Heckethornia, a new genus of dimeropygid trilobites from the Lower Ordovician (Ibexian; Tulean and Blackhillsian) of the Great Basin, western USA

Neo E.B. McAdams and Jonathan M. Adrain

Abstract: ***Heckethornia*** n. gen. is a morphologically striking clade of dimeropygid trilobites known from the Pogonip Group (Ordovician; Ibexian Series, Tulean and Blackhillsian stages) of western Utah and eastern Nevada. It includes seven species based on silicified material. All occur in the Fillmore Formation of western Utah, and four are also known from the Yellow Hill Limestone of eastern Nevada. Diagnostic features of *Heckethornia* include a highly vaulted exoskeleton with a tall pygidial "wall" made of fused outer pleurae, three pairs of large glabellar spines, two to three pairs of prominent pygidial spines, a single (or paired) large occipital spine(s), and an arc of tubercles on the librigenal field. Cladistic parsimony analysis suggests that the genus comprises two subclades, one including species with a single median occipital spine, and species with paired occipital spines or tubercles in the other. New species are ***H. smithi***, ***H. hyndeae***, ***H. numani***, ***H. bowiei***, ***H. morrisseyi***, and ***H. ballionae***.

Résumé : ***Heckethornia*** n. gen. représente un clade frappant sur le plan morphologique de trilobites diméropygidés présents dans le Groupe de Pogonip (Ordovicien, série ibexienne, étages tuléen et blackhillsien) de l'ouest de l'Utah et de l'est du Nevada. Il comprend sept espèces provenant de matériaux silicifiés. Toutes ces espèces sont présentes dans la Formation de Fillmore de l'ouest de l'Utah et quatre d'entre elles sont également présentes dans le Calcaire de Yellow Hill de l'est du Nevada. Parmi les caractères diagnostiques de *Heckethornia* figurent un exosquelette fortement voûté présentant une haute « paroi » pygidiale composée de plèvres externes fusionnées, trois paires de grandes épines glabellaires, de deux à trois paires d'épines pygidiales bien en évidence, une seule grande épine occipitale (ou une paire d'épines) et un arc de tubercules sur le champ librigénal. L'analyse de la parcimonie cladistique porte à croire que le genre compte deux sous-clades, dont un comprend des espèces dotées d'une seule épine occipitale médiane et l'autre, des espèces dotées de paires d'épines ou de tubercules occipitaux. Les nouvelles espèces sont ***H. smithi***, ***H. hyndeae***, ***H. numani***, ***H. bowiei***, ***H. morrisseyi*** et ***H. ballionae***.

[Traduit par la Rédaction]

Introduction

Lower Ordovician (Ibexian) trilobite faunas from the Ibex area of the Tule Valley in western Utah and from Yellow Hill in eastern Nevada were first described by Hintze (1953). These faunas are well preserved as silicified disarticulated sclerites in a limestone matrix and, therefore, yield much information about the constituent trilobites. Although Hintze's (1953) monograph was an extensive and groundbreaking study, most of the trilobite species diversity in the succession remains to be documented. Even those species that have been named suffer from much misassociation of skeletal elements and are in need of modern revision. Adrain et al. (2001) published the first results of ongoing comprehensive field-based revision of the Ibex faunas, as well as those described from coeval faunas from the Garden City Formation in northern Utah and southeastern Idaho by Ross (1951). Aside from new work in the current field-based revision (Adrain et al. 2001, 2003; Adrain and Westrop 2006*a*, 2006*b*, 2007*a*, 2007*b*), only three short papers (Demeter 1973; Terrell 1973; Young 1973) have described new material from Ibex. No subsequent work at all has been done on material from Yellow Hill. This paper continues revision of the Lower Ordovician Ross and Hintze trilobite faunas and begins revision of contemporaneous faunas from Yellow Hill.

Material collected from Ibex and Yellow Hill includes many species of dimeropygids, some of which (e.g., those assignable to *Dimeropygiella* Ross, 1951) are relatively common, and others of which (such as members of *Heckethornia* n. gen.) are generally rare. Adrain and Westrop (2007*a*) reviewed the current state of the systematics of Dimeropygidae and demonstrated that the content and relationships of even the well known members of the group are still in flux. Little is known about Early Ordovician dimeropygids, such as *Heckethornia*, and their relationships to other members of Dimeropygidae Hupé, 1953, are unclear; but data from new collections at Ibex, Yellow Hill, and the Gar-

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den City Formation in Idaho (Ross 1951) may be used to address components of the problem (Adrain et al. 2001; Adrain and Westrop 2006*a*, 2007*a*). The purposes of this paper are (1) to revise *Psalikilopsis* (?) *alticapitis* Young, 1973, on the basis of new collections; (2) to describe six new species related to it; (3) to diagnose a new dimeropygid clade, *Heckethornia*, to which all of the species belong; and (4) to use cladistic parsimony analysis to reconstruct the clade's ingroup phylogeny. Progress in understanding the origins of Dimeropygidae, its membership, and phylogenetic structure can be achieved only via similar descriptive and cladistic studies of the plethora of undescribed or poorly known Lower Ordovician taxa.

Sampling

Sections G and H in the Tule Valley of western Utah (Figs. 1*a*, 1*b*) run through the lower four and upper four members, respectively, of the Fillmore Formation of the Pogonip Group. Hintze (1951, 1953, 1973) measured and clearly marked his horizons at sections G and H in feet with highway paint. Both sections have recently been logged and remeasured in metres, and we use these measurements herein. Correlation with Hintze's (1953) numbered sampling horizons is given under each species where applicable. Section YH at Yellow Hill in eastern Nevada (Figs. 1*a*, 1*c*) is located in the Yellow Hill Limestone (Westgate and Knopf 1932), which is correlative with the middle Fillmore Formation. Horizons at Yellow Hill were not marked, but we were able to locate distinctive beds that Hintze (1953) described near the top of the hill and thus use his reported footage converted to metres. As noted by Adrain et al. (2001, 2003) and Adrain and Westrop (2003, 2006*a*, 2007*a*), many new species assignable to both established and new genera are present in both the classic Ibexian horizons of Hintze (1951, 1953, 1973) and new horizons and sections from the area (e.g., section MME, Adrain and Westrop 2007*a*). Adrain et al. (2001) summarized the probable causes of failure by previous workers to find both common and rarer species at established horizons, with low sampling intensity likely the main culprit. The published record of material from the Ibex area illustrates these problems with regard to *Heckethornia*. Prior to this study, material assignable to three species of *Heckethornia*, *H. alticapitis* (Young, 1973), *H. bowiei* n. sp., and *H. morrisseyi* n. sp., was sampled, but only as a handful of isolated and (or) misassociated sclerites figured in open nomenclature (Hintze 1953). Young (1973) later described three cranidia from section H 191.7 m as *Psalikilopsis* (?) *alticapitis* and also illustrated a single pygidium and librigena of the species. However, the latter were not associated with either the cranidia or each other and were left in open nomenclature.

We sampled species of *Heckethornia* from a total of eleven horizons: two at section G; three at section YH, and six at section H (Fig. 3). These horizons are Hintze's (1951, 1953) sampling localities G-17, G-19; H-7, H-11, H-20, H-23, and H-24; as well as our new collections at H 163.3 m, and at YH 128.9, 128.5, and 175.9 m. In contrast to original sample sizes of approximately 4.5 kg or less (Demeter 1973; Terrell 1973; see Adrain et al. 2001, pp. 947–948), we collected several tens of kilograms of rock per horizon. Our largest sample size was from section H 191.7 m, and was in excess of 100 kg. We collected nearly 30 kg of rock from each of sections H 93.4 m and YH 129.5 m and 50 kg from section H 127.1 m. The trilobite sample size thus acquired permits considerable confidence in association of sclerites, despite the fact that many species of *Heckethornia* are rare components of their respective faunas.

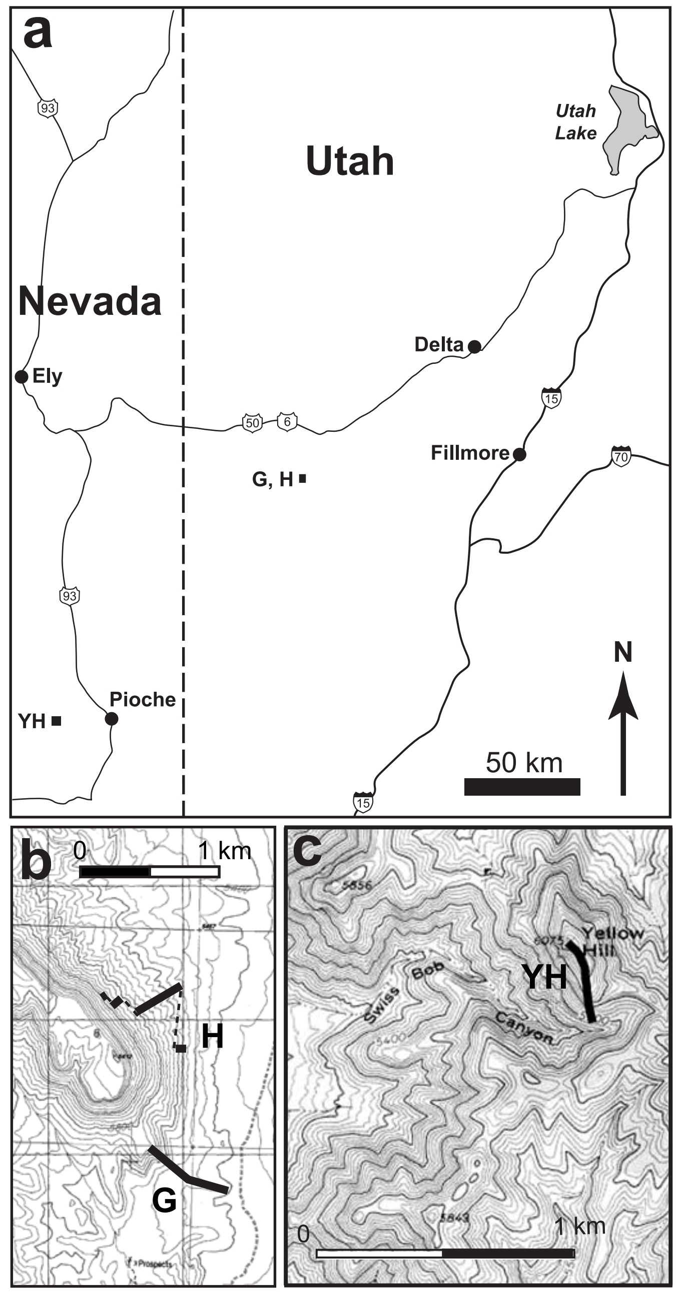


Fig. 1. Maps of collection localities. (*a*) General area map showing location of sections G and H in the southern Confusion Range, Ibex area, Tule Valley, Millard County, western Utah, and section YH at Yellow Hill, near Pioche, Lincoln County, eastern Nevada. Black squares show locations of detailed maps in (*b*) and (*c*). (*b*) Topographical map showing the line of section of sections G and H on the southeast slope of the Confusion Range. (*c*) Topographical map showing the line of section of section YH on the south side of Yellow Hill.

Biostratigraphy

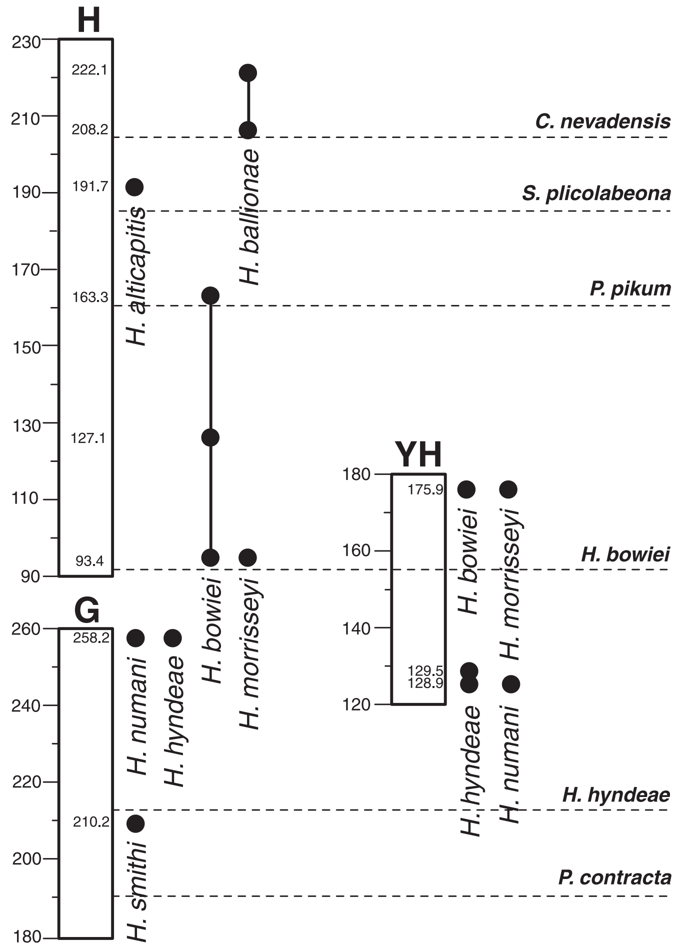
The lowermost Ordovician Ibexian Series and its stages (Ross et al. 1997) were erected on the basis of lettered trilobite faunal zones first established by Ross (1949, 1951) for faunas of the Garden City Formation, southern Idaho and northern Utah, and modified and applied by Hintze (1951, 1953) to faunas in the Pogonip Group of the Ibex area of western Utah and at Yellow Hill in eastern Nevada. Although this biostratigraphic scheme (formalized as named zones by Ross et al. (1997)) has long served as a standard reference for Laurentian trilobite faunas, the zones as originally defined suffer from inadequate sampling and inaccurate taxonomic identifications.

