Lower Ordovician trilobites from the Baumann Fiord Formation, Ellesmere Island, Arctic Canada. *Canadian Journal of Earth Sciences*, 42, 1523–1546.

Adrain, J.M., McAdams, N.E.B. & Westrop, S.R. (2009) Trilobite biostratigraphy and revised bases of the Tulean and Blackhillsian Stages of the Ibexian Series, Lower Ordovician, western United States. *Memoirs of the Association of Australasian Palaeontologists*, 37, 541–610.

Adrain, J.M., McAdams, N.E.B. & Westrop, S.R. (In press) Systematics and affinity of the Lower Ordovician (Tulean; lower Floian) trilobite *Psalikilopsis*. *Memoirs of the Association of Australasian Palaeontologists*.

Adrain, J.M., McAdams, N.E.B. & Westrop, S.R. (In review) Affinities of the Lower Ordovician (Tulean; lower Floian) trilobite *Gladiatoria*, with species from the Great Basin, western United States. *Memoirs of the Association of Australasian Palaeontologists*.

Billings, E. (1859) Fossils of the Calciferous Sandrock, including those of a deposit of white limestone at Mingan, supposed to belong to the formation. *Canadian Naturalist and Geologist*, 4, 345–367.

Billings, E. (1865) *Palaeozoic fossils. Vol. I (4)*. Geological Survey of Canada, Montreal, pp. 169–344.

Boyce, W.D., Knight, I., Rohr, D.M., Williams, S.H. & Measures, E.A. (2000) The upper St. George Group, western Port au Port Peninsula: Lithostratigraphy, biostratigraphy, depositional environments and regional implications. 2000-1, 101–125.

Brett, K.D. & Westrop, S.R. (1996) Trilobites of the Lower Ordovician (Ibexian) Fort Cassin Formation, Champlain Valley regions, New York State and Vermont. *Journal of Paleontology*, 70, 408–427.

Derby, J.R. (1975) Lower Ordovician-Middle Ordovician boundary in western Arbuckle Mountains, Oklahoma. *In*: Ham, W.E. (Ed.), *Regional Geology of the Arbuckle Mountains, Oklahoma. Guidebook for Field Trip No. 5, November 10-11, 1973*. Oklahoma Geological Survey, The University of Oklahoma, Norman, Oklahoma, pp. 24–26.

Fortey, R.A. & Bruton, D.L. (1973) Cambrian-Ordovician rocks adjacent to Hinlopenstretet, North Ny Friesland, Spitsbergen. *Geological Society of America Bulletin*, 84, 2227–2242.

Fortey, R.A. & Droser, M.L. (1996) Trilobites at the base of the Middle Ordovician, western United States. *Journal of Paleontology*, 70, 73–99.

Goloboff, P.A., Farris, J.S., Källersjö, M., Oxelman, B., Ramírez, M.J. & Szumik, C.A. (2003) Improvements to resampling measures of group support. *Cladistics*, 19, 324–332.

Hintze, L.F. (1951) Lower Ordovician detailed stratigraphic sections for western Utah. *Utah Geological and Mineralogical Survey Bulletin*, 39, 1–99.
Hintze, L.F. (1953) Lower Ordovician trilobites from western Utah and eastern Nevada. *Utah Geological and Mineralogical Survey Bulletin*, 48, 1–249. (for 1952)
Hintze, L.F. (1973) Lower and Middle Ordovician stratigraphic sections in the Ibex area, Millard County, Utah. *Brigham Young University Geology Studies*, 20, 3–36.
Hu, C.-H. (1963) Some Lower Ordovician trilobites from Franklin Mountains, Texas. *Transactions and Proceedings of the Palaeontological Society of Japan*, N.S. 51, 86–90.
Hughes, C.P. (1979) The Ordovician trilobite faunas of the Builth-Llandrindod Inlier, central Wales. Part III. *Bulletin of the British Museum (Natural History), Geology Series*, 32, 109–181.
Hupé, P. (1955) Classification des Trilobites. *Annales de Paléontologie*, 41, 111–345.
Jell, P.A. & Adrain, J.M. (2003) Available generic names for trilobites. *Memoirs of the Queensland Museum*, 48, 331–553.
Lochman-Balk, C. & Wilson, J.L. (1967) Stratigraphy of Upper Cambrian-Lower Ordovician subsurface sequence in Williston Basin. *The American Association of Petroleum Geologists Bulletin*, 51, 883–917.
McAdams, N.E.B. & Adrain, J.M. (2007) Phylogenetics of the Ordovician *Acidiphorus*-group bathyurid trilobites. *Geological Society of America Abstracts with Programs*, 39(6), 499.
McAdams, N.E.B. & Adrain, J.M. (2010) A new species of the Lower Ordovician pliomerid trilobite *Pseudocybele* and its biostratigraphic significance. *Zootaxa*, 2550, 21–38.
Poulsen, C. (1927) The Cambrian, Ozarkian and Canadian faunas of northwest Greenland. *Meddelelser om Grønland*, 70, 235–343.
Poulsen, C. (1946) Notes on Cambro-Ordovician fossils collected by the Oxford University Ellesmere Land Expedition 1934-5. *Quarterly Journal of the Geological Society of London*, 102, 299–337.
Raymond, P.E. (1910) Notes on Ordovician trilobites, II. Asaphidae from the Beekmantown. *Annals of the Carnegie Museum*, 7, 35–44.
Raymond, P.E. (1925) Some trilobites of the lower Middle Ordovician of eastern North America. *Bulletin of the Museum of Comparative Zoology, Harvard University*, 67, 1–180.
Ross, R.J., Jr. (1949) Stratigraphy and trilobite faunal zones of the Garden City Formation, northeastern Utah. *American Journal of Science*, 247, 472–491.
Ross, R.J., Jr. (1951) Stratigraphy of the Garden City Formation in northeastern Utah, and its trilobite faunas. *Peabody Museum of Natural History, Yale University, Bulletin*, 6, 1–161.
Ross, R.J., Jr. (1953) Additional Garden City (Early Ordovician) trilobites. *Journal of Paleontology*, 27, 633–646.
Ross, R.J., Jr. (1967) Some Middle Ordovician brachiopods and trilobites from the Basin Ranges, western United States. *United States Geological Survey Professional Paper*, 523-D, 1–43.
Ross, R.J., Jr. (1970) Ordovician brachiopods, trilobites, and stratigraphy in eastern and central Nevada. *United States Geological Survey Professional Paper*, 639, 1–103.
Tremblay, J.V. & Westrop, S.R. (1991) Middle Ordovician (Whiterockian) trilobites from the Sunblood Formation, District of Mackenzie, Canada. *Journal of Paleontology*, 65, 801–824.
Ulrich, E.O. (1927) Fossiliferous boulders in the Ouachita "Caney" shale and the age of the shale containing them. *Oklahoma Geological Survey Bulletin*, 45, 1–48.
Walcott, C.D. (1886) Second contribution to the studies on the Cambrian faunas of North America. *United States Geological Survey Bulletin*, 30, 1–369.
Whittington, H.B. (1948) A new Lower Ordovician trilobite. *Journal of Paleontology*, 22, 567–572.
Whittington, H.B. (1953) North American Bathyuridae and Leiostegiidae (Trilobita). *Journal of Paleontology*, 27, 647–678.
Young, G.E. (1973) An Ordovician (Arenigian) trilobite faunule of great diversity from the Ibex area, western Utah. *Brigham Young University Geology Studies*, 20, 91–115.

PLATE 1

Aponileus latus Hu, 1963, from the Padre Formation (El Paso Group; upper Floian; Blackhillsian), Scenic Drive Section, Franklin Mountains, El Paso County, western Texas, USA.

1, 3, 5. Cranidium, **holotype**, USNM 143342, dorsal, anterior, and left lateral views, x4.
2, 4. Cranidium, USNM 143343a, dorsal and anterior views, x15.
6, 7. Right librigena, USNM 143343b, external and ventrolateral views, x8.
8, 10, 12. Pygidium, USNM 143343c, right lateral, dorsal, and posterior views, x12.
9, 11, 13. Pygidium, USNM 143343d, left lateral, dorsal, and posterior views, x8.

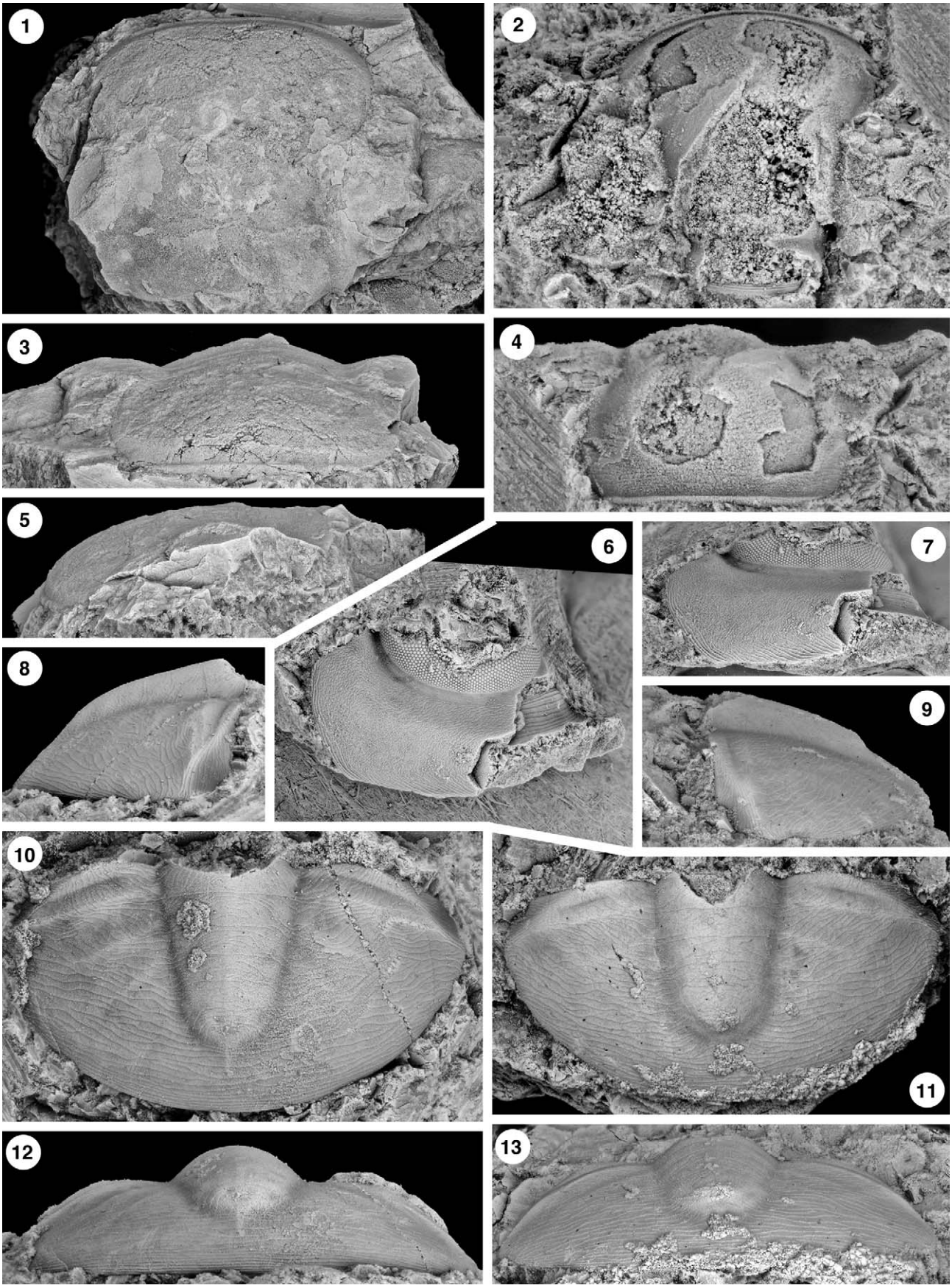

PLATE 2

Aponileus aasei **n. sp.**, from float high in Section H, Fillmore Formation (upper Floian; Blackhillsian; probably *Pseudocybele parana-suta* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

1–6. Dorsal exoskeleton, **holotype**, BYU 19975, dorsal view (x5), lateral detail of left librigena (x.7.5), external detail of left librigena (x7.5.), anterior view (x4.5), left lateral view (x3.5), and detail of cephalon (x9).