Data from new collections permit precise correlation between strata at Ross's (1949, 1951) Garden City localities and Hintze's (1951, 1953, 1973) Tule Valley and Yellow Hill localities, as well as new sections in these areas. This increased level of sampling permits the development of a much more highly resolved trilobite biostratigraphy (Adrain et al. 2009), and this new scheme is used herein (Fig. 2).

The oldest species of *Heckethornia* are found in the upper half of the third stage of the Ibexian, the Tulean. This stage was originally based on two zones (Ross et al. 1997): G(1), *Hintzeia celsaora*; and G(2), *Protopliomerella contracta*. It is now divided into ten zones, with the upper four equivalent to the former G(2). *Heckethornia smithi* n. sp. is found in the lowest of these four, the restricted *Protopliomerella contracta* Zone; *H. numani* n. sp. and *H. hyndeae* n. sp. occur in the overlying *Heckethornia hyndeae* Zone; and *H. bowiei* and *H. morrisseyi* occur in the *Heckethornia bowiei* Zone. Only *H. bowiei* occurs in the *Psalikilus pikum* Zone, the highest zone of the Tulean. Globally, the Tulean corresponds approximately to the uppermost Tremadocian and lowermost Floian.

Younger species of *Heckethornia* are all Blackhillsian in age. The Blackhillsian was formerly divided into the *Trigonocerca typica*, *Presbynileus ibexensis*, and *Pseudocybele nasuta* zones by Ross et al. (1997). In the new scheme, the Blackhillsian contains at least five zones; species of *Heckethornia* were sampled from the lowest two. *Heckethornia alticapitis* (Young, 1973) is found in the *Strigigenalis plicolabeona* Zone, and *H. ballionae* n. sp. occurs in the *Carolinites nevadensis* Zone. The Blackhillsian is middle to upper Floian age in global terms.

Fig. 2. Chart of stratigraphic occurrence of species of *Heckethornia* at sections G, H, and YH. Sections G and H have been remeasured in metres; those measurements are used here. Measurements at section YH are in metres, converted from Hintze's (1953) measurements in feet. Black circles indicate occurrence at sampling horizons; solid vertical lines depict stratigraphic range. Dashed horizontal lines delineate biostratigraphic zones (Adrain et al. 2009), labeled at the right margin.



Parsimony analysis of *Heckethornia*

Taxa

The six newly named species and *H. alticapitis* compose the ingroup. The outgroup is an undescribed Stairsian dimeropygid species from section MME 22.3 m (see Adrain and Westrop 2007*a*, for location of section). The stratigraphically lowest species of *Heckethornia*, *H. smithi*, is found 269.3 m higher (in the composite section) at section G 210.2 m. The outgroup species resembles the ingroup in general cranidial sculpture (paired glabellar sculpture and fixigenal arcs), but lacks the spines that characterize the derived members of *Heckethornia*. The librigenae of the outgroup possess an arc of tubercles on the field similar to that of the ingroup, although composed of more tubercles. They differ in having small, subrectangular librigenal fields instead of large, subtriangular fields. The outgroup pygidia are longer, wider, less vaulted, and contain more segments than those of the ingroup species, but do possess a short "wall." The outgroup species will be described in a forthcoming work.

Characters

38 characters (16 cranidial, 10 librigenal, and 12 pygidial) were used to determine relationships among the ingroup taxa. Characters 3, 10, and 32 were not applicable to all taxa considered in the analysis. We used reductive coding (Wilkinson 1995) in these instances, by coding inapplicable taxa as "?" for a character state. This method allows for coding a structure found in only some taxa as an informative synapomorphy, while minimizing the impact of the character on the phylogenetic placement of taxa that lack the struc-

ture. It also promotes formulation of non-redundant and independent characters (Strong and Lipscomb 1999). Reductive coding is not without drawbacks, however, as phylogenetic software programs treat "?" as missing data, rather than inapplicable data. In the event of multiple most parsimonious trees (MPTs), the tree with the most accurate character optimization must be selected by hand. Likewise, in cases of a single MPT, different character optimizations can cause appearance of a "synapomorphy" in taxa that have been coded as inapplicable. Instances of this problem are discussed under descriptions of individual taxa.

Cranidium

(1) Type of prominent cranidial sculpture: 0, tubercles; 1, spines; 2, none.

(2) Density of cranidial sculpture: 0, dense; 1, sparse; 2, effaced.

(3) Direction of cranidial sculpture: 0, more vertical; 1, more posterior.

(4) Width of anterior border: 0, moderately wide; 1, very narrow; 2, moderately narrow; 3, wide.

(5) Anterior border sculpture: 0, prominent tubercles; 1, effaced or very small tubercles.

(6) Shape of median anterior border in anterior view: 0, flat or very slightly arched; 1, dorsally inflected.

(7) Convexity of glabella in sagittal profile: 0, highly inflated; 1, very highly inflated and bulbous.

(8) Shape of LO: 0, short, evenly arcuate; 1, long medially, tapered laterally.

(9) Type of LO sculpture: 0, tubercles; 1, spines.

(10) Number of LO spines: 0, one; 1, two.

(11) Type of accessory LO sculpture: 0, many more tubercles; 1, one pair flanking spinose tubercles; 2, one pair flanking spinose tubercles and small tubercle on anterior and posterior margins of LO; 3, two pairs flanking spinose tubercles; 4, none.

(12) Shape of LO doublure: 0, even arc; 1, W-shaped.

(13) Size of palpebral lobes: 0, large; 1, small and rim-like.

(14) Shape of palpebral lobes: 0, semilunate; 1, half-teardrop shaped.

(15) Elevation of palpebral lobes in lateral view: 0, low; 1, high.

(16) Shape of posterior fixigena and posterior border: 0, fixigena and border equally wide; 1, fixigena narrow, border laterally extended.

Librigena

(17) Length of posterior branch of facial suture along field compared with anterior branch: 0, longer; 1, shorter; 2, roughly equal.

(18) Eye socle sculpture: 0, none; 1, studded with tubercles.

(19) Density of librigenal field sculpture: 0, sparse; 1, dense; 2, effaced.

(20) Number of tubercles in field arc: 0, five; 1, four; 2, three; 3, multiple arcs; 4, zero.

(21) Course of lateral border furrow: 0, smooth arc; 1, anteriorly arcuate, with sharp posteromedial angle.

(22) Style of lateral border sculpture: 0, low tubercles; 1, spinose tubercles, especially near genal spine.

(23) Lateral border sculpture distribution: 0, even; 1, sparse anteriorly, concentrated posteriorly.

(24) Size of Panderian notch: 0, small; 1, large.

(25) Length of genal spine: 0, short; 1, medium; 2, long; 3, very short.

(26) Width of genal spine: 0, spindly; 1, moderately robust; 2, very robust.

Pygidium

(27) Shape of outline of pygidium: 0, semilunate; 1, more semicircular.

(28) Number of pygidial segments: 0, three and a terminal piece; 1, three; 2, two.

(29) Shape of axis: 0, long, moderately wide; 1, short, wide; 2, short, relatively narrow.

(30) Size variation of prominent sculpture: 0, uniform; 1, variable.

(31) Shape of spine layout defined by spine bases: 0, arc; 1, V-shaped.

(32) Direction of pygidial sculpture: 0, more horizontal; 1, more vertical.

(33) Style of less prominent inner pleural sculpture: 0, tubercles; 1, granules.

(34) Height of "wall" in posterior view: 0, moderate; 1, very tall.

(35) Type of furrow posterior to merged inner pleural region: 0, none; 1, arcing furrow under spine bases; 2, slotted furrow.

(36) Expression of furrows on "wall": 0, visible; 1, effaced.

(37) Thickness of posterior border: 0, thick; 1, moderate.

(38) Presence of median excursion of border onto "wall": 0, absent; 1, present.

Results

The character matrix is shown in Table 1. All characters were treated as unordered. A single most parsimonious tree of length 65, with a consistency index of 0.86, and a retention index of 0.87 (Fig. 3) was found using the implicit enumeration algorithm of TNT (Goloboff et al. 2008). Nonparametric bootstrapping (10 000 replicates, using traditional search), and Bremer support were employed to evaluate nodal support. Synapomorphies are discussed under individual species headings, below.

The seven species of *Heckethornia* include a wide range of morphological variation, but comprise two well-supported sister clades. An older clade includes the type species plus *H. numani*, *H. bowiei*, and *H. hyndeae*. These species are characterized by the possession of paired occipital spines and the prominent retention of primary glabellar and fixigenal tubercles as spines (in some cases very long) in the adult. The clade is also characterized by several c.i.-one synapomorphies: small, rim-like palpebral lobes, spiny tubercles on the librigenal lateral border, a large Panderian notch, a short and relatively narrow pygidial axis, variably sized pygidial spines that project dorsoposteriorly, and a very tall pygidial "wall" with an inflated median projection of the border.

Table 1. Taxon-character matrix for cladistic analysis of *Heckethornia*.

	Characters			
	1	1 1 1 1 1 1 1 1 1 2	2 2 2 2 2 2 2 2 2 3	3 3 3 3 3 3 3 3
Taxa	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8 9 0	1 2 3 4 5 6 7 8
H. alticapitis	1 0 1 0 1 1 1 1 1 0	3 1 0 1 1 1 1 0 1 3	1 0 1 0 1 1 1 1 1 0	1 0 1 0 1 1 1 0
H. ballionae	1 0 1 0 1 1 1 1 1 0	3 1 0 1 1 1 1 0 1 3	1 0 1 0 1 1 1 1 1 0	1 0 1 0 1 1 1 0
H. morrisseyi	2 2 ? 1 1 1 0 1 1 0	4 0 ? ? ? ? 1 0 2 4	1 0 1 0 2 2 ? 1 1 0	1 0 1 0 1 ? 0 ?
H. smithi	1 1 0 2 0 0 0 0 1 1	1 0 1 0 0 0 2 1 0 1	0 1 0 1 0 0 0 1 2 1	0 1 0 1 0 0 0 1
H. numani	1 1 0 2 0 0 0 0 1 1	1 0 1 0 0 0 2 1 0 1	0 1 0 1 0 0 0 2 2 1	0 1 0 1 0 0 0 1
H. bowiei	1 0 0 3 0 1 0 1 1 1	2 0 1 0 0 0 2 0 0 2	0 1 0 1 2 1 0 2 2 1	0 1 0 1 2 0 0 1
H. hyndeae	0 0 ? 1 0 0 1 0 0 ?	0 0 1 0 0 0 1 0 0 3	0 1 0 1 3 0 0 2 2 1	0 1 0 1 0 0 0 1
MME 22.3	0 0 ? 0 0 0 0 0 0 ?	0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0	0 ? 0 0 0 0 0 0

Note: The outgroup taxon, an undescribed dimeropygid from section MME 22.3 m at Middle Mountain (Wah Wah Mountains, Millard County, western Utah) is labeled "MME 22.3". *Heckethornia alticapitis* (Young, 1973) codes identically with *H. ballionae* for the purposes of this analysis, but the two species are differentiated in their respective species descriptions and remarks.

Fig. 3. Single most parsimonious cladogram retrieved by implicit enumeration search of the taxon-character matrix of Table 1. Length, consistency index (c.i.), and retention index (r.i.) of the cladogram are recorded in the shadowed box. Characters with a c.i. of 1.0 are represented by black boxes; homoplasious characters (c.i. < 1.0) are represented by white boxes. (*a*) Character-state transitions are optimized using the accelerated transformation (ACCTRAN) criterion. Bold numbers at nodes are (upper) nonparametric bootstrap support values derived from 10 000 pseudoreplicates using traditional search and (lower) Bremer support values. (*b*) Character-state transitions are optimized using the delayed transformation (DELTRAN) criterion.

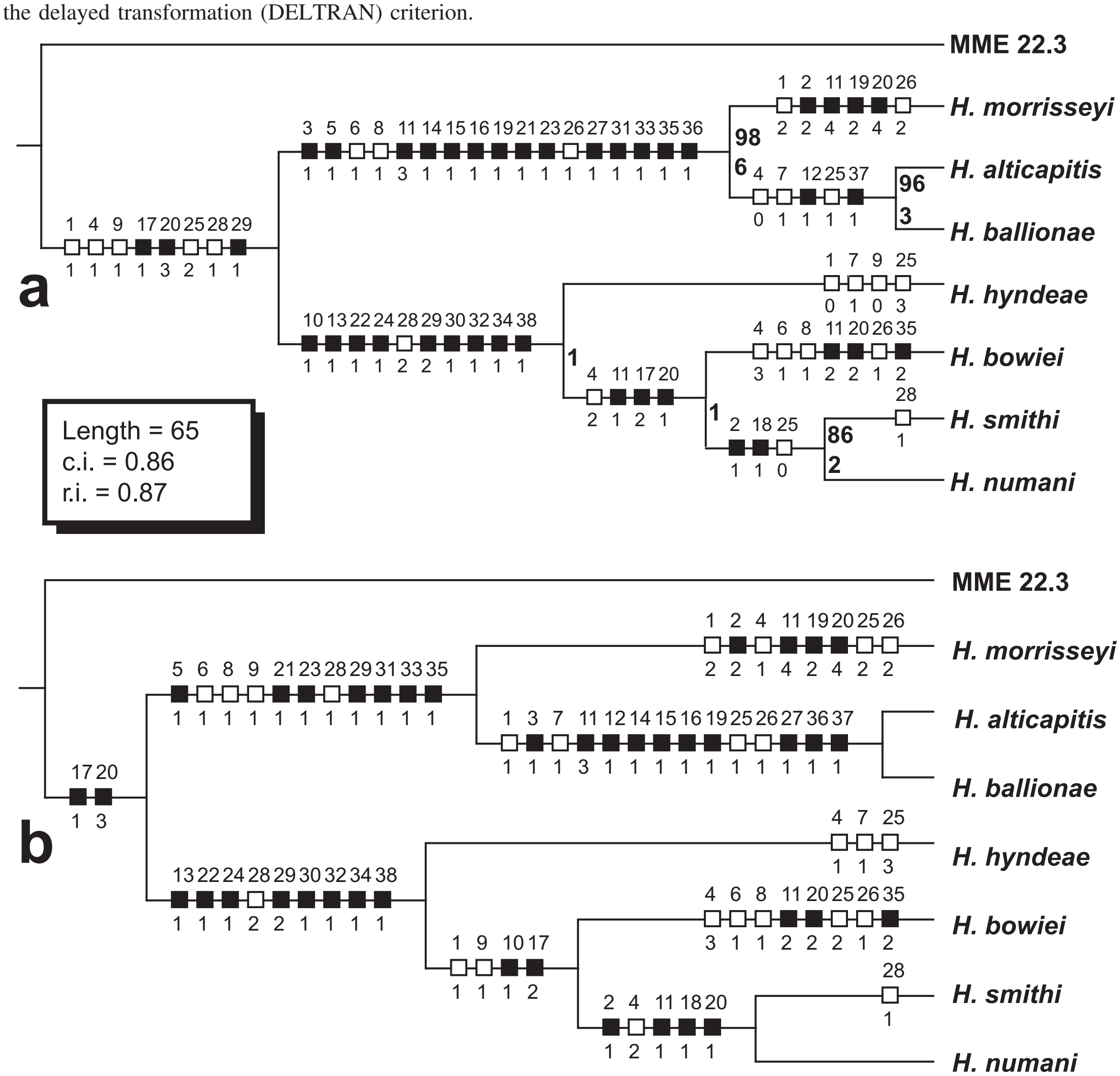


Fig. 4. *Heckethornia smithi* n. sp., from section G 210.2 m, Fillmore Formation (Ibexian; Tulean), southern Confusion Range, Ibex area, Tule Valley, Millard County, western Utah. (*a*, *e*, *j*) Cranidium, SUI 113342, dorsal, left lateral, and anterior views, ×10. (*b*, *f*, *k*), Cranidium, **holotype**, SUI 113343, dorsal, left lateral, and anterior views, ×10. (*c*, *g*, *l*) Cranidium, SUI 113344, dorsal, left lateral, and anterior views, ×10. (*d*, *h*, *i*, *m*) Cranidium, SUI 113345, dorsal, left lateral, ventral, and anterior views, ×10. (*n*, *r*, *v*) Cranidium, SUI 113346, dorsal, left lateral, and anterior views, ×12. (*o*, *s*, *t*, *w*) Cranidium, SUI 113347, dorsal, right lateral, ventral, and anterior views, ×12. (*p*, *q*, *u*, *bb*) Cranidium, SUI 113348, dorsal, anterior, right lateral, and oblique views, ×12. (*x*, *ee*, *ff*) Cranidium, SUI 113349, dorsal, right lateral, and anterior views, ×12. (*y*, *z*, *aa*) Cranidium, SUI 113350, dorsal, right lateral, and anterior views, ×12. (*cc*, *gg*, *hh*) Cranidium, SUI 113351, left lateral, dorsal, and anterior views, ×15. (*dd*, *ii*, *jj*) Cranidium, SUI 113352, left lateral, dorsal, and anterior views, ×15.

A younger clade includes *H. morrisseyi*, *H. alticapitis*, and *H. ballionae*. These species have a prominent median occipital spine and either effaced dorsal sculpture or a densely tuberculate background sculpture surrounding the primary tubercles, which are not as prominently developed as in the *H. smithi* clade. They also have pygidial spines that project only a little above horizontal. Further c.i.-one synapomorphies include effaced anterior border sculpture, librigenal lateral border furrows that are arcuate anteriorly and steeply angled posteriorly, librigenal lateral borders with the sculpture effaced anteriorly, short and wide pygidial axes, uniformly sized pygidial spines in a V-shaped layout, granulose sculpture on the inner pleurae, and an arcuate furrow underneath the bases of the pygidial spines.

A case could be made for recognition of two genus-group taxa, as the most derived members of either group are quite strikingly distinct from one another. As there seems little doubt that the clade as a whole is monophyletic, however, we prefer for the time being to refer all species to a single taxon.

Systematic paleontology

Repository

All figured material is housed in the Paleontology Repository, Department of Geoscience, University of Iowa, Iowa City, Iowa, USA, with specimen number prefix SUI.

Terminology

Morphological terms follow Whittington and Kelly (1997).

Family Dimeropygidae Hupé, 1953
= Dimeropygidae Whittington and Evitt, 1954
= Toernquistiidae Hupé, 1953

REMARKS: *Heckethornia* n. gen. is assigned to Dimeropygidae, although it lacks the diagnostic features (Adrain and Westrop 2007*a*, p. 346) of typical dimeropygids, such as *Dimeropyge* Öpik, 1937; *Chomatopyge* Whittington and Evitt, 1954; *Mesotaphraspis* Whittington and Evitt, 1954; and *Toernquistia* Reed, 1896. It belongs to Adrain and Westrop's (2007*a*, p. 342) "group 4" of Lower Ordovician genera, such as *Bearriverops* Adrain and Westrop, 2007*a* and *Tulepyge* Adrain and Westrop, 2006*a*.

Genus ***Heckethornia*** n. gen.

TYPE SPECIES: *Heckethornia smithi*, n. sp., from the Ibexian (Tulean) of western Utah, USA.

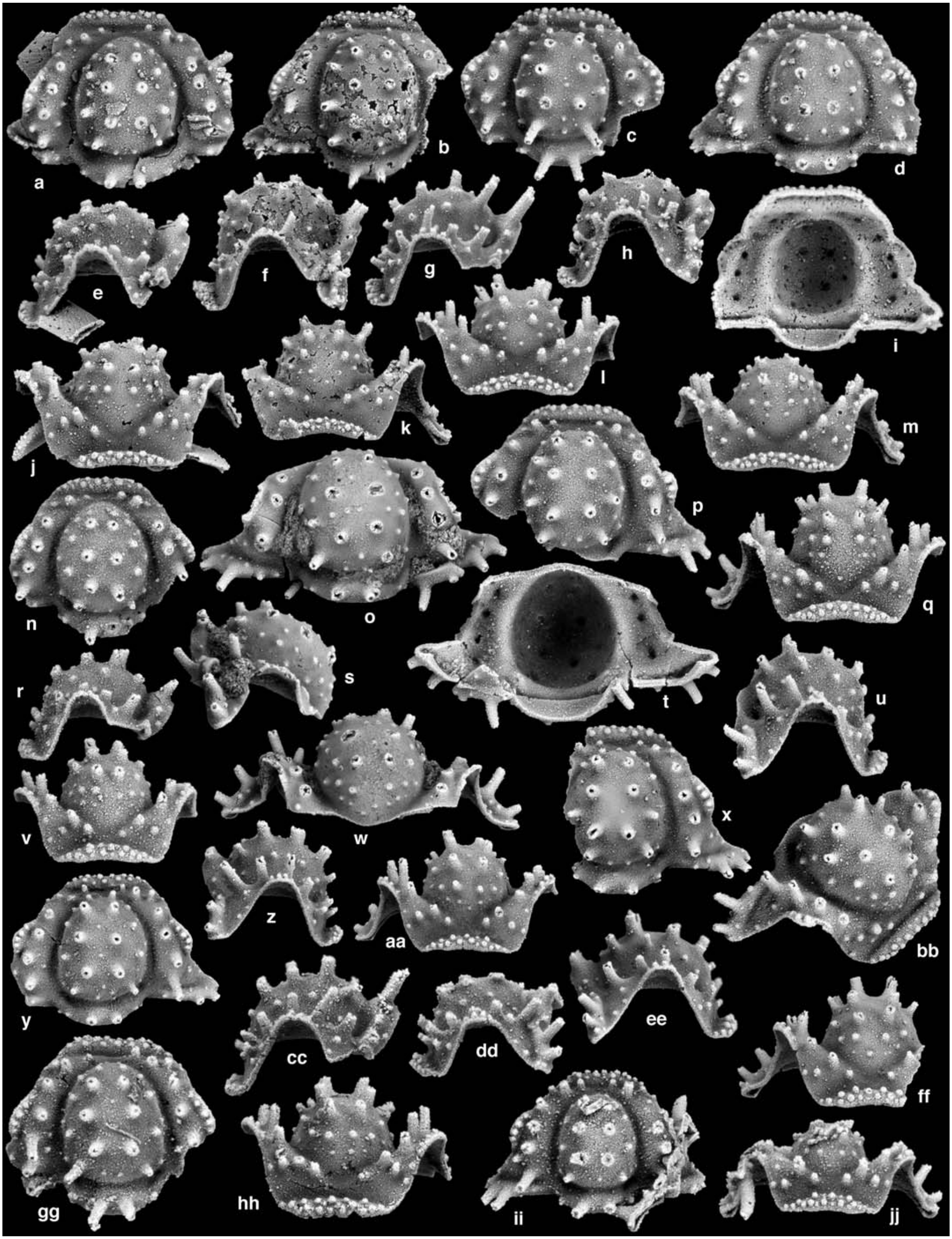
OTHER SPECIES: All from the Ibexian of western Utah; *Heckethornia numani* n. sp., from the Tulean; *Heckethornia hyndeae* n. sp., from the Tulean; *Heckethornia bowiei* n. sp. from the Tulean; *Heckethornia morrisseyi* n. sp. from the Tulean; *Heckethornia alticapitis* (Young, 1973), from the Blackhillsian; and *Heckethornia ballionae* n. sp. from the Blackhillsian.

ETYMOLOGY: After the Heckethorn Hills, southern Confusion Range, which contain the type locality of the type species. Gender is feminine.

DIAGNOSIS: Cranidium and pygidium highly vaulted; cranidium with trapezoidal outline; anterior border usually with median dorsal inflection, and with doublure expressed as anterior face; glabella ovoid to thimble-shaped, highly inflated, with three prominent pairs of spines or tubercles in non-effaced species, lateral lobes not clearly defined; interocular fixigenae narrow, with arc of five or six spines in most species; LO typically with prominent median spine(s); librigena with large, subtriangular field and often with arc of three or four tubercles or spines; pygidium of two or three segments with one or two axial rings expressed; with a prominent spine projecting from the fulcra of each posterior pleural band; and with outer pleurae merged into a tall "wall" structure.

REMARKS: No articulated thoracic material is known from any species of *Heckethornia*, although all species are represented by at least a single thoracic segment, and the thorax of *H. bowiei* is very well known. Unfortunately, no thoracic material is known for the outgroup. Despite this incomplete knowledge, some putative synapomorphies are expressed in the thoracic segments. All taxa (except the less well known and plesiomorphic *H. hyndeae*) possess segments with prominent paired axial and fulcral spines. *Heckethornia ballionae*, *H. alticapitis*, and *H. bowiei* share segments with tuberculate axes and large fulcral spines, as well as segments with very large inset articulating half rings, paired axial spines, and small, posterolaterally projecting pleural spines.

Heckethornia is a striking taxon due to its highly vaulted and inflated exoskeleton and robustly spinose sculpture. These features are unusual among mature aulacopleuroidean trilobites, but bear strong resemblance to juvenile features of several species of *Dimeropyge* Öpik, 1937. The cranidial spine array of *Heckethornia* closely resembles that of juveniles of *Dimeropyge speyeri* Chatterton, 1994, pl. 5 and *D. spinifera* Whittington and Evitt, 1954, pl. 22. However, the species of *Dimeropyge* possess either two or four pairs of main glabellar spines, never the three seen in all members of *Heckethornia*. The arc of fixigenal spines is basically identical. The key difference is that in species of *Dimeropyge*, the spinose sculpture reduces ontogenetically to tubercles (as in *D. speyeri*) or blends into a general dense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jj

Fig. 5. *Heckethornia smithi* n. sp., from section G 210.2 m, Fillmore Formation (Ibexian; Tulean), southern Confusion Range, Ibex area, Tule Valley, Millard County, western Utah. (*a*, *e*, *j*) Cranidium, SUI 113353, dorsal, left lateral, and anterior views, ×12. (*b*, *f*, *g*) Cranidium, SUI 113354, dorsal, left lateral, and anterior views, ×12. (*c*, *h*, *n*) Cranidium, SUI 113355, dorsal, left lateral, and anterior views, ×15. (*d*, *i*, *o*) Cranidium, SUI 113356, dorsal, left lateral, and anterior views, ×15. (*k–m*) Cranidium, SUI 113357, dorsal, right lateral, and anterior views, ×15. (*p*, *q*) Left librigena, SUI 113358, external and internal views, ×12. (*r*, *x*) Left librigena, SUI 113359, external and ventrolateral views, ×12. (*s*, *t*, *y*) Left librigena, SUI 113360, external, internal, and ventrolateral views, ×12. (*u*, *v*) Right librigena, SUI 113361, external and ventrolateral views, ×15. (*w*) Left librigena, SUI 113362, external view, ×12. (*z*, *aa*) Right librigena, SUI 113363, external and ventrolateral views, ×12. (*bb*) right librigena, SUI 113364, external view, ×15. (*cc*) Left librigena, SUI 113365, external view, ×12. (*dd*) right librigena, SUI 113366, external view, ×12. (*ee*) Right librigena, SUI 113367, external view, ×15. (*ff*, *pp*, *qq*) Thoracic segment, SUI 113368, left lateral, anterior, and dorsal views, ×15. (*gg–ii*, *rr*) Thoracic segment, SUI 113369, right lateral, dorsal, ventral, and anterior views, ×15. (*jj*) Right librigena, SUI 113370, external view, ×12. (*kk–oo*) Thoracic segment, SUI 113371, dorsal, posterior, ventral, anterior, and left lateral views, ×12.

spinotuberculate sculpture (as in *D. spinifera*), whereas in most species of *Heckethornia*, the spines stand out above a relatively effaced background.