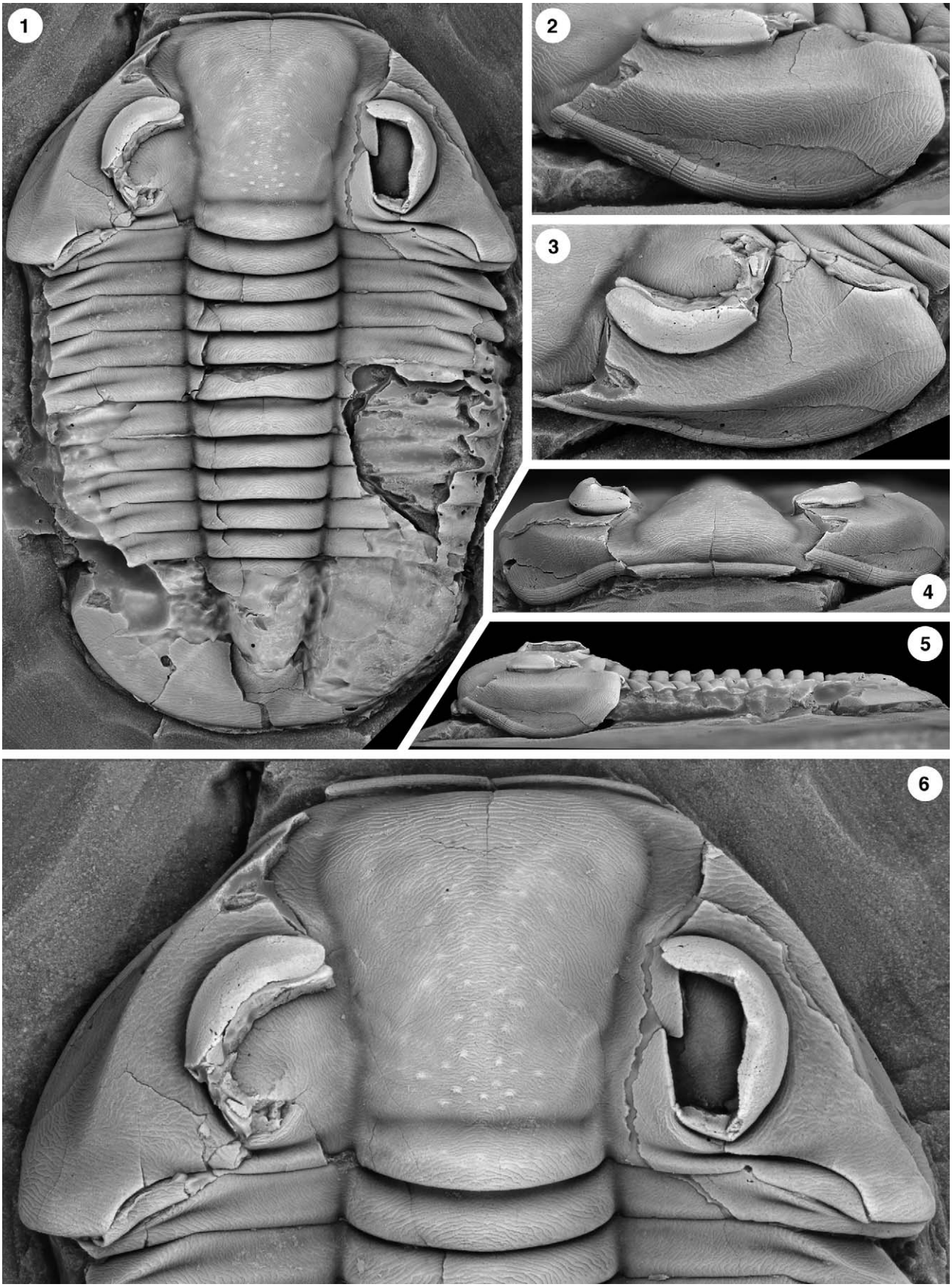

PLATE 3

Aponileus laikaae **n. sp.**, from Section H 256–261T m and H 264–267T m, Fillmore Formation (upper Floian; Blackhillsian; *Presbynileus ibexensis* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

1, 4, 8, 10. Cranidium, **holotype**, SUI 129234, dorsal, ventral, left lateral, and anterior views, x12 (H 256–261T m).
2, 5, 9, 11, 13. Cranidium, SUI 129235, dorsal, ventral, left lateral, oblique, and anterior views, x15 (H 256–261T m).
3, 6, 7. Cranidium, SUI 129236, dorsal, right lateral, and anterior views, x12 (H 256–261T m).
12, 14, 18. Cranidium, SUI 129237, dorsal, anterior, and left lateral views, x7.5 (H 256–261T m).
15, 16, 19, 20. Hypostome, SUI 129238, ventral, left lateral, posterior, and dorsal views, x15 (H 256–261T m).
17, 21-23. Thoracic segment, SUI 129239, right lateral, posterior, anterior, and dorsal views, x12 (H 264–267T m).

PLATE 4

Aponileus laikaae **n. sp.**, from Section H 256–261T m, Fillmore Formation (upper Floian; Blackhillsian; *Presbynileus ibexensis* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

1. Left librigena, SUI 129240, external view, x5.
2, 4, 5. Left librigena, SUI 129241, internal, external, and ventrolateral views, x5.
3, 6. Right librigena, SUI 129242, internal and external views, x6.
7. Right librigena, SUI 129243, external view, x10.
8. Left librigena, SUI 129244, external view, x7.5.
9. Left librigena, SUI 129245, external view, x12.
10–13. Thoracic segment, SUI 129246, dorsal, anterior, posterior, and right lateral views, x6.
14. Left librigena, SUI 129247, external view, x12.
15, 17, 20, 21, 23. Thoracic segment, SUI 129248, ventral, dorsal, anterior, left lateral, and posterior views, x10.
16, 18, 19, 22, 24. Thoracic segment, SUI 129249, dorsal, left lateral, ventral, anterior, and posterior views, x6.
25–29. Thoracic segment, SUI 129250, anterior, dorsal, posterior, left lateral, and ventral views, x12.

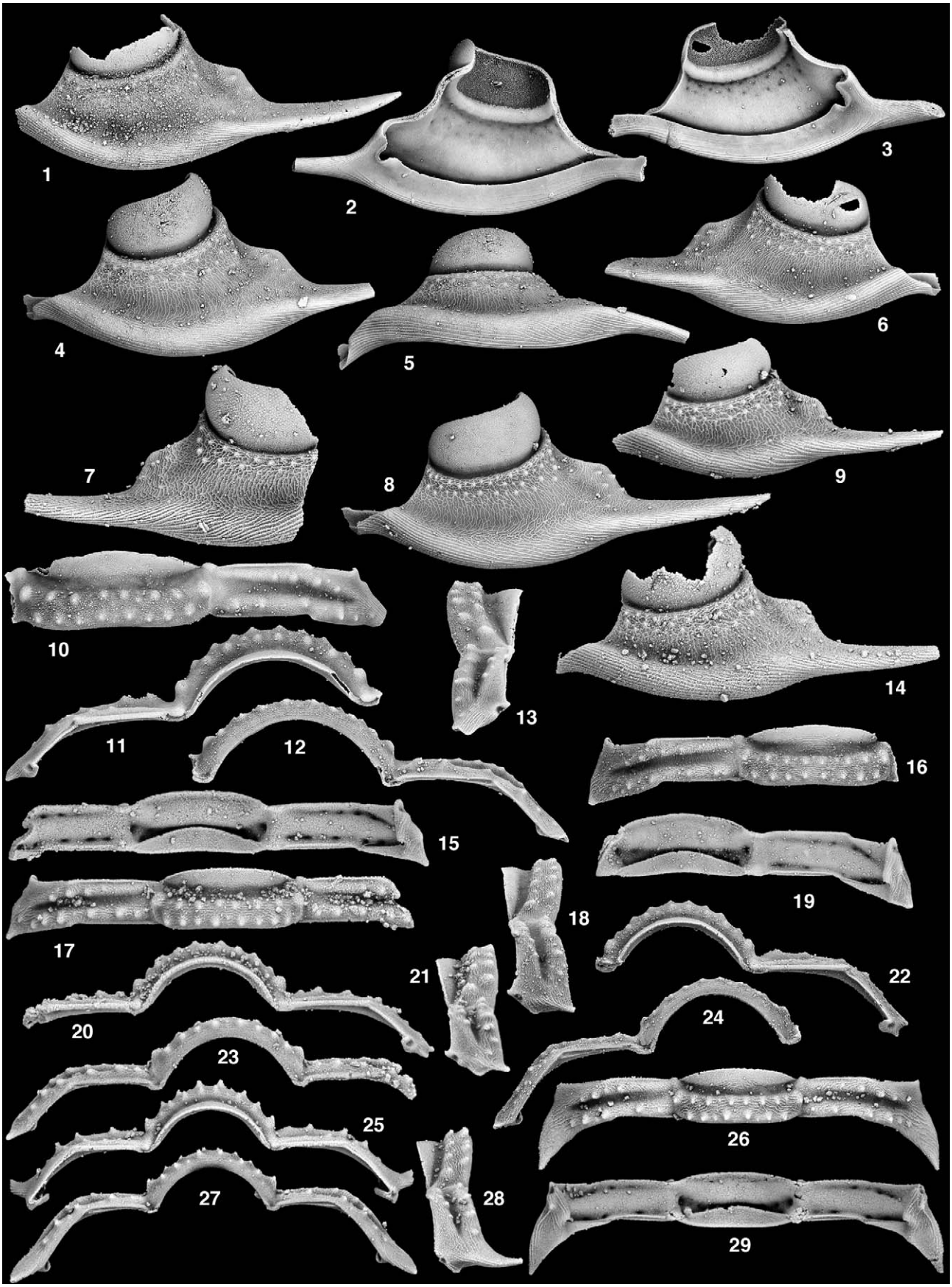

PLATE 5

Aponileus laikaae **n. sp.**, from Section H 256–261T m, Fillmore Formation (upper Floian; Blackhillsian; *Presbynileus ibexensis* Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

1, 4, 6, 9. Pygidium, SUI 129251, dorsal, posterior, right lateral, and ventral views, x10.
2, 3, 5, 7, 8. Pygidium, SUI 129252, posterior, dorsal, anterior, left lateral, and ventral views, x12.
10, 12, 13. Pygidium, SUI 129253, posterior, dorsal, and left lateral views, x12.
11, 14, 15. Pygidium, SUI 129254, posterior, right lateral, and dorsal views, x10.

Aponileus belkaae n. sp., from Section J 16.0 m, Wah Wah Formation (upper Floian; Blackhillsian; "*Pseudocybele nasuta*" Zone), southern Confusion Range, Ibex area, Millard County, western Utah.

16, 20, 23, 24. Cranidium, SUI 129255, dorsal, anterior, right lateral, and oblique views, x8.
17–19. Cranidium, SUI 129256, right lateral, anterior, and dorsal views, x9.
21, 22, 25. Cranidium, SUI 129257, right lateral, anterior, and dorsal views, x10.