Thoracic segments of these genera are also highly similar in overall arched shape, possession of an inset articulating half ring with the axial ring wrapped and tapered around it anterolaterally, and similarly positioned spines. Again, in some species of *Dimeropyge*, the spines transform to tubercles (*D. speyeri*; cf. Chatterton 1994, pl. 5, fig. 25, with pl. 6, fig. 15), but in other species (*Dimeropyge spinifera*; Whittington and Evitt, 1954, pl. 23, figs. 1–8, 13–16), the spines are retained as in *Heckethornia*. There is one major difference between even the most spinose thorax of *Dimeropyge* and that of *Heckethornia*: species of the latter do not possess any segments with a single median axial spine, which is diagnostic of core-group dimeropygids. This can be assessed despite a lack of articulated thoracic material for *Heckethornia*, because no dimeropygid thoracic segments with single median spines occur in the faunas.

Librigenal morphologies of *Dimeropyge* and *Heckethornia* are very different, with the former possessing yoked cheeks with long and narrow librigenal fields, very thick lateral borders, and flattened, highly tapered genal spines. Pygidial morphologies are also dissimilar. Although traditional dimeropygid pygidia are "walled," it is developed much less in *Dimeropyge* than in *Heckethornia*, and *Dimeropyge* lacks the prominent spines protruding from the fulcra of the posterior band of each segment.

Adrain and Fortey (1997) also compared their *Dimeropyge*? *ericina* with juvenile material of *Dimeropyge*. The spine array of *D.*? *ericina* compares closely with that of *Heckethornia*, except that it bears only two pairs of glabellar spines, and possesses a much more spinose anterior border. Ontogenetic material of *Heckethornia*, however, suggests that the anteriormost pair of glabellar spines is last to develop. Furthermore, its librigenae are like those of *Heckethornia* in overall shape, and in that they possess a spine arc (though of two spines, not four or five tubercles). The thoracic segments are also very similar. These potential synapomorphies leave open the possibility that *D.*? *ericina* could be a derived and paedomorphic species of *Heckethornia*. Unfortunately, the pygidium of *D.*? *ericina* is unknown, and until it is better represented, we leave it tentatively assigned to *Dimeropyge*.

Comparison with otarionine trilobites also reveals interesting points of similarity. *Harpidella spinifrons* (Williams *in* Cooper and Williams, 1935; Adrain and Chatterton 1995, fig. 8) and *Maurotarion messieri* Adrain and Chatterton (1995, fig. 9) both display three large pairs of glabellar tubercles like those of *Heckethornia*. In *M. messieri*, these tubercles become effaced during ontogeny, but they remain as large tubercles among smaller background tubercles in *Harpidella spinifrons*. Juvenile cranidia of *Cyphaspis lowei* Adrain and Chatterton, 1996, not only display paired glabellar tubercles (though only two main pairs) and fixigenal tubercle arcs, but they also have a large median spine on LO that diminishes through ontogeny. The librigenae of *C. mactavishi* Adrain and Chatterton, 1996 and *Harpidella greggi* Adrain and Chatterton, 1995, resemble those of some species of *Heckethornia* in their overall shape (subtriangular field, rolled and inflated border, long and conical spine) and also possess an arc of four or five tubercles. All of these taxa are clearly not closely related to *Heckethornia*, but the similar spine arrays could be indicative of broader relationships among aulacopleuroidean taxa.

Heckethornia smithi n. sp.
(Figs. 4–6)

DERIVATION OF NAME: After Robert Smith.

HOLOTYPE: Holotype cranidium, SUI 113343, from section G 210.2 m (Hintze's (1953) 690/ G-17), Fillmore Formation (Ibexian; Tulean), southern Confusion Range, Ibex area, Tule Valley, Millard County, western Utah.

MATERIAL: Assigned specimens SUI 113342 – SUI 113380 from section G 210.2 m, Fillmore Formation (Ibexian; Tulean), southern Confusion Range, Ibex area, Tule Valley, Millard County, western Utah.

DIAGNOSIS: Cranidium lacking background sculpture of scattered small tubercles; librigena with a long, wide field, arc of four or five tubercles, a short, incised lateral border furrow, and a short, very slender genal spine; pygidium with three pairs of large, tall (posterodorsally projecting) spines alternating with small peglike tubercles.

DESCRIPTION: Cranidium with sagittal length 83.0% (77.3%–87.1%) width across midpoint of palpebral lobes, with granulose sculpture overlain by prominent spines; anterior branch of facial suture slightly bowed outward, strongly posteriorly divergent; anterior border moderately short and narrow, somewhat dorsally inflated, with moderately dense

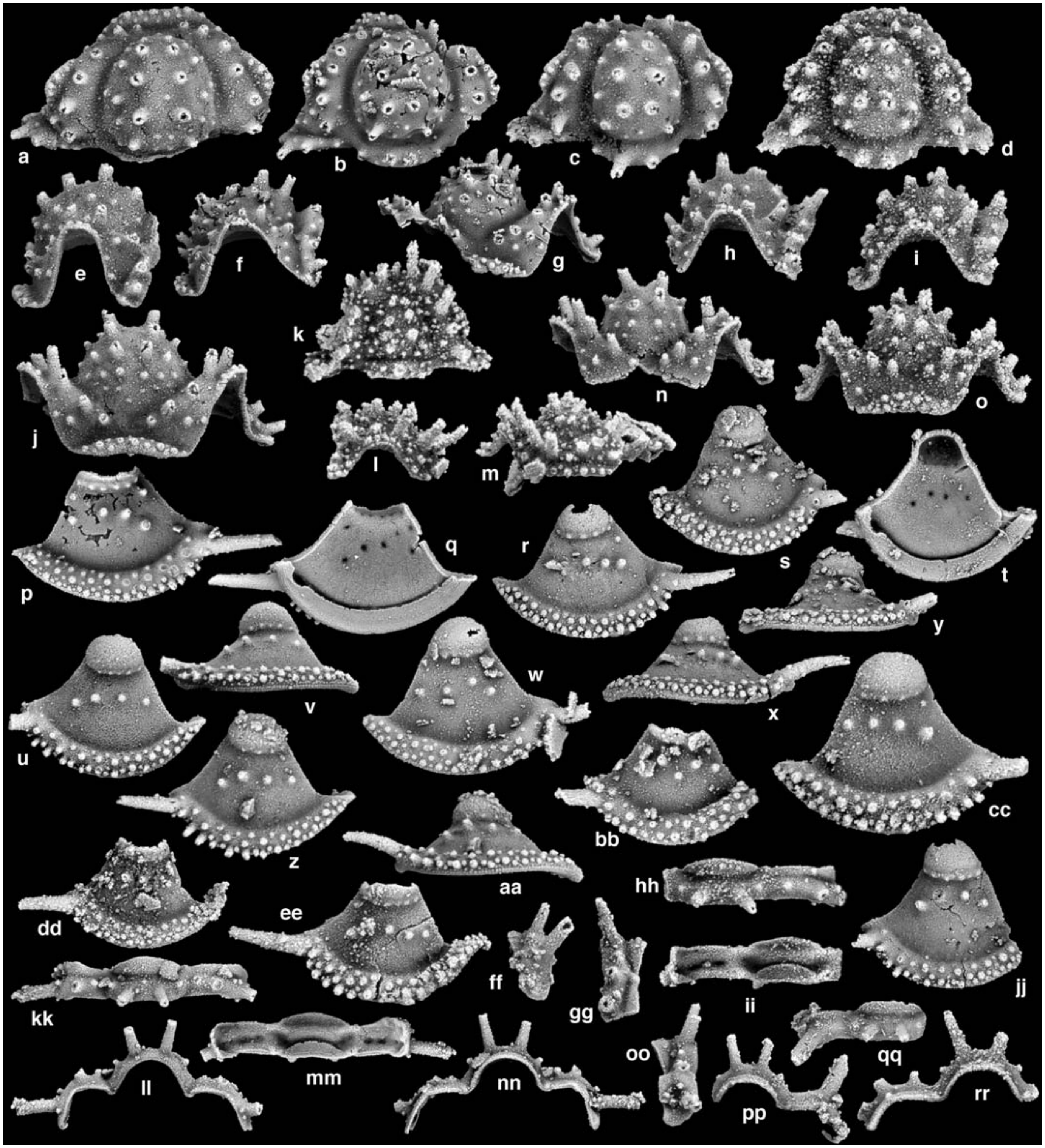
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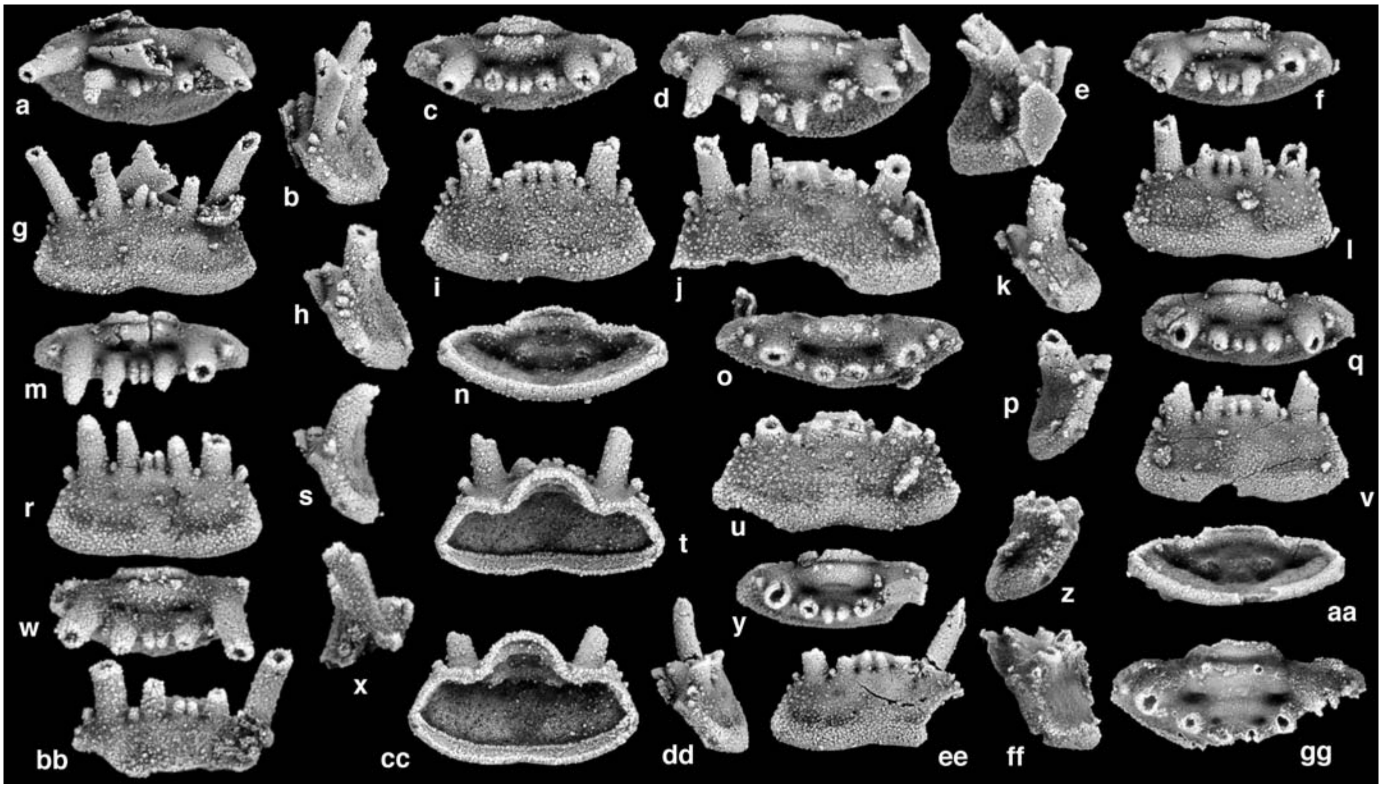
Fig. 6. *Heckethornia smithi* n. sp., from section G 210.2 m, Fillmore Formation (Ibexian; Tulean), southern Confusion Range, Ibex area, Tule Valley, Millard County, western Utah. Magnifications are ×15, except where noted. (*a*, *b*, *g*) Pygidium, SUI 113372, dorsal, left lateral, and posterior views, ×12. (*c*, *h*, *i*, *n*, *t*, *cc*) Pygidium, SUI 113373, dorsal, left lateral, posterior, ventral, anterior, and anteroventral views. (*d*, *e*, *j*) Pygidium, SUI 113374, dorsal, right lateral, and posterior views. (*f*, *k*, *l*) Pygidium, SUI 113375, dorsal, left lateral, and posterior views. (*m*, *r*, *s*) Pygidium, SUI 113376, dorsal, posterior, and left lateral views, ×20. (*o*, *u*, *z*) Pygidium, SUI 113377, dorsal, posterior, and right lateral views. (*p*, *q*, *v*, *aa*) Pygidium, SUI 113378, right lateral, dorsal, posterior, and ventral views. (*w*, *x*, *bb*) Pygidium, SUI 113379, dorsal, right lateral, and posterior views, ×20. (*y*, *dd*, *ee*) Pygidium, SUI 113380, dorsal, left lateral, and posterior views. (*ff*, *gg*) Pygidium, SUI 113381, left lateral and dorsal views.



tuberculate sculpture; anterior border furrow short, moderately shallow; preglabellar field short, narrow, slightly depressed, effaced; frontal areas moderately wide anteriorly, tapered dorsoposteriorly, steeply sloped to subvertical, with linear arrangement of spines; preglabellar furrow short, shallow, strongly anteriorly convergent to a point, slightly overhung by glabella, nearly connected to anterior border furrow through depressed preglabellar field; glabella with width at midlength 89.1% (80.4%–97.6%) length, with highest point of inflation at posteriormost pair of main glabellar spines, with spinose sculpture of three large pairs straddling sagittal axis alternating with wide-set paired smaller spines, and with widely spaced small spinose tubercles outlining the base; axial furrow moderately wide and deep, deepest along mid-glabella, separated from SO by raised ridge, anteriorly divergent until midlength of glabella, then strongly convergent; interocular fixigena slightly inflated, steeply sloped upward from axial furrow, subhorizontal adjacent to palpebral lobes, with linear arrangement of five or six spines extending forward down frontal areas and backward onto posterior fixigenae, with some additional tubercles anteriorly and posteriorly; palpebral furrow narrow, shallow medially, deeper anteriorly and posteriorly, course diagonal to gently outwardly convex; palpebral lobes narrow, tapered anteriorly and posteriorly, widest slightly posterior of midlength, with five or six tubercles on rim; posterior branch of facial suture moderately long in dorsal view, actually slightly longer than anterior branch, strongly posterolaterally divergent, sloped at about 45°; posterior fixigena moderately wide, triangular; SO moderately long, shallow medially, deeper laterally, deepest in apodemal pits, arcuate in course (convex posteriorly); LO moderately long, slightly longer than anterior border, tapered laterally, moderately inflated, with sculpture of prominent pair of median spines flanked by pair of smaller spines, with some additional tubercles; LO doublure long, with smooth anterior margin; posterior border furrow short, shallow proximally and distally, slightly deeper along midwidth of posterior border, transverse to slightly anterolaterally curved in course; posterior border short sagittally, flared exsagittally, moderately inflated, moreso laterally, with two pairs of small spinose tubercles flanking axis and two pairs of medium sized spines near distal edge; posterior border doublure of short rim proximally, and triangular incurvature distally.

Rostral plate unknown.

Librigena sub-equilaterally triangular in outline, with width of field under midpoint of eye 56.3% (52.4%–62.3%) length along lateral border; anterior branch of facial suture long, very steep, with short subhorizontal section along anterior projection of lateral border; posterior branch of facial suture slightly more gently sloped and curved, about equal to anterior branch in length; eye highly domed, elliptical, separated from eye socle by narrow, shallow furrow; eye socle of single, thin band, with sculpture of four to eight small tubercles, separated from librigenal field by moderately broad and shallow furrow; librigenal field about twice as long at lateral border than under eye, gently convex, with flat to convex-inward arc of four or five prominent tubercles and some smaller interspersed tubercles overlying a smooth or anastomosing ridge sculpture; lateral border furrow gently curved in course, moderately broad and deep, deepest anteriorly; lateral border moderately wide, slightly tapered anteriorly, with maximum width occurring slightly anterior of genal spine, highly inflated, with heavily tuberculate sculpture of two major arcs of larger tubercles following curve of border with smaller interspersed tubercles, with spinose tubercles near genal spine, border continues about one half spine-width posterior of genal spine; genal spine short, convexly posteriorly arched, slender, tapered to fine point, with sparsely tuberculate sculpture; border doublure wide, slightly narrower posteriorly, with large, semicircular Panderian opening opposite base of genal spine.

Total number of thoracic segments unknown. Segments highly arched and vaulted axially and pleurally, with axial width 43.2% (41.1%–45.5%) maximum width of segment; articulating half ring longest medially, tapered laterally, with maximum length slightly shorter than axial ring; ring furrow moderately deep, deepest laterally in apodemal pits, describes shallow "W" shape on larger specimens; axial ring moderately long and wide, gently inflated, with sculpture of pair of large spines flanking axis, flanked by small, nubby spines midway down side of ring; axial furrow narrow and shallow; inner pleurae nearly horizontal; fulcral angle steep and outer pleurae steeply sloped to subvertical; anterior pleural band short medially, flared laterally into prominent triangular articulating facet, with very short articulating flange along anterior edge of inner pleurae, some segments (Figs. 5*kk*–5*oo*) with distinctive sinuous anterior margin; pleural furrow short, moderately shallow near axis, deeper laterally, slightly posteriorly curved; posterior pleural band nearly as long as axial ring, gently inflated, with slight articulating flange (visible as short raised edge) on posterior edge of inner pleurae, and with strong paired spinose sculpture of spines at fulcrum, between fulcrum and axial ring, and between fulcrum and lower edge of pleurae on most segments, and some additional spines on some segments; with slight triangular doublure under posteroventralmost corners of pleurae, and semilunate doublure under axial ring.

Pygidium of three segments, moderately short and wide, with sagittal length excluding articulating half ring 36.4% (32.8%–44.6%) maximum width, highly vaulted pleurally and moderately vaulted axially, with robust sculpture of spines on posterior bands alternating with tubercles; articulating half ring moderately short, semilunate; articulating furrow short, moderately deep, deepest laterally in apodemal pits; axis short, moderately wide, slightly more than about 1/3 maximum pygidial width, strongly posteriorly tapered, moderately inflated; first axial ring moderately long, wide, moderately independently inflated, with one or two pairs of small tubercles at midlength; pseudo-articulating half ring (more prominent on larger specimens) short, slightly recessed, set off by very short, shallow furrows; inter-ring furrow very shallow medially (over pseudo-articulating half ring), very deeply slotted laterally; second axial ring short, fairly narrow, obscured on smaller specimens by spines; second inter-ring furrow absent; third axial ring short, narrow, obscured by paired spines; axial furrow moderately narrow and moderately deep, wider and shallower on larger specimens, strongly anteriorly divergent; inner pleurae ill-defined into anterior and posterior bands (except first segment), subhorizontal; fulcral angle very steep; anterior pleural band of first segment short, shorter near axis, with very short ventrally tapered articulating facet and large tubercle in front of fulcrum; pleural furrow short, shallow, slightly deeper laterally, posterolaterally directed; posterior pleural band of first segment roughly as long as axial ring proximally, ill-defined laterally, with large, conical, posterolaterally curved spine at fulcrum; second and third anterior and posterior pleural bands merged; not well defined by pleural furrows, obscured by tubercle-spine pairs; interpleural furrows inferred to pass between first spine and second tubercle, second spine and second tubercle, and either side of central small spine pair; outer pleural "wall" structure tall, posteriorly convex, with coarse granulose sculpture; posterior border furrow very shallow medially, moderately shallow laterally, with gentle W-shaped course (posterior view); posterior border thick, gently inflated, with raised median section reaching halfway up "wall," and with moderate median dorsal inflection of ventral margin; posterior border doublure long, slightly shorter than border, with even anterior margin.

ONTOGENY: Although *H. smithi* is known from relatively little ontogenetic material, some morphological changes can be documented. The smallest illustrated cranidium (Figs. 5*k*, 5*l*, 5*m*) has a small, strongly anteriorly tapered (thimble- or bullet-shaped) cranidium; sculpture of dense tubercles overlain by long spines; flat, wider anterior border; and lower arch of facial suture – palpebral lobe (lateral view). Small librigenae (Figs. 4*bb*, 4*ee*) have less robust eye socle studs; smaller librigenal fields; wider lateral borders; and slightly more robust genal spines than larger librigenae. Large pygidia of *Heckethornia smithi* (e.g., Figs. 6*d*, 6*e*, 6*j*) express a well-developed pseudo-articulating half ring on the second axial ring and have three tubercle-spine pairs of posterior pleural band sculpture. Small pygidia (e.g., Figs. 6*m*, 6*r*, 6*s*) have a small pseudo-articulating half ring (if any) and lack tubercles with the third spine pair, and sometimes also with the second pair.

REMARKS: Intraspecific variation in *Heckethornia smithi* is low, and most notable differences are ontogenetic. Cranidial variation includes the degree of median dorsal inflection of the anterior border (cf. Figs. 4*j*, 4*l*); expression of secondary glabellar spines and tubercles (cf. Figs. 4*a*, 4d, 4*o*); degree of inflation of the glabella (Fig. 4*f*, high; Fig. 4*h*, low);

Fig. 7. *Heckethornia numani* n. sp., from section YH 128.9 – YH 129.5 m, "Yellow Hill Beds" (Ibexian; Tulean), Yellow Hill, near Pioche, Lincoln County, eastern Nevada and section G 258.2 m, Fillmore Formation (Ibexian; Tulean), southern Confusion Range, Ibex area, Tule Valley, Millard County, western Utah. (*a*, *b*, *e*, *j*) Cranidium, **holotype**, SUI 113382, dorsal, oblique, left lateral, and anterior views, ×10 (YH 128.9 m). (*c*, *d*, *h*, *i*) Cranidium, SUI 113383, dorsal, ventral, right lateral, and anterior views, ×12 (YH 128.9 m). (*f*, *g*, *k*, *m*) Cranidium, SUI 113384, right lateral, dorsal, anterior, and ventral views, ×12 (YH 128.9 m). (*l*, *q*, *r*, *v*) Thoracic segment, SUI 113385, left lateral, dorsal, ventral, and anterior views, ×12 (YH 128.9 m). (*n–p*) Right librigena, SUI 113386, ventrolateral, internal, and external views, ×20 (YH 128.9 m). (*s*, *w*, *x*) Cranidium, SUI 113387, dorsal, left lateral, and anterior views, ×15 (G 258.2 m). (*t*, *dd*, *ii*) Cranidium, SUI 113388, dorsal, anterior, and left lateral views, ×12 (YH 129.5 m). (*u*) Left librigena, SUI 113389, external view, ×15 (YH 128.9 m). (*y*, *ee*) Right librigena, SUI 113390, external and internal views, ×15 (YH 128.9 m). (*z*, *aa*, *ff*) Pygidium, SUI 113391, dorsal, left lateral, and posterior views, ×20 (YH 128.9 m). (*bb*, *cc*, *gg*, *hh*, *jj*) Pygidium, SUI 113392, dorsal, right lateral, ventral, anterior, and posterior views, ×20 (YH 128.9 m).

depth of the axial furrow (cf. Figs. 4*c*, 4*d*); shape of the palpebral lobes (Fig. 4*a*, diagonal; Fig. 4*c*, arcuate); and the number of accessory tubercles on LO. Librigenal variation is expressed in the number and robustness of the eye socle tubercles (Fig. 5*p*, many robust tubercles; Fig. 5*cc*, few weak tubercles); size (length vs. width) of the librigenal field (cf. Figs. 5*p*, 5*r* with Figs. 5*w*, 5*cc*); and shape of the arc of field tubercles (Fig. 5*r*, flat; Fig. 5*p*, concave-outward).

Pygidia differ mainly according to size, as discussed earlier in the text. However, the number of tubercles on the first axial ring does vary. Some pygidia (e.g., Figs. 6*a*, 6*c*, 6*f*, 6*q*) have a centered pair of tubercles. Others (e.g., Figs. 6*d*, 6*o*, 6*y*, 6*gg*) have the center pair and a flanking pair. The posterior border also differs on some pygidia. It is nearly uninflected medially in Figs. 6*l*, 6*r*; but distinctly inflected in Figs. 6*u*, 6*ee*. One pygidium (Figs. 6*o*, 6*p*, 6*u*) may not express the third segment at all, as only two tubercle-spine pairs are apparent. The first two pairs of spines of the pygidium of Figs. 6*a*, 6*b*, 6*g* are about the same thickness.

Heckethornia smithi most closely resembles its sister taxon, *H. numani*, with which it is compared through differential description. *Heckethornia hyndeae* is also differentially described with respect to *H. smithi*. *Heckethornia smithi* is compared with *H. bowiei* in the remarks section of the latter species.

Heckethornia numani n. sp.

(Fig. 7)

DERIVATION OF NAME: After Gary Numan.

HOLOTYPE: Holotype cranidium, SUI 113382, from section YH 128.9 m, "Yellow Hill Beds" (Ibexian; Tulean), Yellow Hill, near Pioche, Lincoln County, eastern Nevada.

MATERIAL: Assigned specimens SUI 113382 – SUI 113392 from section YH 128.9–129.5 m, "Yellow Hill Beds" (Ibexian; Tulean), Yellow Hill, near Pioche, Lincoln County, eastern Nevada and section G 258.2 m (Hintze's (1953) 758′/ G-19), Fillmore Formation (Ibexian; Tulean), southern Confusion Range, Ibex area, Tule Valley, Millard County, western Utah.

DIAGNOSIS: Cranidium with long, narrow, oval glabella and with arc of spines outlining axial furrow growing inward across furrow; librigena with arc of spines on field; thoracic segment with fine raised line sculpture on articulating half ring doublure; pygidium with pair of tubercles on axial ring and two pairs of tall, similarly sized conical spines with tubercles interspaced.

DESCRIPTION: *Heckethornia numani* is sufficiently similar to *H. smithi* that it is treated via extended comparison. These taxa share four c.i.-one synapomorphies: studded eye socle sculpture, sparsely distributed cranidial sculpture, one pair of tubercles flanking the paired occipital spines, and four tubercles in the librigenal tubercle arc.

Measurements are given to enable comparison of *H. numani* with other species of the clade. The sagittal length of the cranidium is 87.8% (85.6%, 89.9%) the width across the midpoint of the palpebral lobes, and the glabella (measured at midlength) is 85.2% (79.8%–87.3%) as wide as the sagittal length. Cranidia of *H. numani* and *H. smithi* are highly similar. Differences include the former's slightly narrower and more robustly tuberculate anterior border; longer, narrower, more ovoid, and more inflated glabella; deeper axial furrows; narrower interocular fixigenae; slightly shorter palpebral lobes; broader posterior fixigena; shallower SO and SO apodemal pits; and denser, more spinose sculpture, including an arc of fixigenal tubercles growing across the axial furrow.

The width of the librigenal field at the midpoint of the eye is 51.0% (49.0%, 52.9%) the length along the lateral border. Librigenae of *H. numani* and *H. smithi* are also alike, but differ in that those of *H. numani* possess a slightly narrower field, more robust eye socle tubercles, spinose librigenal field sculpture, a shallower lateral border furrow, a slightly thicker genal spine, and a somewhat narrower doublure.