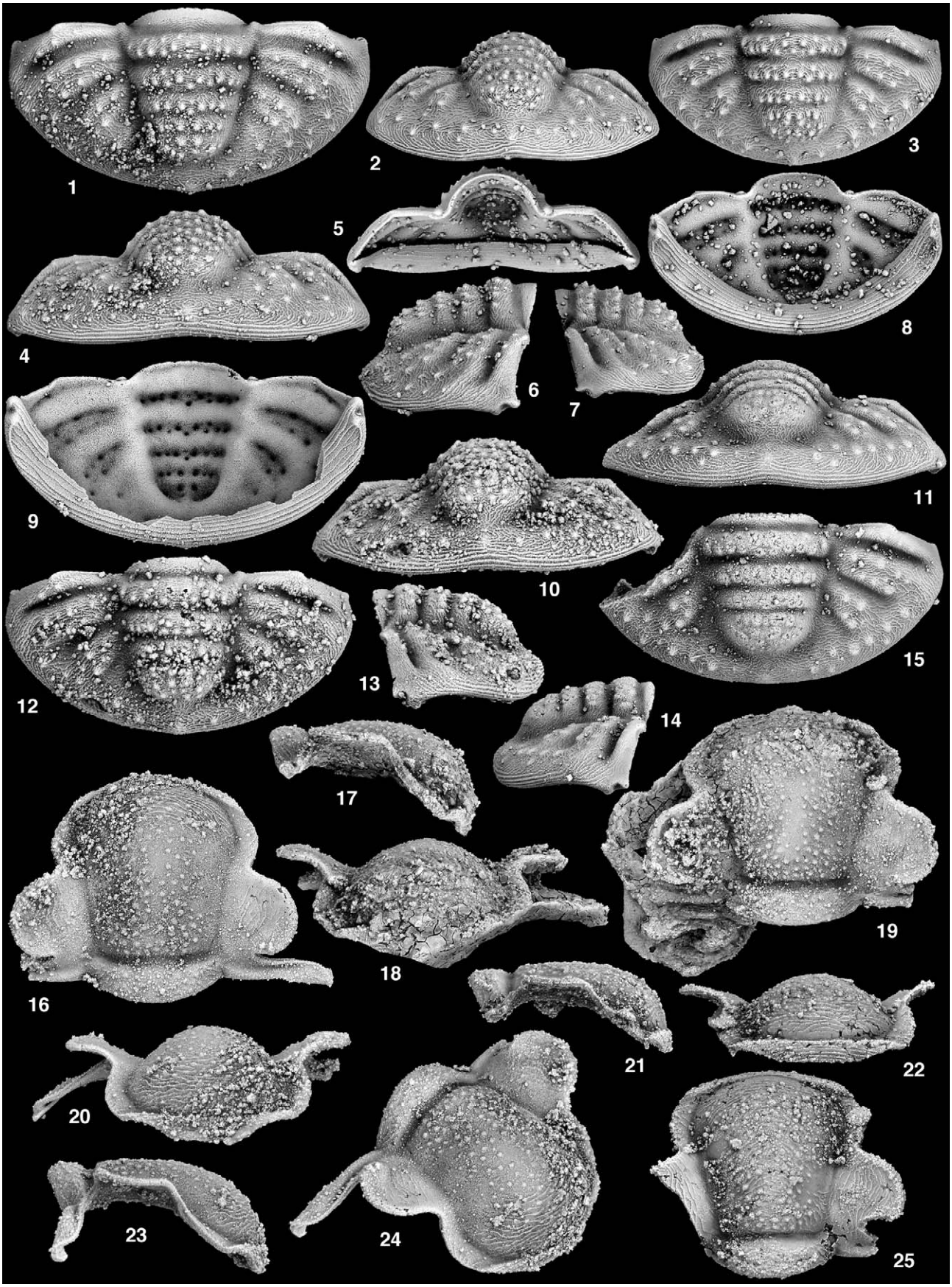

PLATE 6

Aponileus belkaae **n. sp.**, from Section J 16.1 m and J 20.0 m, Wah Wah Formation (upper Floian; Blackhillsian; "*Pseudocybele nasuta*" Zone), southern Confusion Range, Ibex area, Millard County, western Utah.

1, 6, 9, 12. Cranidium, **holotype**, SUI 129258, dorsal, ventral, anterior, and left lateral views, x10 (J 16.1 m).
2, 7, 11. Cranidium, SUI 129259, dorsal, anterior, and left lateral views, x15 (J 20.0 m).
3, 4, 5. Cranidium, SUI 129260, dorsal, anterior, and right lateral views, x10 (J 16.1 m).
8, 10, 13–15. Cranidium, SUI 115403, anterior, dorsal, oblique, right lateral, and anterior views, x12 (J 16.1 m).
16-18. Cranidium, SUI 129261, dorsal, right lateral, and anterior views, x15 (J 16.1 m).

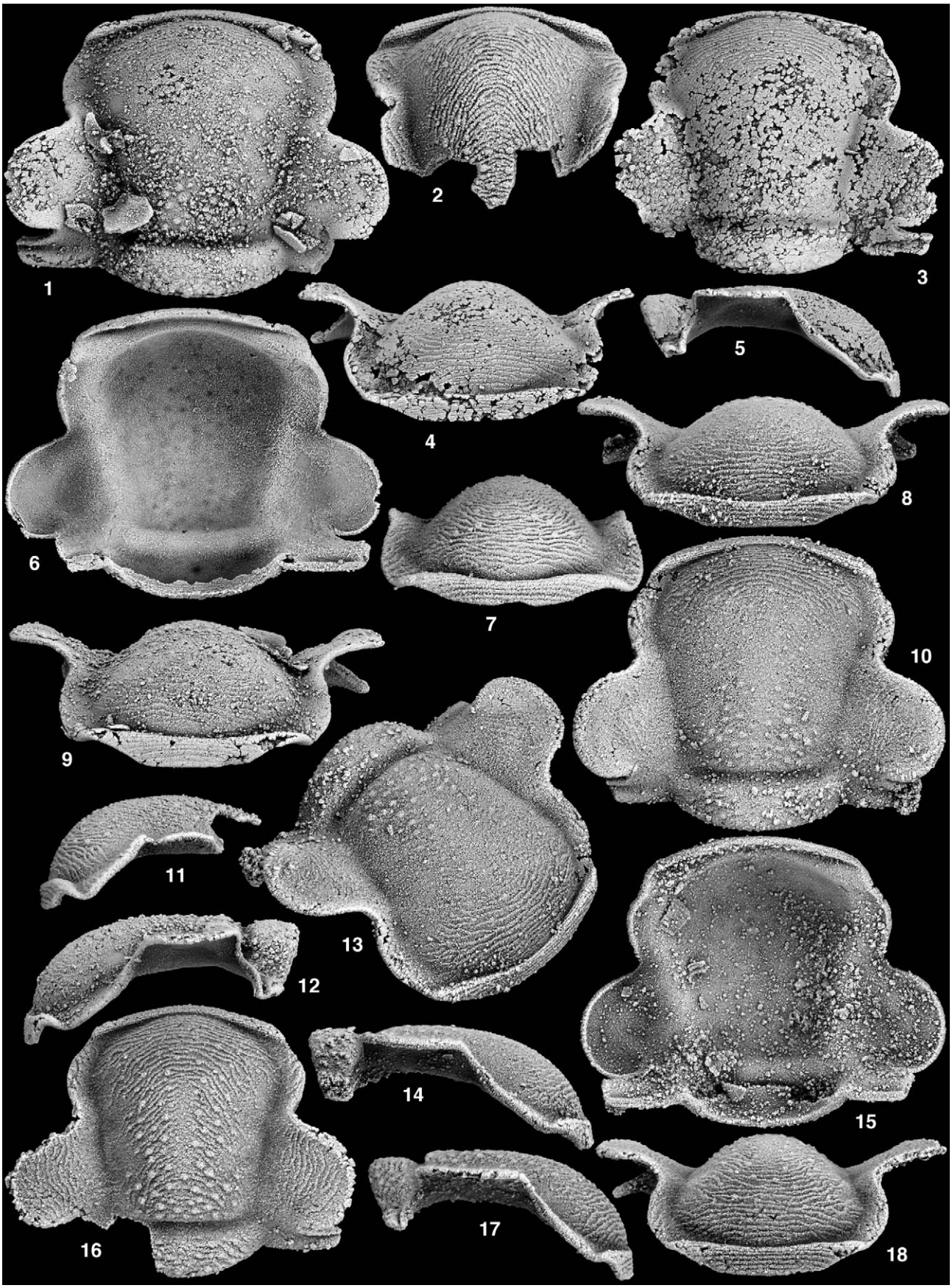

PLATE 7

Aponileus belkaae **n. sp.**, from Section H 294.2 m, Fillmore Formation (upper Floian; Blackhillsian; "*Pseudocybele nasuta*" Zone), southern Confusion Range, Ibex area, Millard County, western Utah.

1, 3, 5, 8, 11. Cranidium, SUI 129262, dorsal, right lateral, anterior, ventral, and oblique views, x10.
2, 4, 6, 7. Cranidium, SUI 129263, right lateral, dorsal, ventral, and anterior views, x12.
9, 10, 12, 13. Cranidium, SUI 129264, left lateral, dorsal, ventral, and anterior views, x15.
14, 17, 18. Cranidium, SUI 129265, right lateral, dorsal, and anterior views, x17.
15, 16, 19. Cranidium, SUI 129266, right lateral, dorsal, and anterior views, x17.