The width of the axis is 35.8% the total width of the thoracic segment. Although only a single thoracic segment assignable to *H. numani* is known, it compares closely to those of *H. smithi*. They differ most strikingly in that *H. numani* possesses one or two additional pairs of large spines, with a pair on the axial ring, one midway between the axial furrow and the fulcrum, one on the fulcrum, and one near the ventral tip of the segment. There are also additional smaller spines between the major pairs. More subtle differences include the narrower axis of *H. numani*; its longer articulating half ring, but shorter axial ring; its deeper articulating and pleural furrows; and its wider inner pleurae.

The sagittal length of the pygidium of *H. numani* is 27.8% the width. Pygidia of *H. numani* are relatively shorter and broader than those of *H. smithi*; with one fewer segments; only two pairs of thinner spines; a slightly more inflated, less dorsally inflected posterior border; a less prominent me-

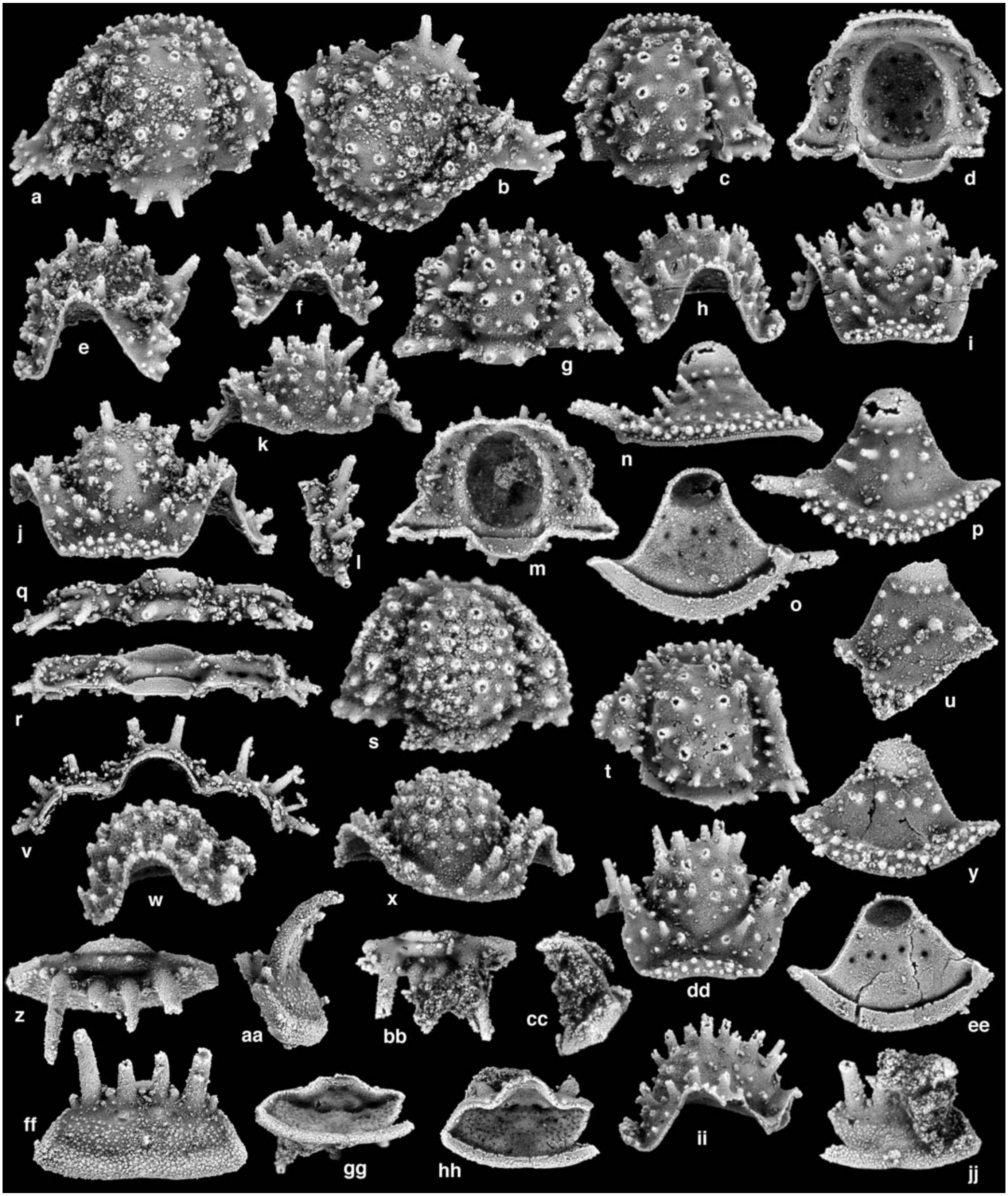

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Fig. 8. *Heckethornia hyndeae* n. sp., from section YH 128.9 m, "Yellow Hill Beds" (Ibexian; Tulean), Yellow Hill, near Pioche, Lincoln County, eastern Nevada. (*a*, *e*, *j*, *n*) Cranidium, **holotype**, SUI 113393, dorsal, right lateral, anterior, and oblique views, ×12. (*b*, *f*, *g*, *k*, *o*) Cranidium, SUI 113394, dorsal, ventral, right lateral, anterior, and oblique views, ×12. (*c*, *d*, *i*) Cranidium, SUI 113395, dorsal, right lateral, and anterior views, ×12. (*h*, *l*, *m*) Cranidium, SUI 113396, right lateral, dorsal, and anterior views, ×12. (*p*, *s*, *t*) Cranidium, SUI 113397, dorsal, anterior, and right lateral views, ×15. (*q*, *u*, *v*) Cranidium, SUI 113398, dorsal, right lateral, and anterior views, ×15. (*r*, *w*, *x*) Cranidium, SUI 113399, dorsal, anterior, and left lateral views, ×15. (*y*, *aa*, *bb*) Cranidium, SUI 113400, dorsal, left lateral, and anterior views, ×15. (*z*, *cc*, *dd*) Cranidium, SUI 113401, dorsal, anterior, and right lateral views, ×15.

dian projection of the border onto the "wall"; and coarser, sparser granulose sculpture on the "wall" and border. *H. numani* pygidia also lack one or more pairs of the small spinose tubercles exsagittal to the largest spine pair.

ONTOGENY: *Heckethornia numani* is known from less material than the other species, but some ontogenetic changes in the cranidium, librigena, and pygidium can be observed. The smallest cranidium (Figs. 7*f*, 7*g*, 7*k*) is relatively shorter and narrower than the largest (Figs. 7*a*, 7*b*, 7*e*, 7*i*); possesses shorter facial suture branches; a relatively shorter, wider glabella; narrower interocular and posterior fixigenae; denser and more spinose sculpture; and deeper furrows. The smallest of the three librigenae (Figs. 15*n*–15*p*) has more and smaller eye socle tubercles and more spinose field and border tubercles. The smaller pygidium (Figs. 7*bb*, 7*cc*, 7*gg*, 7*hh*, 7*jj*) is relatively shorter and narrower than the larger one, with a narrower and less vaulted axis, poorly developed posterior pleural band tubercles, more closely spaced spines, and a relatively thinner posterior border.

REMARKS: Cranidial variation in *Heckethornia numani* is difficult to evaluate, as there is only one large cranidium (Figs. 7*a*, 7*b*, 7*e*, 7*j*). One cranidium (Figs. 7*s*, 7*w*, 7*x*) has a shorter, wider glabella; longer, narrower palpebral lobes; and much denser glabellar sculpture, with rows of five or six small tubercles between each major spine pair and two pairs of small tubercles flanking each major spine pair. This may be geographic variation, as this cranidium is the single specimen from section G 258.2 m, rather than the Yellow Hill section. These differences are also possibly ontogenetic, as the cranidium is slightly smaller than the other figured specimens. Likewise, librigenal variation is difficult to evaluate. One specimen (Figs. 7*y*, 7*ee*) has an extra tubercle in the arc on the field and is possibly missing its genal spine. However, the genal spine could also be reduced during ontogeny. Pygidial variation is likely ontogenetic, as discussed earlier in the text.

Heckethornia numani is compared with *H. hyndeae* in the the differential description of the latter species. *Heckethornia numani* less closely resembles *H. bowiei*, mainly in that its cranidium is narrower overall, and its sculpture is much less robust. Also, *H. numani* possesses a narrower anterior border; longer preglabellar field; more ovoid glabella; a fixigenal tubercle arc growing across the axial furrow; smaller, less inflated palpebral lobes; less divergent LO spines; a studded eye socle; a much smaller librigenal field with four or five fixigenal spines; a short, slender genal spine; more pairs of small and large spines on the thoracic segment; a longer pygidial axial ring, with a pair of tubercles; shorter, thinner pygidial spines; a shorter "wall"; and a thicker posterior border.

Heckethornia hyndeae n. sp.
(Figs. 8–10)

DERIVATION OF NAME: After Chrissie Hynde.

HOLOTYPE: Holotype cranidium, SUI 113393, from section YH 128.9 m, "Yellow Hill Beds" (Ibexian; Tulean), Yellow Hill, near Pioche, Lincoln County, eastern Nevada.

MATERIAL: Assigned specimens SUI 113393 – SUI 113441 from section YH 128.9 m, "Yellow Hill Beds" (Ibexian; Tulean), Yellow Hill, near Pioche, Lincoln County, eastern Nevada.

DIAGNOSIS: Cranidium with narrow and highly inflated anterior border, very bulbously inflated subcircular to ovoid (outline shape) glabella with sculpture of short spines - spinose tubercles and transverse belts of smaller tubercles, axial–preglabellar and anterior border furrows crossing on preglabellar field, making strikingly effaced "X"; librigena with short, very slender genal spine and very wide (compared with field width) lateral border doublure; thoracic segments with short, nubby spinose and tuberculate sculpture; pygidium with four or more tubercles on axial ring, and spines on first (of two) posterior pleurae much more robust than second pair of spines.

DESCRIPTION: *Heckethornia hyndeae* is not morphologically distinct enough from *H. smithi* to warrant a full description. It is instead described via extended comparison with *H. smithi* and *H. numani*. Ratios are given to allow comparison with other members of *Heckethornia*.

The sagittal length of the cranidium is 88.4% (82.4%–98.2%) the width across the palpebral lobes, and the width of the glabella is 87.0% (79.6%–93.0%) its sagittal length. The most easily observed cranidial difference between *H. hyndeae* and *H. smithi* is the former's dense tuberculate sculpture. The typical paired glabellar and occipital spines are instead expressed as large, coarse tubercles. The cranidium of *H. hyndeae* is also longer and wider than that of *H. smithi*, with a longer, narrower, and more highly inflated anterior border; longer preglabellar field; a larger and more highly inflated glabella; deeper and narrower axial furrows; narrower interocular fixigenae; shorter and narrower palpebral lobes; and a shorter LO.

The width of the librigenal field at the midpoint of the eye is 53.4% (45.4%–58.6%) the length along the lateral border furrow. Librigenae of *H. hyndeae* and *H. smithi* are closely comparable. Those of *H. hyndeae* possess a smooth eye socle; two arcs of tubercles on the field; a deeper lateral

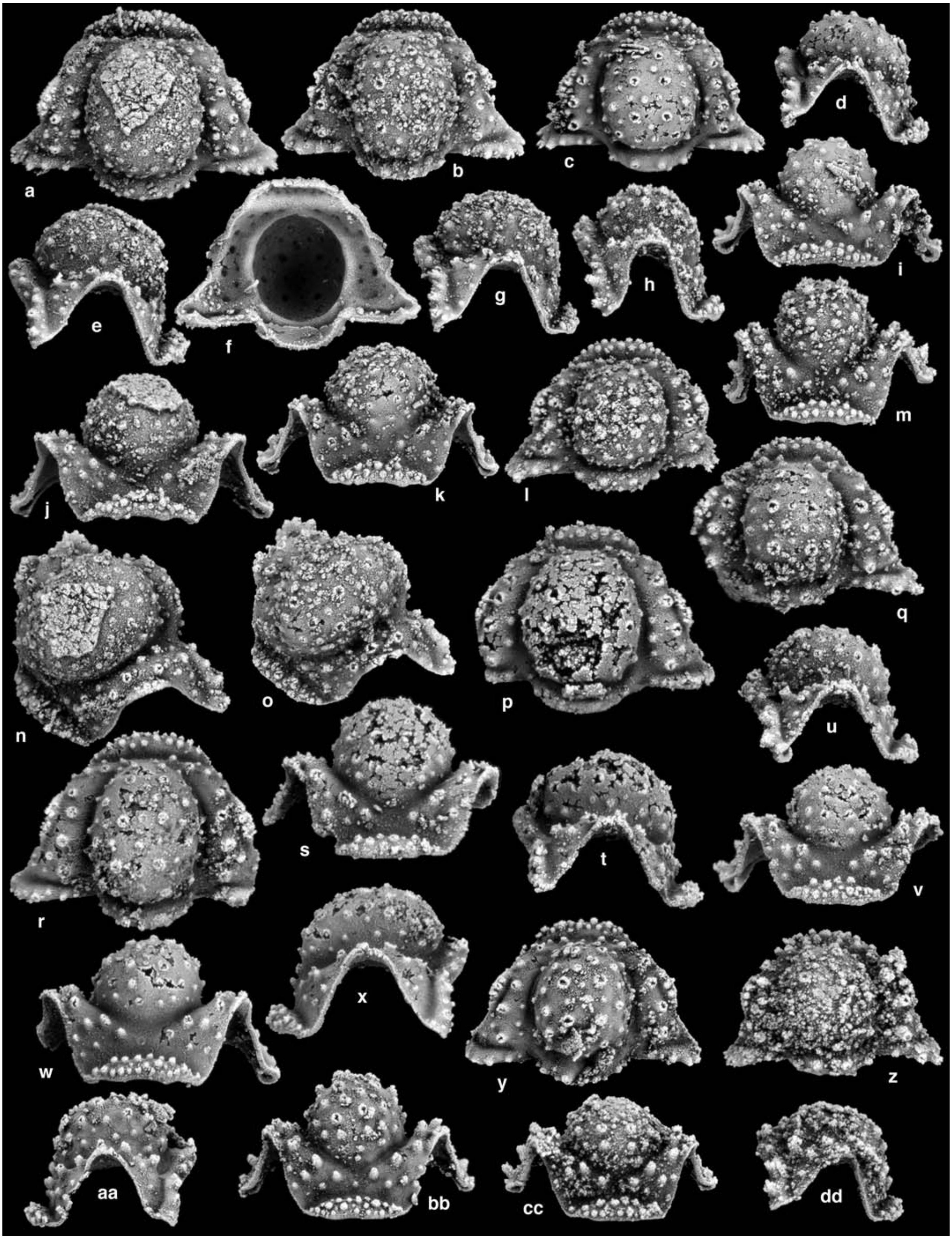
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Fig. 9. *Heckethornia hyndeae* n. sp., from section YH 128.9 m, "Yellow Hill Beds" (Ibexian; Tulean), Yellow Hill, near Pioche, Lincoln County, eastern Nevada. Magnifications are ×15, except where noted. (*a*) Left librigena, SUI 113402, external view. (*b*, *f*) Left librigena, SUI 113403, external and internal views. (*c*, *d*, *g*) Left librigena, SUI 113404, external, internal, and ventrolateral views. (*e*) Right librigena, SUI 113405, external view. (*h*) Left librigena, SUI 113406, external view. (*i*) Left librigena, SUI 113407, external view. (*j*) Left librigena, SUI 113408, external view. (*k*, *q*) Right librigena, SUI 113409, external and ventrolateral views. (*l*) Left librigena, SUI 113410, external view, ×20. (*m*) Right librigena, SUI 113411, external view, ×20. (*n*) Right librigena, SUI 113412, external view. (*o*) Left librigena, SUI 113413, external view. (*p*) Left librigena, SUI 113414, external view. (*r*) Right librigena, SUI 113415, external view, ×20. (*t*) Left librigena, SUI 113416, external view, ×20. (*u–w*) Thoracic segment, SUI 113417, dorsal, anterior, and right lateral views. (*x*, *dd*, *hh*) Thoracic segment, SUI 113418, right lateral, dorsal, and anterior views. (*y*, *ee*, *ii*) Thoracic segment, SUI 113419, left lateral, dorsal, and anterior views. (*z*, *aa*) Pygidium, SUI 113420, dorsal and right lateral views, ×20. (*bb*, *ff*, *jj*) Pygidium, SUI 113421, left lateral, dorsal, and posterior views, ×20. (*cc*, *gg*, *kk*, *rr*, *ss*) Pygidium, SUI 113422, ventral, anterior, dorsal, posterior, and left lateral views. (*ll*, *mm*, *tt*) Pygidium, SUI 113423, left lateral, dorsal, and posterior views. (*nn–pp*, *uu*) Pygidium, SUI 113424, posterodorsal, right lateral, dorsal, and posterior views. (*qq*, *vv*, *ww*) Pygidium, SUI 113425, dorsal, left lateral, and posterior views, ×20.

border furrow; a wider lateral border; and a shorter, thinner genal spine.

Thoracic segments of *H. hyndeae* possess longer articulating half rings and axial rings, and many closely spaced pairs of spinose tubercles, in contrast to the sparsely and distinctly spinose segments of *H. smithi*. The axis is 42.9% (40.4%–45.2%) of the total width of the segment.

The sagittal length of the pygidium of *H. hyndeae* is 30.5% (26.3%–36.5%)themaximumwidth(acrossthearticulatingfacet). Itisdistinguishedfromthatof*H.smithi*bypossessingonlytwosegments; four or more axial ring tubercles; thinner anterior spines; thicker posterior spines; a single tubercle between the posterior spines;andamoreprominentmedianprojectionoftheanteriorborderontothe"wall."

Heckethornia hyndeae and *H. numani* are also morphologically similar. *H. hyndeae* mainly differs in its more effaced sculpture; belts of small tubercles between main glabellar spine pairs; rounder, more highly inflated glabella; longer, narrower palpebral lobes; narrower posterior fixigenae; deeper glabellar furrows; unstudded eye socle; wider lateral border; slightly thinner genal spine; four (instead of two) tubercles on the first pygidial axial ring; and slightly thicker pygidial spines. The arc of fixigenal tubercles closest to the axial furrow also grow over the furrow in *H. numani*, but remain just adjacent in *H. hyndeae*.

ONTOGENY: The smallest cranidium of *Heckethornia hyndeae* (Figs. 10*u*, 10*aa*, 10*ee*) is relatively much shorter and less vaulted than the largest cranidium (Figs. 10*a*, 10*e*, 10*i*), with denser, more robustly spinose sculpture; a narrower, much less inflated glabella; smaller palpebral lobes; and has a prominent pair of spines on LO. The smallest librigenae (e.g., Fig. 9*l*) have relatively larger eyes; narrower and slightly shorter librigenal fields; and longer genal spines than larger specimens. Small pygidia are considerably relatively shorter and wider, with a narrow axis; few axial tubercles; slender spines without well-developed tubercle pairs; and slightly steeper "wall" structures.

REMARKS: Intraspecific variation in *Heckethornia hyndeae* is very low. The curvature of the anterior border varies (Fig. 8*j*, curvy; 8*bb*, flat), as does the density of the cranidial sculpture (Figs. 8*c*, 8*r*). The eye socle is more effaced on some specimens (e.g., Figs. 9*j*, 9*k*, 9*o*); the number of librigenal field tubercles in the exsagittal arc ranges from two (Figs. 9*b*, 9*c*) to 5 (Fig. 9*m*); and the pattern of the arcs is erratic. Pygidia of *H. hyndeae* have different numbers of tubercles on the axial ring (Figs. 9*kk*, 9*mm*, 9*qq*).

Heckethornia hyndeae is compared with *H. bowiei* under the latter species.

Heckethornia bowiei n. sp.
(Figs. 11–15)

Undetermined gen. and sp. locality (loc.) H-7. Zone G-2. (Not described); Hintze 1953, pl. 19, fig. 14.

DERIVATION OF NAME: After David Bowie.

HOLOTYPE: Holotype cranidium, SUI 113443, from section H 127.1 m (Hintze's (1953) 276′/ H-11), Fillmore Formation (Ibexian; Tulean), southern Confusion Range, Ibex area, Tule Valley, Millard County, western Utah.

MATERIAL: Assigned specimens SUI 113442 – SUI 113492 from section H 93.4–163.3 m (Hintze's (1953) 190′/ H-7–163.3 m, new horizon), Fillmore Formation (Ibexian; Tulean), southern Confusion Range, Ibex area, Tule Valley, Millard County, western Utah and section YH 175.9 m (Hintze's (1953) 577′/ YH-16), "Yellow Hill Beds" (Ibexian; Tulean), Yellow Hill, near Pioche, Lincoln County, eastern Nevada.

DIAGNOSIS: Cranidium with wide anterior border, thimble-shaped glabella, very tall glabellar and fixigenal spines, and very tall, widely splayed occipital spine pair; librigena with very large field and long, moderately slender spine; thoracic segments with very long, robust, posterodorsally directed spines at fulcra (some segments with smaller, thinner spines), and with node on sagittal axis at anterior and posterior margins of axial ring; pygidium with very short axial ring followed by deep, slot-like inter-ring furrow, with extremely tall, posteriorly curved spines on first segment and short (in comparison), conical spines on second segment, and with pair of slot-like furrows on upper portion of "wall."

DESCRIPTION: Cranidium with sagittal length 83.5% (77.9%–86.1%) width at midpoint of palpebral lobes, with robust tuberculospinose sculpture; anterior branch of facial suture slightly anteriorly convergent; anterior border wide, moderately short, slightly tapered exsagittally, inflated with semicylindrical cross-section, with moderately dense sculpture of

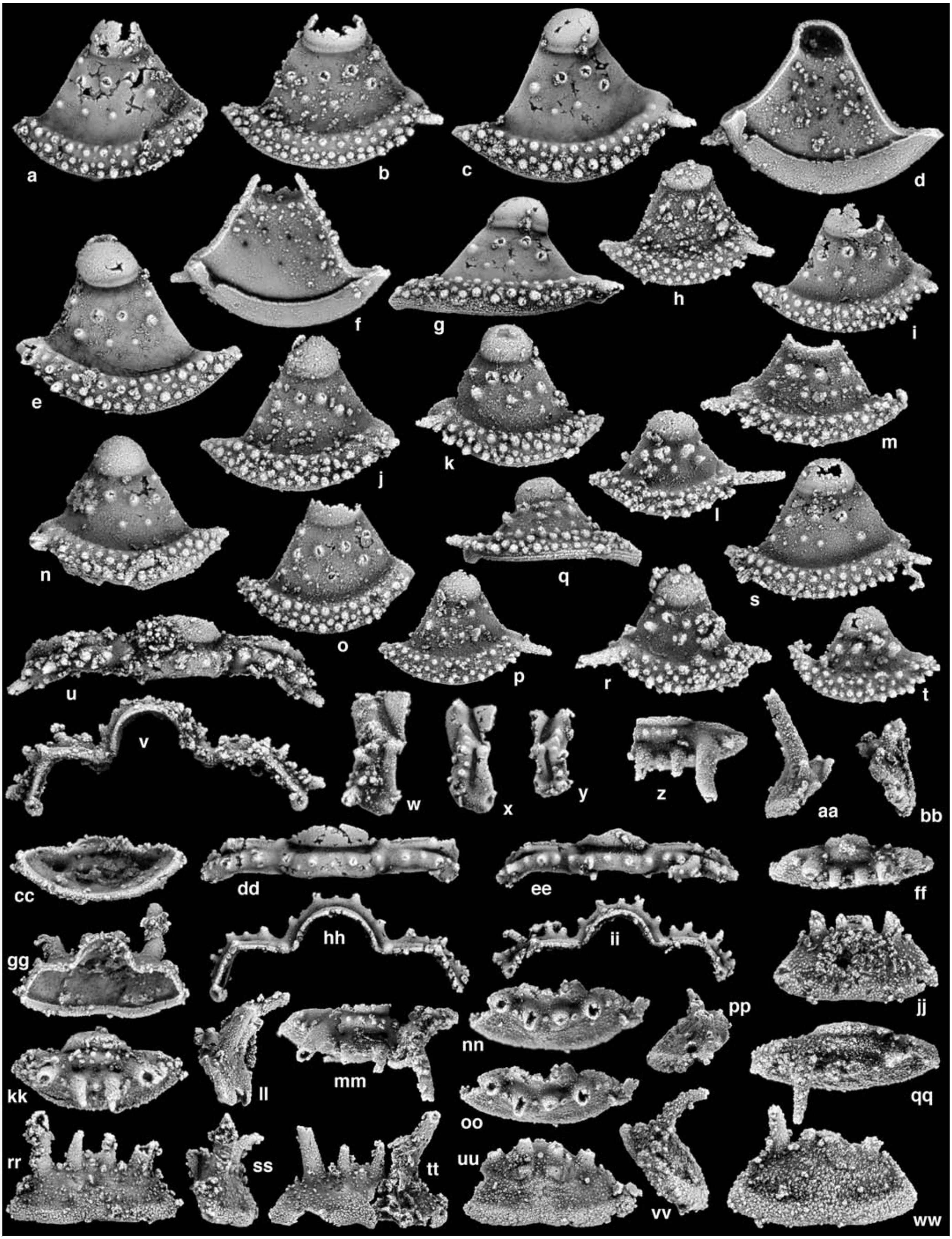
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Fig. 10. *Heckethornia hyndeae* n. sp., from section YH 129.5 m, “Yellow Hill Beds” (Ibexian; Tulean), Yellow Hill, near Pioche, Lincoln County, eastern Nevada and section G 258.2 m, Fillmore Formation (Ibexian; Tulean), southern Confusion Range, Ibex area, Tule Valley, Millard County, western Utah. Specimens are from YH 129.5 m, except where noted. (*a*, *e*, *j*) Cranidium, SUI 113426, dorsal, right lateral, and anterior views, ×12. (*b*, *f*, *g*, *l*) Cranidium, SUI 113427, dorsal, ventral, right lateral, and anterior views, ×12. (*c*, *h*, *m*) Cranidium, SUI 113428, dorsal, left lateral, and anterior views, ×12. (*d*, *i*, *n*) Cranidium, SUI 113429, dorsal, right lateral, and anterior views, ×15. (*k*, *o*, *p*) Cranidium, SUI 113430, right lateral, dorsal, and anterior views, ×15. (*q*, *r*, *w*) Cranidium, SUI 113431, dorsal, right lateral, and anterior views, ×15. (*s*, *t*, *x*) Cranidium, SUI 113432, dorsal, anterior, and right lateral views, ×15. (*u*, *aa*, *ee*) Cranidium, SUI 113433, dorsal, right lateral, and anterior views, ×17. (*v*, *bb*, *cc*) Cranidium, SUI 113434, dorsal, left lateral, and anterior views, ×15. (*y*) Right librigena, SUI 113435, external view, ×15. (*z*, *jj*, *kk*) Cranidium, SUI 113436, dorsal, left lateral, and anterior views, ×15 (G 258.2 m). (*dd*, *gg*, *hh*) Thoracic segment, SUI 113437, right lateral, dorsal, and anterior views, ×12. (*ff*, *ll*, *mm*, *tt*) Thoracic segment, SUI 113438, left lateral, dorsal, anterior, and ventral views, ×12. (*ii*, *qq*, *rr*) Cranidium, SUI 113439, dorsal, anterior, and left lateral views, ×12 (G 258.2 m). (*nn*, *oo*, *pp*, *uu*) Thoracic segment, SUI 113440, left lateral, dorsal, anterior, and ventral views, ×12. (*ss*) Left librigena, SUI 113441, external view, ×10 (G 258.2 m).