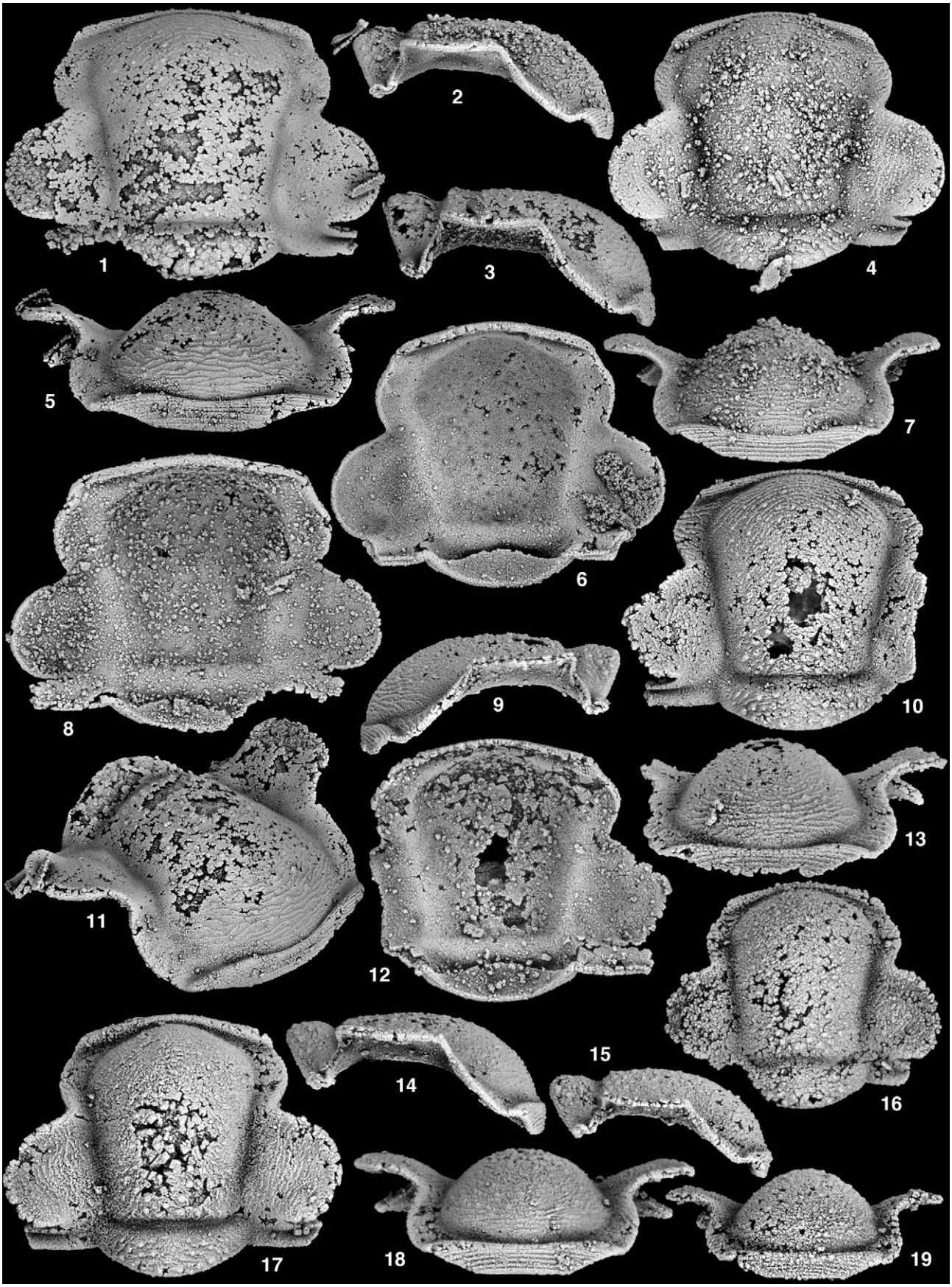

PLATE 8

Aponileus belkaae **n. sp.**, from Section H 294.2 m, Fillmore Formation, and Section J 16.0 m, J 16.1 m, and J 20.1 m, Wah Wah Formation (upper Floian; Blackhillsian; "*Pseudocybele nasuta*" Zone), southern Confusion Range, Ibex area, Millard County, western Utah.

1, 2. Right librigena, SUI 129267, external and ventrolateral views, x7.5 (J 16.0 m).
3, 4, 6. Right librigena, SUI 129268, external, internal, and ventrolateral views, x7.5 (J 16.1 m).
5, 8. Right librigena, SUI 129269, external and ventrolateral views, x7.5 (J 16.0 m).
7. Right librigena, SUI 129270, external view, x12 (J 20.1 m).
9. Left librigena, SUI 129271, external view, x7.5 (J 16.0 m).
10. Right librigena, SUI 129272, external view, x12 (J 16.0 m).
11. Left librigena, SUI 129273, external view, x15 (J 16.0 m).
12, 16. Left librigena, SUI 129274, external and internal views, x10 (H 294.2 m).
13. Right librigena, SUI 129275, external view, x12 (H 294.2 m).
14, 17. Left librigena, SUI 129276, ventrolateral and external views, x15 (H 294.2 m).
15. Right librigena, SUI 129277, external view, x10 (H 294.2 m).
18, 21, 22. Left librigena, SUI 129278, external, ventrolateral, and internal views, x7.5 (J 20.1 m).
19, 20. Left librigena, SUI 129279, external and internal views, x10 (H 294.2 m).

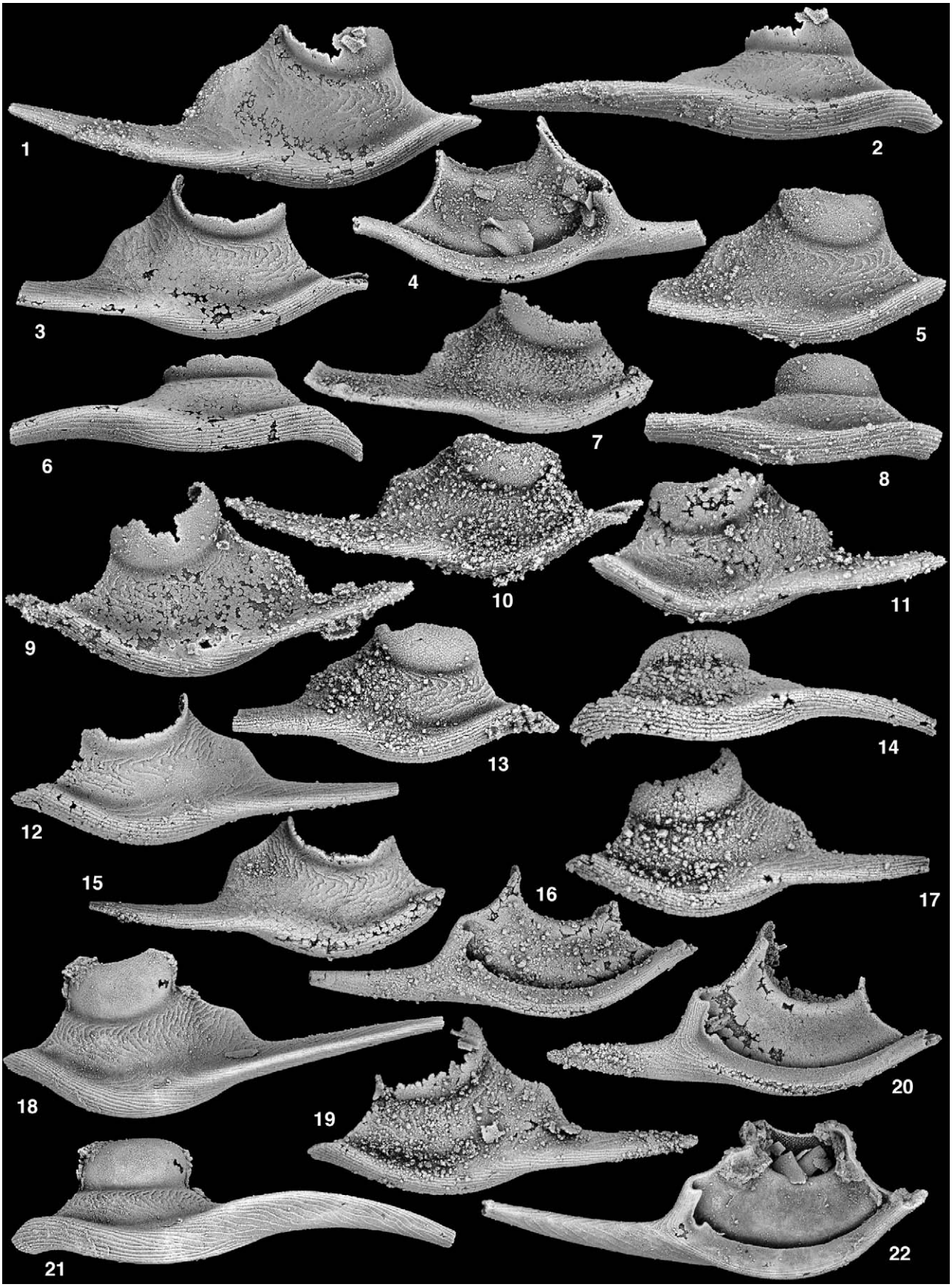

PLATE 9

Aponileus belkaae **n. sp.**, from Section H 294.2 m, Fillmore Formation, and Section J 16.0 m, J 16.1 m, J 20.0 m, and J 20.1 m, Wah Wah Formation (upper Floian; Blackhillsian; "*Pseudocybele nasuta*" Zone), southern Confusion Range, Ibex area, Millard County, western Utah.

1, 3, 6, 8, 11. Pygidium, SUI 129280, dorsal, posterior, ventral, anterior, and right lateral views, x10 (H 294.2 m).
2, 4, 5. Pygidium, SUI 129281, dorsal, right lateral, and posterior views, x10 (H 294.2 m).
7, 9, 10. Pygidium, SUI 129282, dorsal, left lateral, and posterior views, x12 (J 20.0 m).
12, 14, 21. Pygidium, SUI 129283, left lateral, dorsal, and posterior views, x10 (J 16.0 m)
13, 25, 26. Pygidium, SUI 129284, right lateral, dorsal, and posterior views, x15 (H 294.2 m).
15, 16, 18. Pygidium, SUI 129285, dorsal, right lateral, and posterior views, x15 (H 294.2 m).
17, 22, 23. Pygidium, SUI 129286, right lateral, dorsal, and posterior views, x12 (J 20.1 m).
19, 20, 24. Pygidium, SUI 129287, dorsal, posterior, and right lateral views, x15 (J 16.1 m).

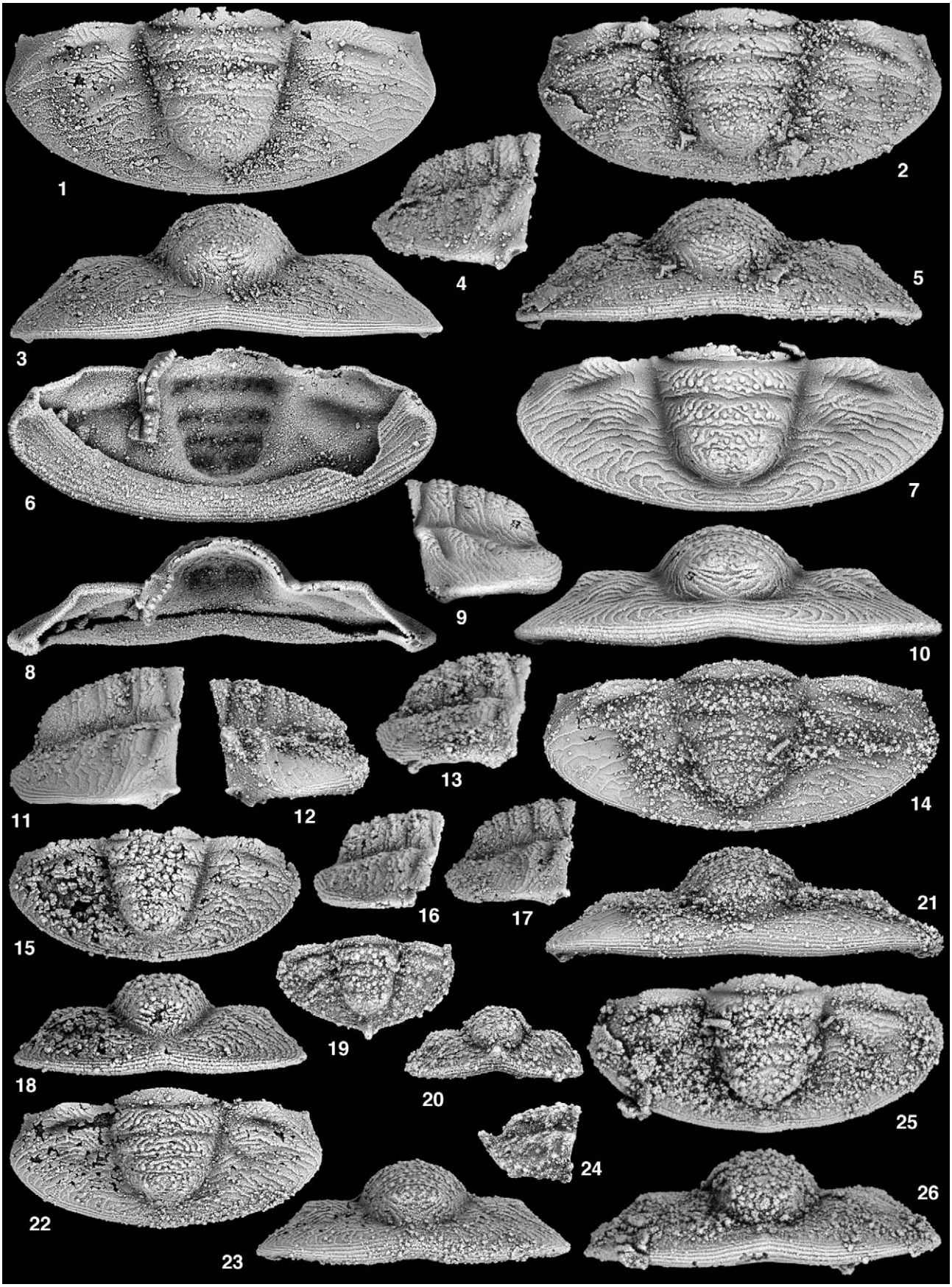

PLATE 10

Aponileus belkaae **n. sp.**, from Section J 16.0 m, J 16.1 m, J 20.0 m, and J 20.1 m, Wah Wah Formation (upper Floian; Blackhillsian; "*Pseudocybele nasuta*" Zone), southern Confusion Range, Ibex area, Millard County, western Utah.

1, 2, 5. Pygidium, SUI 129288, dorsal, right lateral, and posterior views, x12 (J 16.0 m).
3, 4, 6. Pygidium, SUI 129289, right lateral, dorsal, and posterior views, x6 (J 16.0 m).
7, 10, 13. Pygidium, SUI 129290, posterior, dorsal, and right lateral views, x10 (J 16.1 m).
8, 11, 12. Pygidium, SUI 129291, dorsal, posterior, and left lateral views, x10 (J 20.1 m).
9. Pygidium, SUI 129292, dorsal view, x15 (J 20.1 m).
14, 17, 21. Pygidium, SUI 129293, dorsal, posterior, and left lateral views, x15 (J 16.1 m).
15, 16, 20. Pygidium, SUI 129294, dorsal, posterior, and left lateral views, x10 (J 16.1 m).
18, 19, 23. Pygidium, SUI 129295, dorsal, right lateral, and posterior views, x15 (J 16.1 m).
22, 26, 30, 33. Pygidium, SUI 115404, right lateral, dorsal, posterior, and ventral views, x12 (J 16.1 m).
24, 25, 29, 32. Pygidium, SUI 129296, posterior, right lateral, dorsal, and ventral views, x20 (J 16.1 m).
27, 28, 31. Pygidium, SUI 129297, right lateral, dorsal, and posterior views, x12 (J 20.0 m).

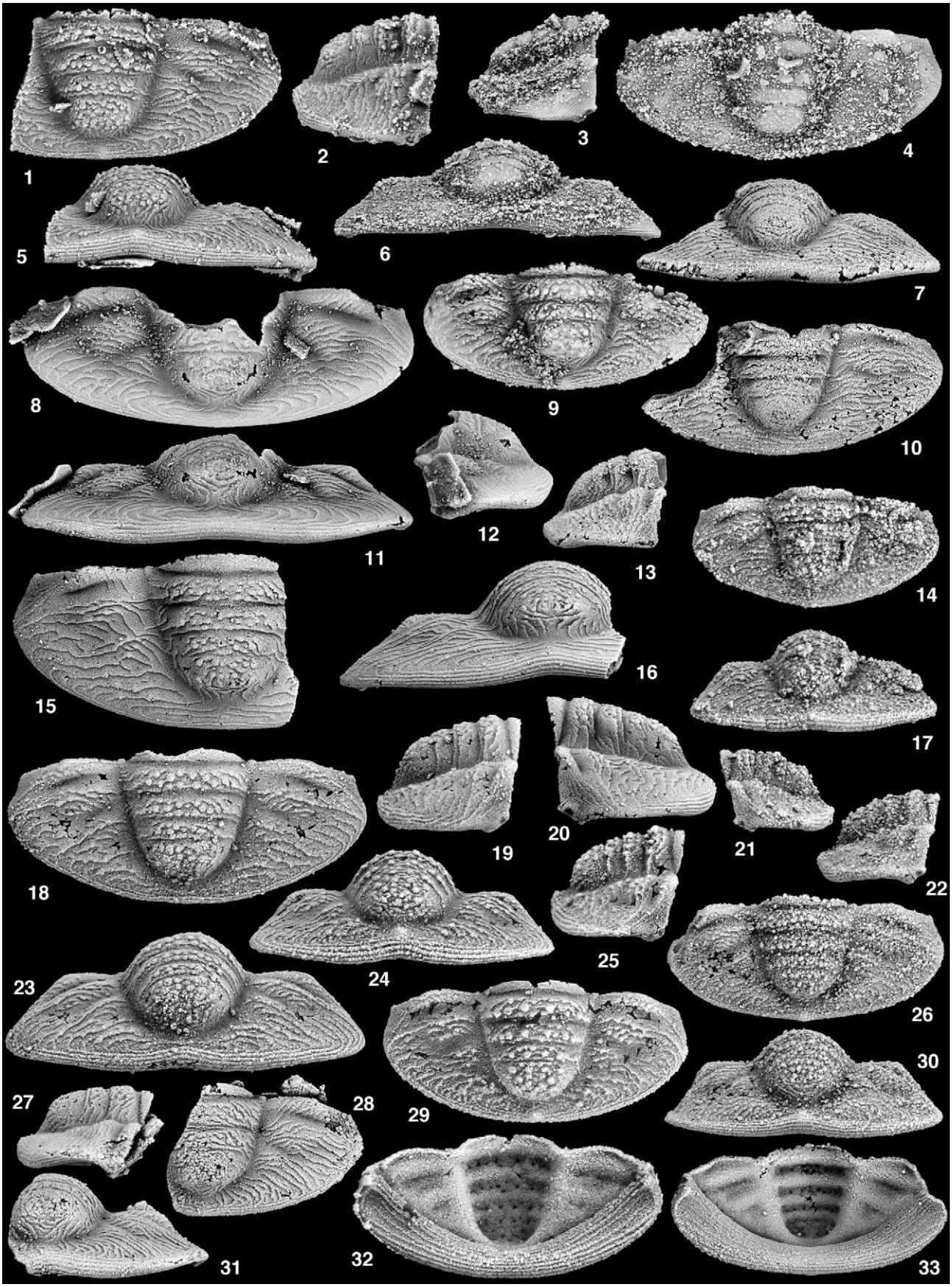

PLATE 11

Aponileus strelkaae **n. sp.**, from Section J 28.1 m, Wah Wah Formation (upper Floian; Blackhillsian; "*Pseudocybele nasuta* Zone"), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

1, 2, 4, 6, 9. Cranidium, **holotype**, SUI 129298, dorsal, ventral, left lateral, anterior, and oblique views, x10.
3, 5, 7, 8. Cranidium, SUI 129299, dorsal, left lateral, anterior, and ventral views, x10.
10, 12, 16. Cranidium, SUI 129300, dorsal, left lateral, and anterior views, x12.
11, 13, 14. Cranidium, SUI 129301, dorsal, anterior, and left lateral views, x15.
15, 19, 20. Cranidium, SUI 129302, dorsal, left lateral, and anterior views, x10.
17, 18, 21. Cranidium, SUI 129303, right lateral, dorsal, and anterior views, x15.

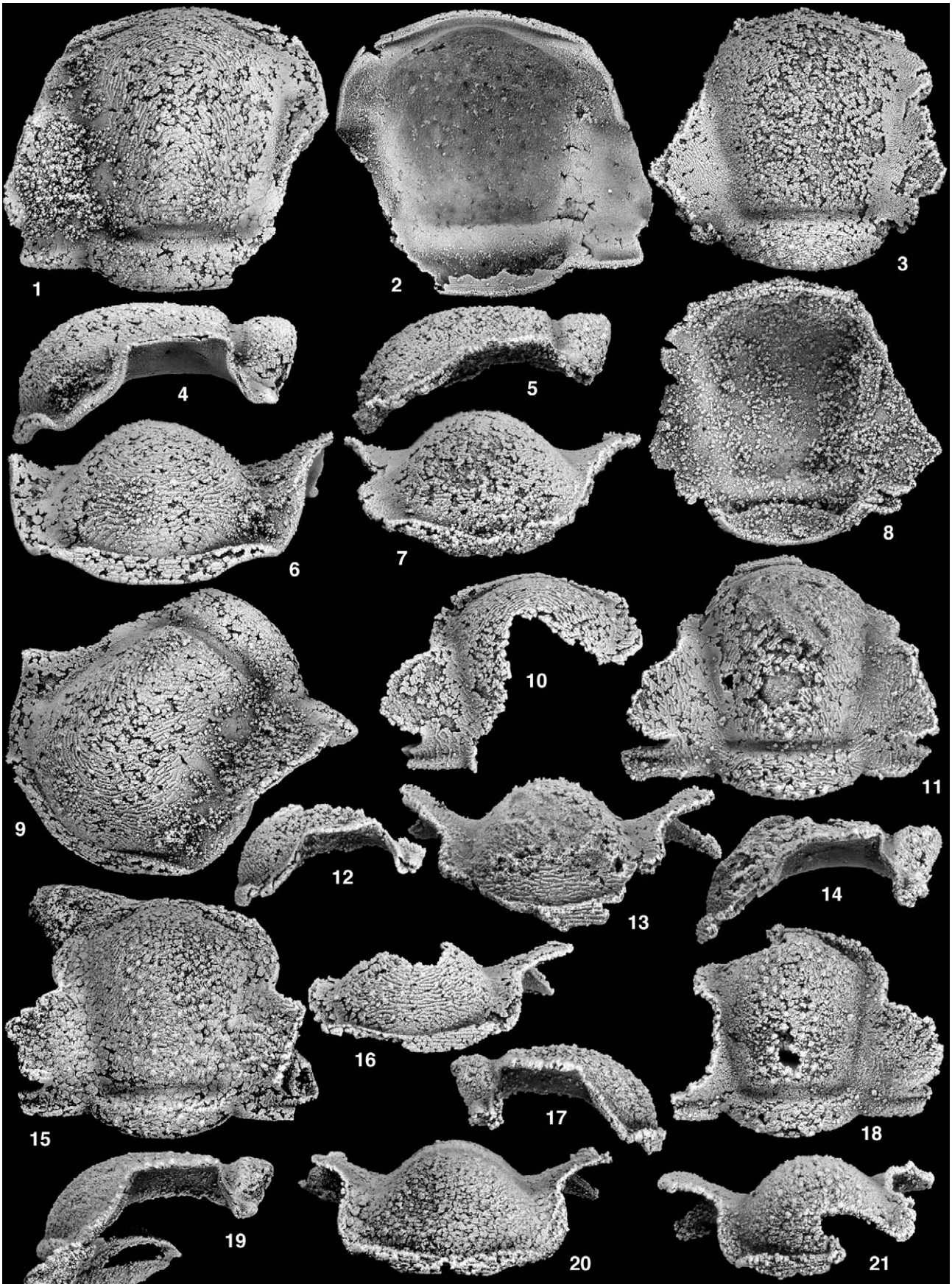

PLATE 12

Aponileus strelkaae **n. sp.**, from Section J 28.1 m, Wah Wah Formation (upper Floian; Blackhillsian; "*Pseudocybele nasuta* Zone"), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

1, 4, 7. Left librigena, SUI 129304, external, internal, and ventrolateral views, x7.5.
2, 3. Left librigena, SUI 129305, ventrolateral and external views, x12.
5. Left librigena, SUI 129306, external view, x7.5.
6, 8. Right librigena, SUI 129307, external and internal views, x10.
9, 11, 14, 18, 23. Pygidium, SUI 129308, left lateral, posterior, dorsal, ventral, and anterior views, x10.
10, 12, 15, 19. Pygidium, SUI 129309, dorsal, right lateral, ventral, and posterior views, x10.
13, 16, 17. Pygidium, SUI 129310, dorsal, right lateral, and posterior views, x15.
20, 22, 24. Pygidium, SUI 129311, right lateral, dorsal, and posterior views, x12.

Aponileus ugolekae **n. sp.**, from Section J 46.8 m, Wah Wah Formation (upper Floian; Blackhillsian; "*Pseudocybele nasuta* Zone"), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

21, 33, 35, 36. Pygidium, SUI 129312, left lateral, dorsal, posterior, and ventral views, x7.5.
25, 26, 29, 30, 34. Pygidium, SUI 129313, anterior, posterior, dorsal, right lateral, and ventral views, x7.5.
27, 28, 31. Left librigena, SUI 129314, external, internal, and ventrolateral views, x7.5.
32. Left librigena, SUI 129315, external view, x6.

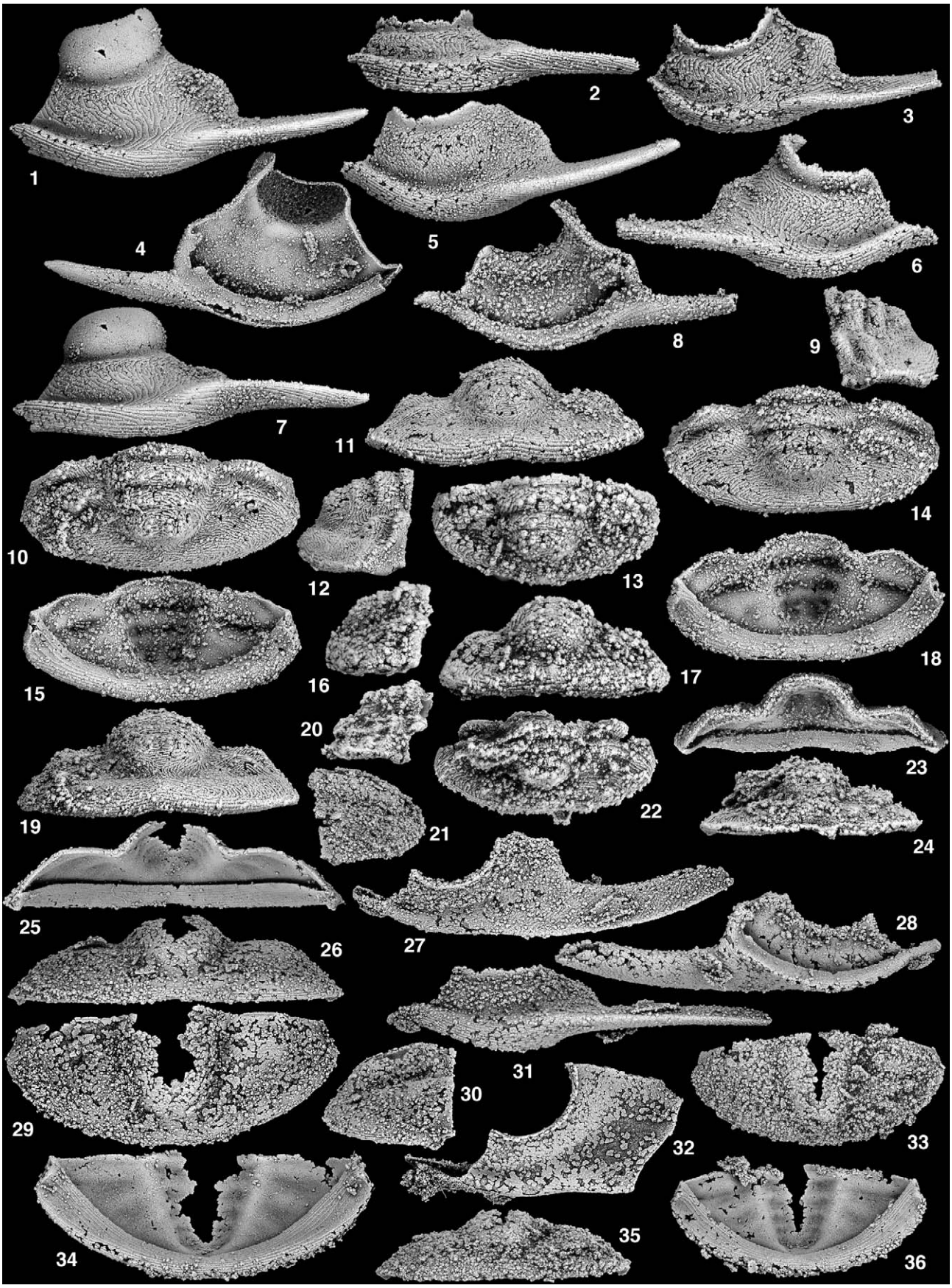

PLATE 13

Aponileus ugolekae **n. sp.**, from Section J 46.3 m, Wah Wah Formation (upper Floian; Blackhillsian; "*Pseudocybele nasuta* Zone"), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

1, 3, 5, 9. Cranidium, **holotype**, SUI 131127, dorsal, right lateral, oblique, and anterior views, x9.
2, 4, 8. Cranidium, SUI 131128, left lateral, dorsal, and anterior views, x5.
6, 11, 14. Cranidium, SUI 131129, right lateral, dorsal, and anterior views, x5.
7, 10, 12, 13, 15. Cranidium, SUI 131130, left lateral, dorsal, oblique, anterior, and ventral views, x9.
16–19. Cranidium, SUI 131131, anterior, dorsal, right lateral, and ventral views, x9.

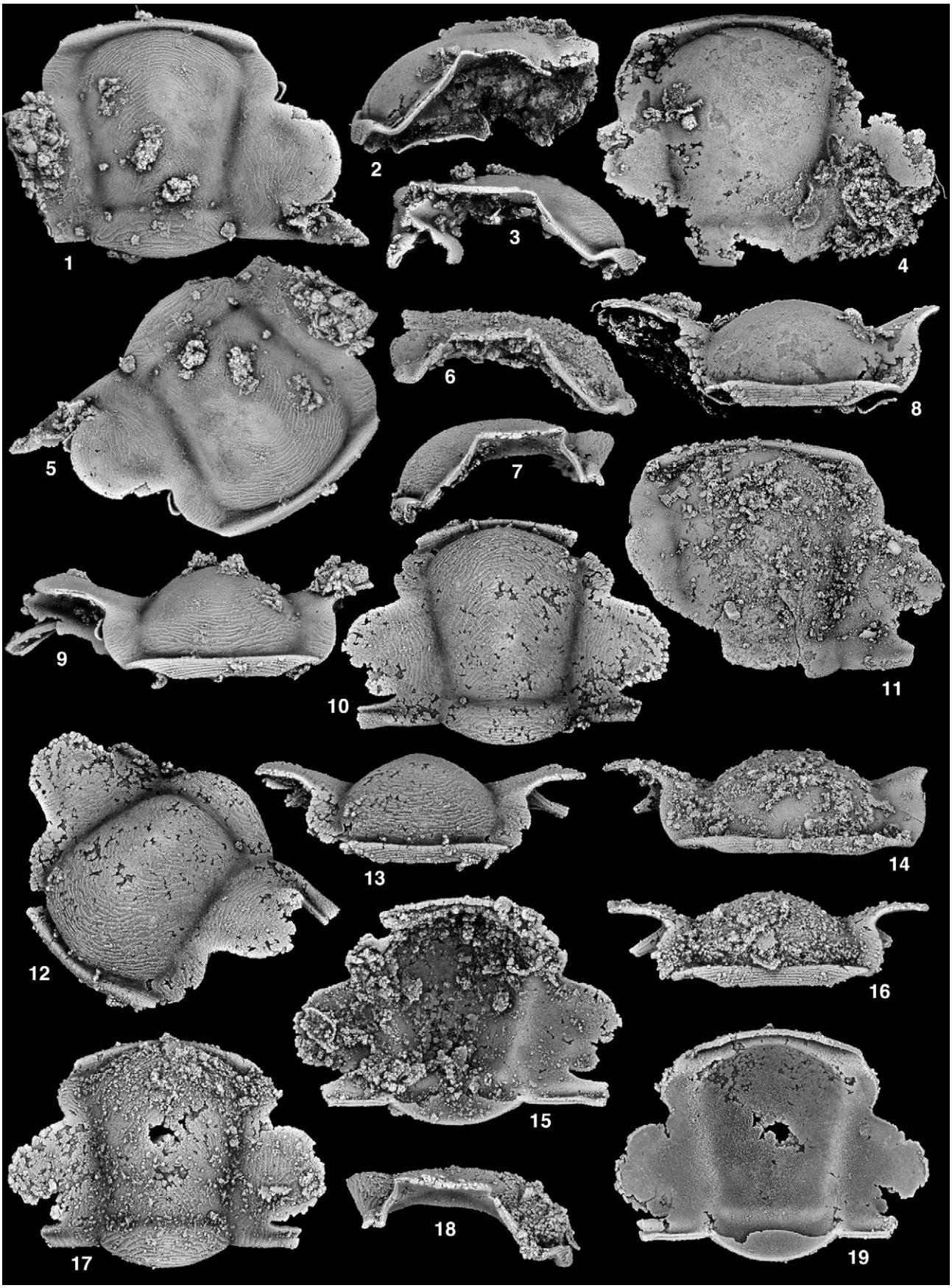

PLATE 14

Aponileus ugolekae **n. sp.**, from Section J 46.3 m, Wah Wah Formation (upper Floian; Blackhillsian; "*Pseudocybele nasuta* Zone"), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

1, 3, 5. Cranidium, SUI 131132, dorsal, left lateral, and anterior views, x12.
2, 4, 6. Cranidium, SUI 131133, left lateral, anterior, and dorsal views, x15.
7–9, 11. Left librigena, SUI 131134, internal, dorsal, ventral, and lateral views, x5.
10, 13, 14, 16. Right librigena, SUI 131135, ventral, internal, lateral, and dorsal views, x6.
12. Right librigena, SUI 131136, external view, x10.
15, 17–19. Left librigena, SUI 131137, internal, ventral, lateral, and dorsal views, x6.
20, 22, 23. Right librigena, SUI 131138, dorsal, lateral, and ventrolateral views, x10.
21. Right librigena, SUI 131139, external view, x12.
24, 25. Right librigena, SUI 131140, external and lateral views, x6.
26. Left librigena, SUI 131141, external view, x10.

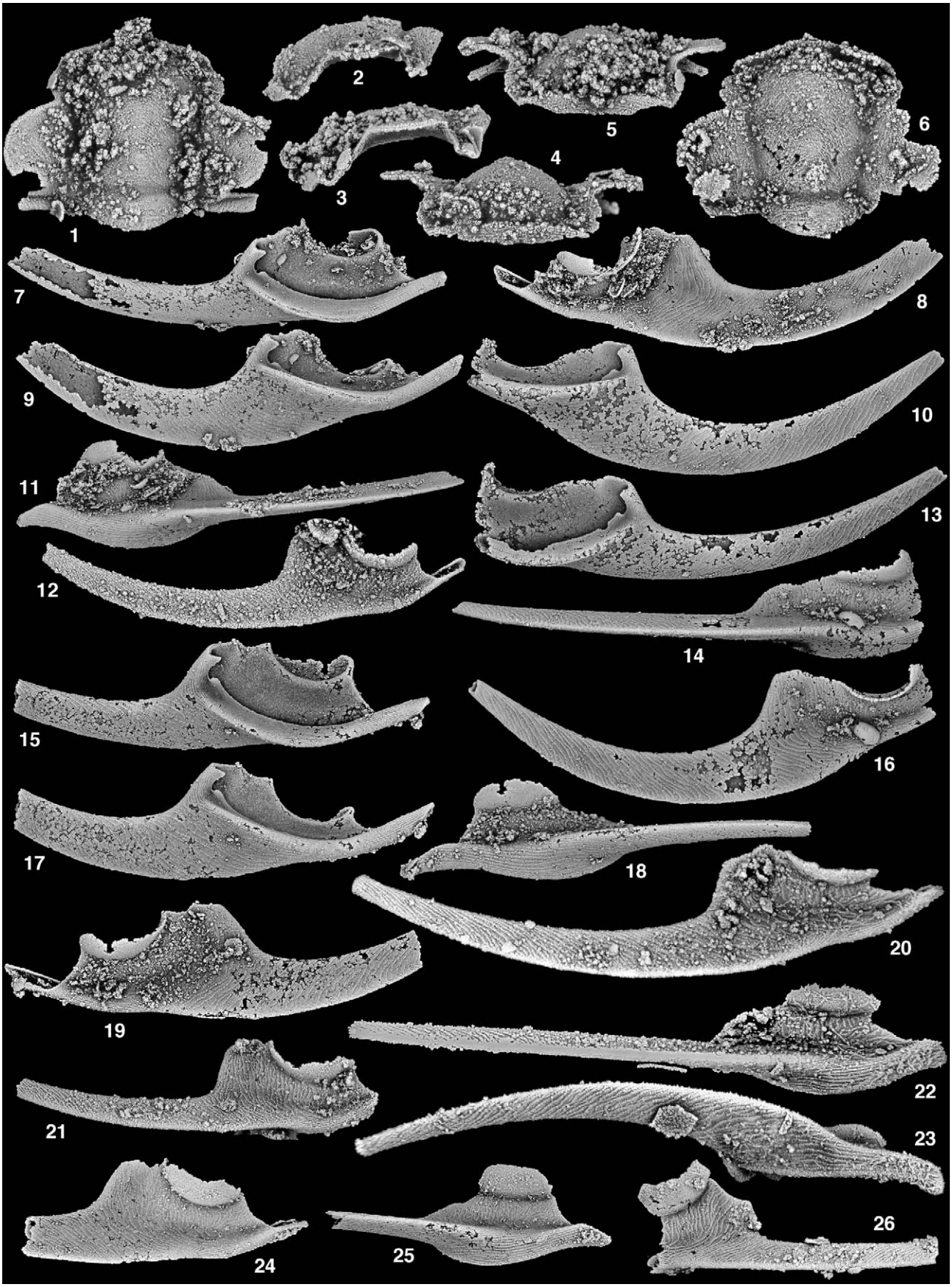

PLATE 15

Aponileus ugolekae **n. sp.**, from Section J 46.3 m, Wah Wah Formation (upper Floian; Blackhillsian; "*Pseudocybele nasuta* Zone"), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

1, 4, 5. Pygidium, SUI 131142, dorsal, posterior, and right lateral views, x10.
2, 3, 6, 9, 13. Pygidium, SUI 131143, left lateral, dorsal, posterior, ventral, and anterior views, x6.
7, 8, 10. Pygidium, SUI 131144, dorsal, left lateral, and posterior views, x12.
11, 12, 14. Pygidium, SUI 131145, left lateral, posterior, and dorsal views, x12.
15, 16, 19. Pygidium, SUI 131146, right lateral, dorsal, and posterior views, x12.
17, 18, 20. Pygidium, SUI 131147, dorsal, posterior, and left lateral views, x12.
21, 25, 28. Pygidium, SUI 131148, right lateral, dorsal, and posterior views, x12.
22–24, 27, 31. Pygidium, SUI 131149, right lateral, anterior, posterior, dorsal, and ventral views, x12.
26, 29, 30. Pygidium, SUI 131150, dorsal, left lateral, and posterior views, x15.

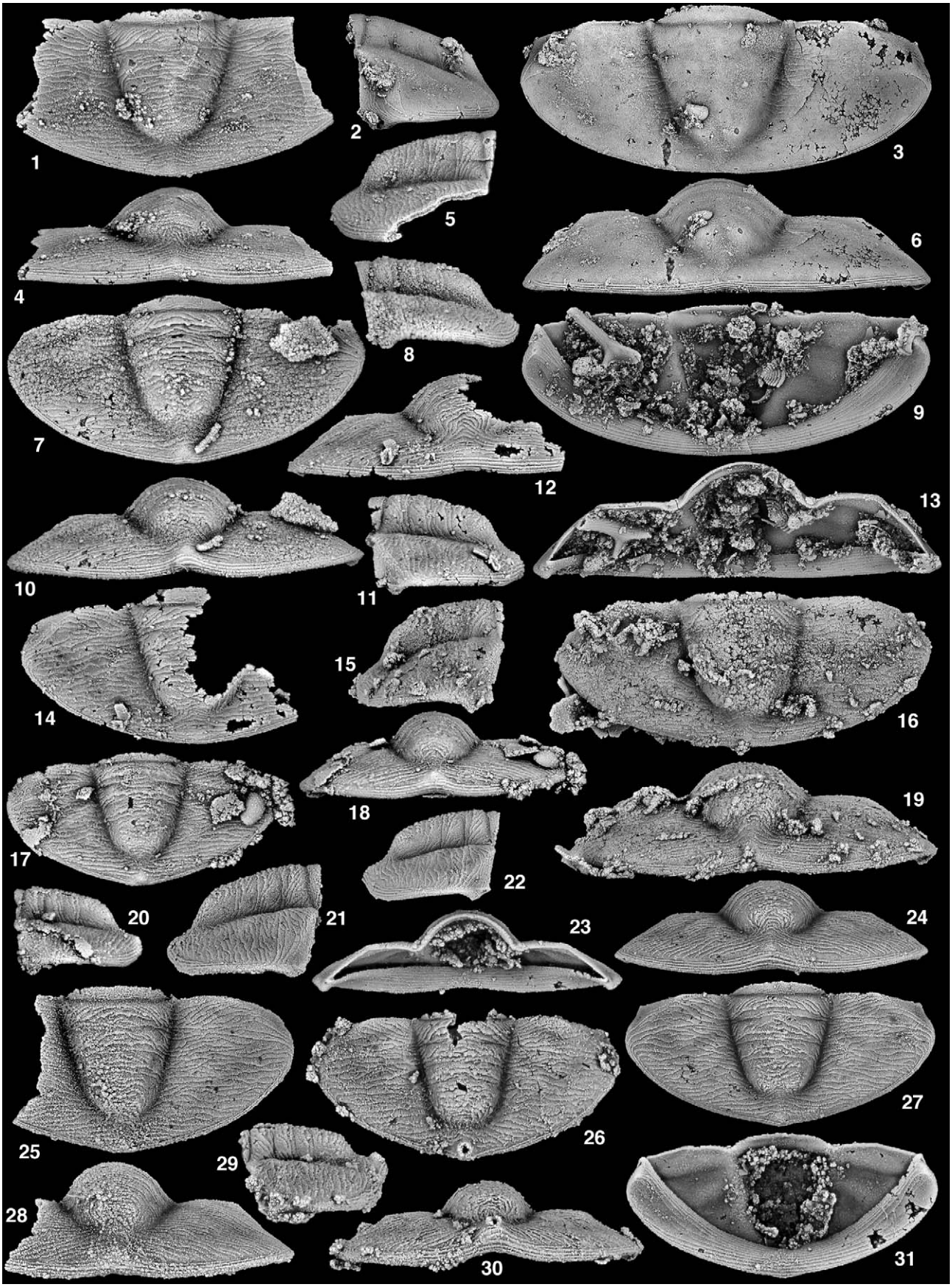

PLATE 16

Aponileus ? *veterokae* **n. sp.**, from Section J 48.1 m, Wah Wah Formation (upper Floian; Blackhillsian; "*Pseudocybele nasuta* Zone"), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

1, 2. Right librigena, SUI 129321, external and internal views, x6.
3, 5. Left librigena, SUI 129322, external and ventrolateral views, x7.5.
4. Right librigena, SUI 129323, external view, x12.
6. Right librigena, SUI 129324, external view, x7.5.
7. Right librigena, SUI 129325, external view, x10.
8. Right librigena, SUI 129326, external view, x12.
9. Left librigena, SUI 129327, external view, x12.
10. Left librigena, SUI 129328, internal view, x10.
11, 13. Right librigena, SUI 129329, external and ventrolateral views, x15.
12, 14. Left librigena, SUI 129330, external and ventrolateral views, x12.

Aponileus ugolekae **n. sp.**, from Section J 40.0 m, Wah Wah Formation (upper Floian; Blackhillsian; "*Pseudocybele nasuta* Zone"), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

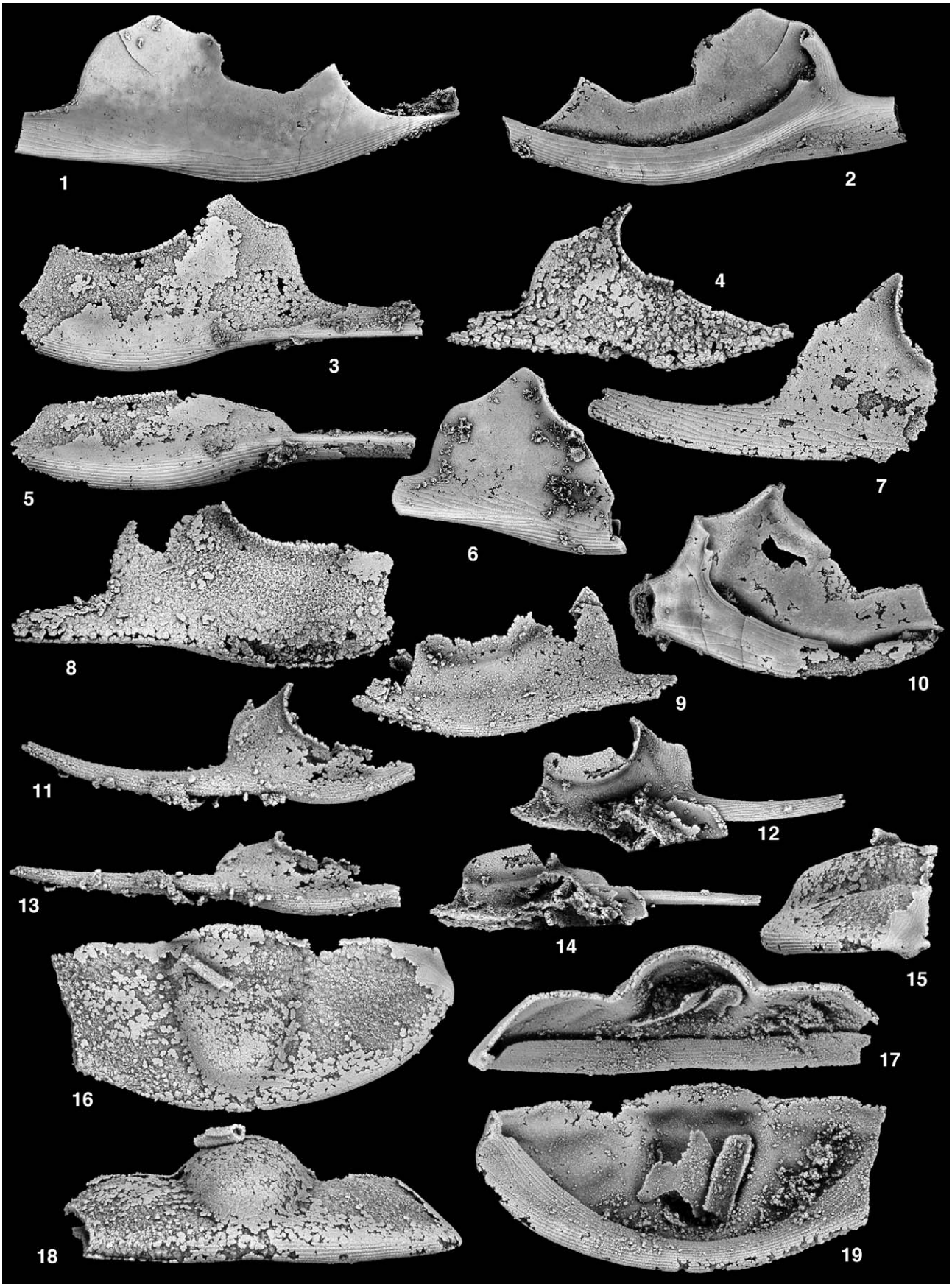

PLATE 17

Aponileus ? *veterokae* **n. sp.**, from Section J 48.1 m, Wah Wah Formation (upper Floian; Blackhillsian; "*Pseudocybele nasuta* Zone"), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

1, 5, 8, 11, 14. Cranidium, **holotype**, SUI 129316, dorsal, right lateral, anterior, ventral, and oblique views, x12.
2, 6, 9, 12. Cranidium, SUI 129317, dorsal, left lateral, anterior, and ventral views, x15.
3, 4, 7. Cranidium, SUI 129318, dorsal, right lateral, and anterior views, x7.5.
10, 13, 16. Cranidium, SUI 129319, dorsal, right lateral, and anterior views, x15.
15, 17–19. Cranidium, SUI 129320, dorsal, anterior, right lateral, and ventral views, x20.

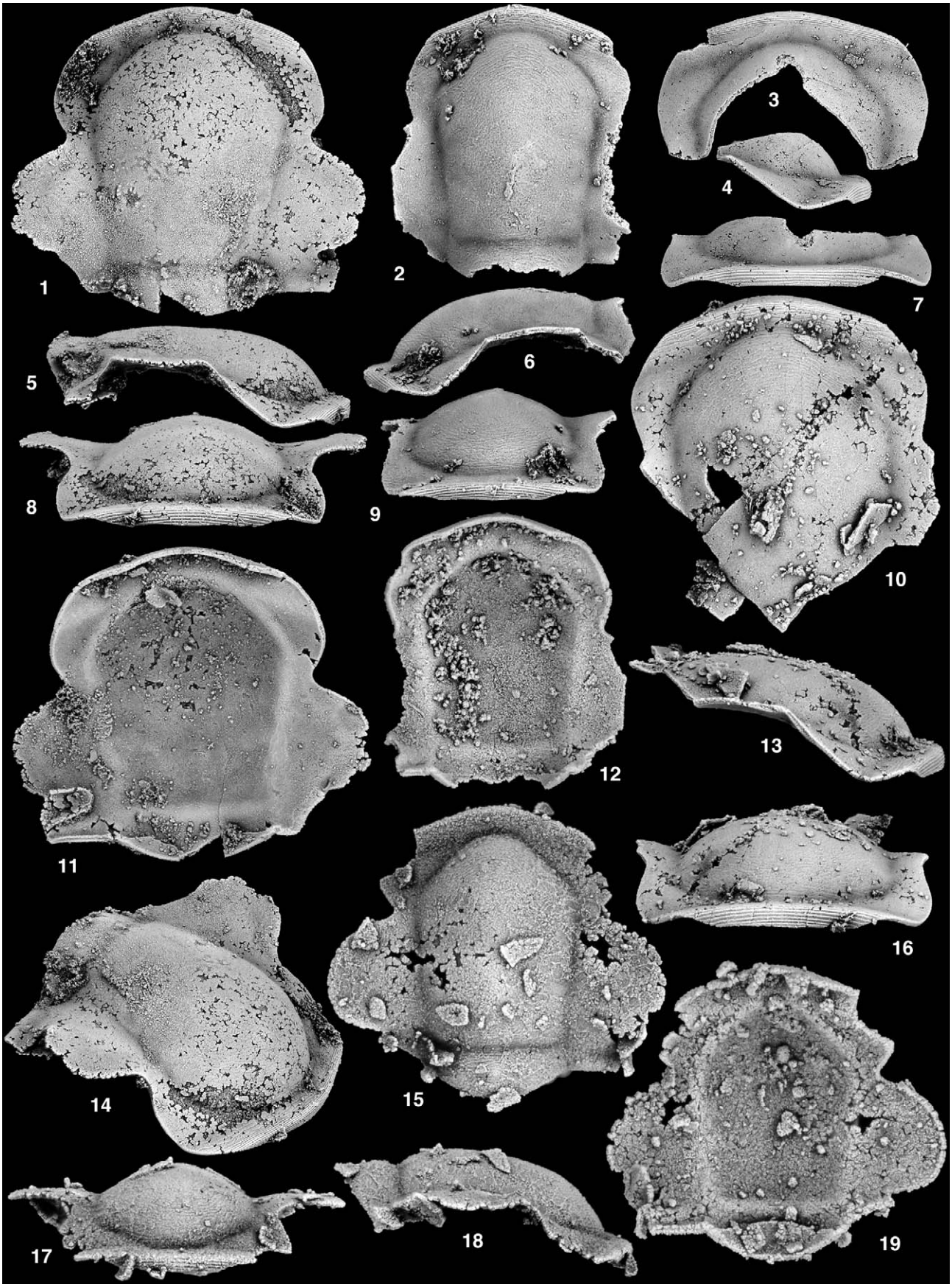

PLATE 18

Aponileus ? *veterokae* **n. sp.**, from Section J 48.1 m, Wah Wah Formation (upper Floian; Blackhillsian; "*Pseudocybele nasuta* Zone"), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

1–4, 6. Pygidium, SUI 129332, dorsal, posterior, right lateral, ventral, and anterior views, x12.
5, 8, 9. Pygidium, SUI 129333, dorsal, left lateral, and posterior views, x12.
7, 11, 18. Pygidium, SUI 129334, right lateral, dorsal, and posterior views, x12.
10, 14, 19, 21. Pygidium, SUI 129335, posterior, dorsal, ventral, and right lateral views, x6.
12, 13, 16. Pygidium, SUI 129336, dorsal, posterior, and left lateral views, x12.
15, 17, 20. Pygidium, SUI 129337, left lateral, dorsal, and posterior views, x12.

PLATE 19

Psephosthenaspis glabrior Fortey and Droser, 1996, from Locality K-1, Kanosh Formation (Dapingian), base of Section K-South, Fossil Mountain, southern Confusion Range, Ibex area, Millard County, western Utah, USA.

1, 4, 7, 12, 19. Cranidium, SUI 129338, dorsal, left lateral, anterior, ventral, and oblique views, x20.
2, 5, 8, 9. Cranidium, SUI 129339, dorsal, ventral, right lateral, and anterior views, x10.
3, 6, 11. Cranidium, SUI 129340, dorsal, left lateral, and anterior views, x7.5.
10, 14, 15. Cranidium, SUI 129341, dorsal, anterior, and right lateral views, x10.
13, 17, 20. Cranidium, SUI 129342, right lateral, dorsal, and anterior views, x10.
16, 18, 21. Cranidium, SUI 129343, left lateral, dorsal, and anterior views, x12.

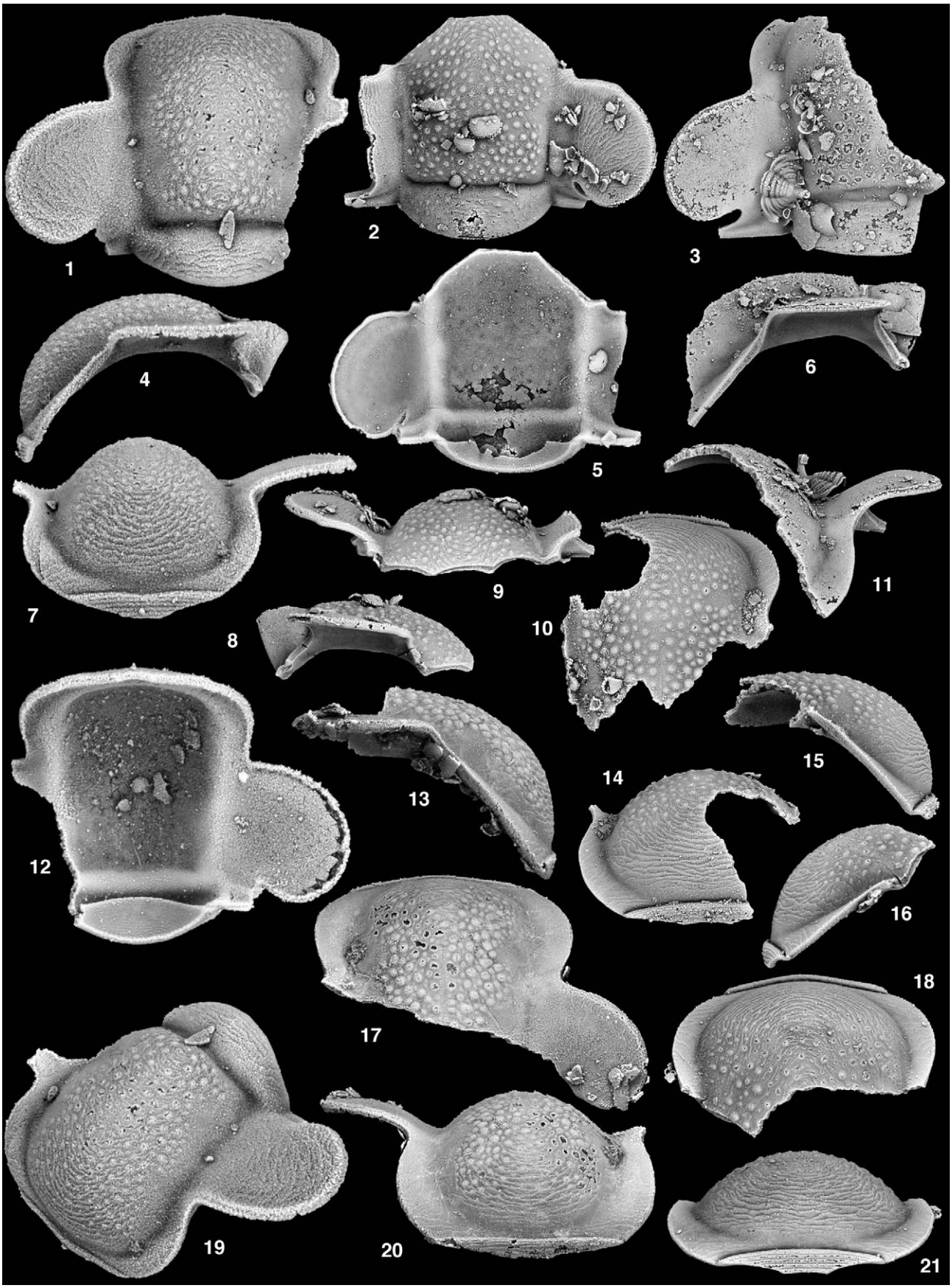

PLATE 20

Psephosthenaspis glabrior Fortey and Droser, 1996, from Locality K-1, Kanosh Formation (Dapingian), base of Section K-South, Fossil Mountain, southern Confusion Range, Ibex area, Millard County, western Utah, USA.

1, 4, 5, 9. Left librigena, SUI 129344, external, ventrolateral, internal, and dorsal views, x9.
2. Right librigena, SUI 129345, external view, x12.
3, 6, 7. Right librigena, SUI 129346, external, ventrolateral, and internal views, x12.
8. Right librigena, SUI 129347, external view, x9.
10. Left librigena, SUI 129348, external view, x9.
11. Left librigena, SUI 129349, external view, x6.
12, 14. Left librigena, SUI 129350, external and ventrolateral views, x10.
13. Left librigena, SUI 129351, external view, x12.
15. Left librigena, SUI 129352, external view, x6.
16–18, 20, 21. Pygidium, SUI 129353, dorsal, right lateral, posterior, anterior, and ventral views, x12.
19. Left librigena, SUI 129354, external view, x6.
22, 25, 28. Pygidium, SUI 129355, dorsal, left lateral, and posterior views, x7.5.
23, 24, 27, 29. Pygidium, SUI 129356, dorsal, left lateral, ventral, and posterior views, x6.
26, 30, 31. Pygidium, SUI 129357, posterior, right lateral, and dorsal views, x15.