small tubercles; anterior border furrow moderately short, very short and incised distally; preglabellar field extremely short, depressed, effaced, allows convergence of anterior border and preglabellar furrows; frontal areas very broad, highly posterodorsally tapered, steeply sloped to subvertical, with linear spinose sculpture (discussed on fixigenae) underlain by moderately densely spaced tiny tubercles on most cranidia; preglabellar furrow short, moderately deep, slightly overhung by anterior of glabella, anteriorly convergent to a point at sagittal axis; glabella thimble-shaped, anteriorly tapered, with width at midlength 92.3% (88.2%–96.5%) sagittal length, moderately highly inflated, with highest point even with posteriormost main spine pair, without defined lateral lobes or furrows (lateral furrows sometimes discernible as slight lateral indentations in glabellar outline), with complex tuberculospinose sculpture of three pairs of large spines decreasing in size anteriorly, flanked by one or two pairs of tubercles, alternating with transverse belts of closely spaced small tubercles (posteriormost at anterior edge of SO), and with scattered small tubercles, but some specimens more effaced; axial furrow moderately wide, narrower anteriorly, moderately strongly outwardly bowed and anteriorly convergent, separated from SO by low ridge; fixigenae moderately broad, steeply inclined adaxially, subhorizontal distally, with lineation of five or six large spines running anteriorly onto frontal areas and posteriorly onto posterior fixigenae, closely spaced line of small tubercles near axial furrow following its course, and scattered small tubercles (some specimens more effaced); palpebral furrow moderately narrow and deep, incised, course diagonal to gently outwardly convex; palpebral lobes very slightly inflated, narrow, moderately long, arcuate, with about six small tubercles along the rim; posterior branch of facial suture long, roughly equal to anterior suture length, posterolaterally angled; posterior fixigenae large, triangular, moderately steeply posteriorly sloped, with tuberculospinose sculpture (see earlier in the text); posterior border furrow moderately short, shallow laterally, deeper medially; posterior border short, slightly longer at distal tips, mildly inflated like anterior border, with two or three paired small tubercles medially and a large spine just adaxial to distal edge; border doublure just a short rim medially, curved under triangularly under lateral spine; SO long, shallow medially, very deep laterally in large apodemal pits; LO long sagittally, highly tapered exsagittally, highly inflated, with sculpture of pair of extremely large, widely splayed conical spines flanked by one or two pairs of tiny spines, with tiny tubercle on sagittal axis just behind SO, and one on posterior margin, and some specimens with additional tiny tubercles; LO doublure long, crescentic.

Rostral plate unknown.

Librigena with width at midlength of eye 60.4% (54.0%–64.8%) length along lateral border; anterior branch of facial suture long, steep, except along short anterior projection of lateral border; posterior branch of facial suture slightly shorter and less steep, gently posterolaterally curved; eye ovoid in outline, highly inflated, set off from socle by narrow, incised furrow; eye socle of single narrow band, separated from librigenal field by narrow, shallow furrow; librigenal field gently convex, with prominent arc of three or four large tubercles near eye (most arcs convex-outward, but some flat or concave-outward), some specimens with additional scattered small tubercles, some with anastomosing ridges – caecal trunks radiating from base of tubercles; librigenal border furrow narrow, moderately deep anteriorly to spine base (deeper on some specimens), then very shallow along genal spine and posteriorly, strongly arcuate in course; lateral border broad, broadest near base of spine, highly inflated, with semicylindrical cross-section, with sculpture of two arcs of medium-sized tubercles (more spinose near genal spine) and interspersed smaller tubercles, extends posteriorly beyond genal spine; genal spine large, very long, more than thrice length of field under eye, moderately thick, cylindrical, tapered to a blunt point, gently posteromedially curved, lightly granulose; lateral border doublure broad, slightly tapered anteriorly and posteriorly, with arcuate margin following lateral border furrow, with large semicircular Panderian notch located just posterior from center of genal spine.

Total number of thoracic segments unknown. Thoracic segments highly arched axially and moderately arched pleurally, with width of axial ring 42.3% (39.2%–48.4%) maximum width of segment, and prominent spinose sculpture; articulating half ring semilunate, inset posteriorly from anterior margin of segment; ring furrow moderately long, highly tapered laterally, shallow medially, deep laterally in apodemal pits; axial ring gently dorsally inflated, equal to or

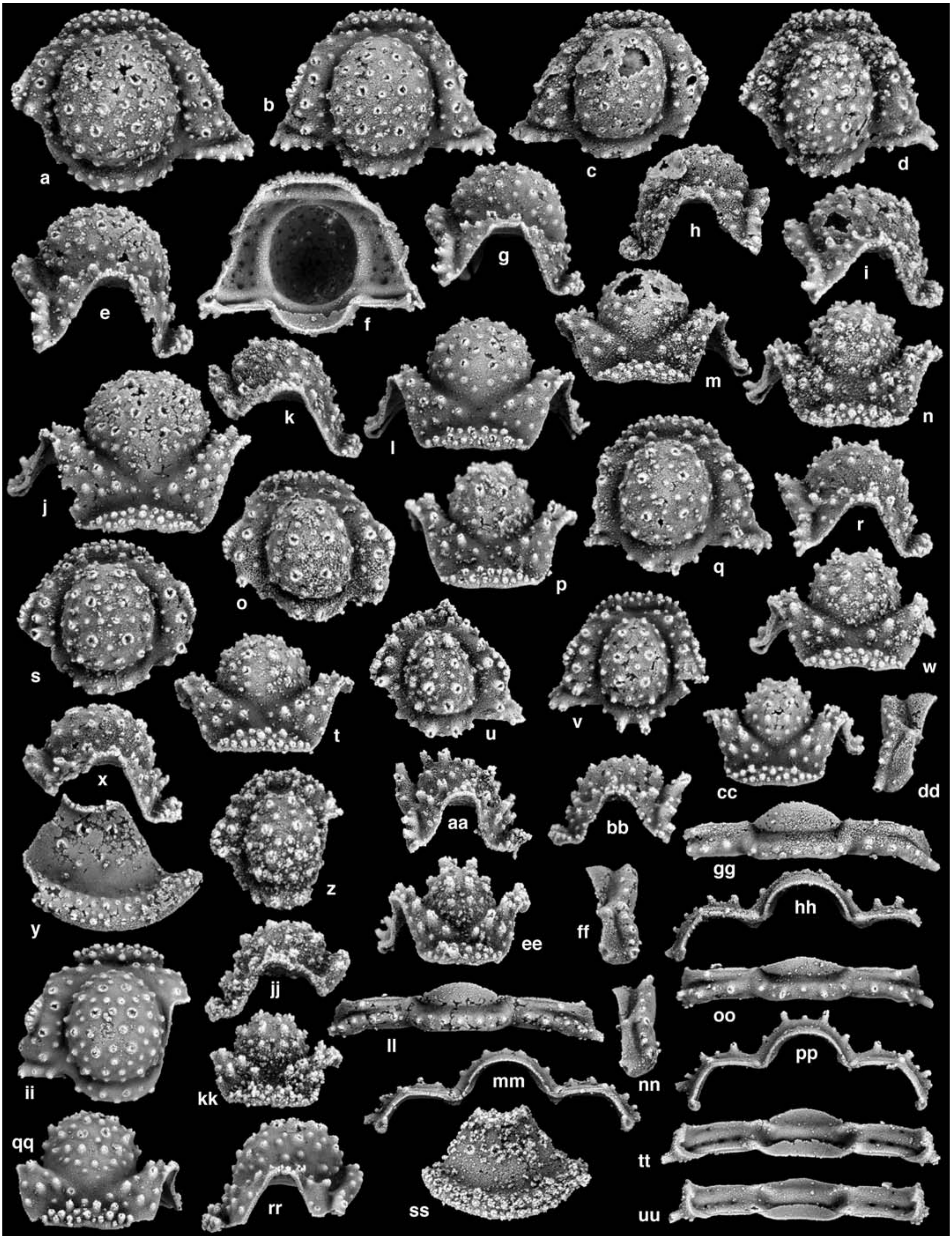
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Fig. 11. *Heckethornia bowiei* n. sp., from section H 93.4–127.1 m, Fillmore Formation (Ibexian; Tulean), southern Confusion Range, Ibex area, Tule Valley, Millard County, western Utah. (*a*, *e*, *j*) Cranidium, SUI 113442, dorsal, right lateral, and anterior views, ×7.5 (H 127.1 m). (*b*, *f*, *k*, *l*) Cranidium, **holotype**, SUI 113443, dorsal, left lateral, anterior, and oblique views, ×7.5 (H 127.1 m). (*c*, *d*, *g*, *h*) Cranidium, SUI 113444, dorsal, ventral, left lateral, and anterior views, ×7.5 (H 127.1 m). (*i*, *m*, *r*, *w*) Cranidium, SUI 113445, right lateral, dorsal, anterior, and ventral views, ×10 (H 127.1 m). (*n*, *s*, *x*) Cranidium, SUI 113446, dorsal, left lateral, and anterior views, ×7.5 (H 127.1 m). (*o*, *t*, *y*, *hh*) Cranidium, SUI 113447, dorsal, left lateral, anterior, and oblique views, ×10 (H 127.1 m). (*p*, *u*, *z*) Cranidium, SUI 113448, dorsal, right lateral, and anterior views, ×10 (H 127.1 m). (*q*, *v*, *aa*, *ff*) Cranidium, SUI 113449, dorsal, left lateral, anterior, and ventral views, ×10 (H 93.4 m). (*bb*, *cc*, *gg*) Cranidium, SUI 113450, dorsal, right lateral, and anterior views, ×10 (H 127.1 m). (*dd*, *ii*, *jj*) Cranidium, SUI 113451, dorsal, right lateral, and anterior views, ×12 (H 93.4 m). (*ee*, *ll*, *mm*) Cranidium, SUI 113452, dorsal, right lateral, and anterior views, ×15 (H 127.1 m).

slightly longer than sagittal length of articulating half ring, tapered laterally, U-shaped in dorsal view (wraps anteriorly around sides of articulating half ring), with sculpture of very large pair of spines moderately wide-set across axis, flanked by pair of spinose tubercles on most specimens, some specimens (e.g., Figs. 13*a*, 13*d*, 13*i*) have additional scattered tubercles, all specimens show two tubercles on sagittal axis like those on LO; axial ring doublure long medially, tapered laterally, closely resembles LO doublure; axial furrow narrow and incised over posterior band (on most segments, some with only faint furrow), unimpressed anteriorly, anteriorly divergent in course; inner pleurae subhorizontal; fulcral angle steep; outer pleurae steeply sloped to subvertical; anterior pleural band short, slightly longer laterally, then tapered posteroventrally, with line of small tubercles on inner pleurae on some specimens, also with very short ridge on anterior margin of inner pleurae for articulation with depression near axis and ridge on posterior margin of inner pleurae of posterior band; articulating facet short, small, triangular; pleural furrow moderately long, very shallow near axis, deeper laterally, with slightly posterolaterally directed course; posterior pleural band not quite twice length of anterior band, slightly inflated, with prominent spinose sculpture; spines on posterior pleural band vary, but all known segments with very large, conical, posterodorsally directed spine at fulcra, some with spine between fulcrum and axial furrow and one or more between fulcrum and pleural tips; pleural doublure just a short rim, except slightly more curved under at pleural tips.

Pygidium of two segments, short and wide, with sagittal length from articulating furrow 32.3% (26.6%–37.4%) maximum width, highly vaulted, with robust spinose sculpture; articulating half ring large, semilunate; articulating furrow short, deep, incised, deeper laterally; axis very short, moderately wide, moderately inflated, ill-defined; axial furrow narrow, shallow, unimpressed over axial rings, strongly anteriorly divergent; first axial ring short, moderately narrow, independently dorsally inflated; inter-ring furrow moderately long, very deep, slot-like, separated from axial furrow by bases of first spine pair; second axial ring long, narrow, independently inflated, mostly obscured by pair of spines; inner pleurae narrow, subhorizontal; fulcral angle very steep; articulating facet short, triangular; anterior and posterior pleural bands not well delineated, without pleural furrows, with inner areas merged into raised arc and outer areas subsumed in "wall," posterior bands conflated with large spines projecting from fulcra; large tubercle at fulcrum just anterolateral from first spine pair; first spine pair extremely long, robust, with broad bases gradually tapered to blunt tips, diverges dorsoposteriorly at about 45°, with tips slightly ventrally curved; followed by depressed area (probably merged anterior pleural band of second segment plus interpleural furrow) with small tubercle; second spine pair much shorter, more delicate, closely set, with depressed area and tubercle between; raised arc of merged inner pleurae–spine array set off posteriorly by pair of short, deep, slot-like furrows running along on "wall" below depressed area after first spine pair, most furrows slanted ventrolaterally (e.g., Fig. 15*y*), but one pair (Fig. 15*v*) slanted medioventrally; "wall" very tall, tapered laterally, with coarsely granulose sculpture; posterior border furrow short, shallow, not well defined; posterior border inflated, very tall laterally, tapered medially, with moderate dorsal median inflection and raised, broadly V-shaped area spreading up onto wall from inflection, and with very dense granulose sculpture; border doublure short, with anterior margin following ventral contour of border.

ONTOGENY: *Heckethornia bowiei* is known from several small cranidia and librigenae, as well as several transitory and small pygidia. Changes among the small cranidia include growth of the anteriormost pair of glabellar tubercles (cf. Figs. 12*m*, 12*n*, 12*p*); reduction and definition of axial furrow tubercles; vaulting of the cranidium and inflation of the glabella; reduction and effacement of the preglabellar field; lateral expansion of the palpebral lobes; and the growth of a flanking spine pair on LO. The smallest cranidia differ most notably from the large cranidia (cf. Figs. 11, 12) in possessing much narrower and flatter anterior borders; longer preglabellar fields; narrower fixigenae and posterior borders; smaller and less inflated glabellae; shallower axial furrows filled with granules; shorter, less inflated occipital rings; and more robust, less splayed paired spines, with fewer small interspersed tubercles.

Librigenal changes (cf. Figs. 14*a*, 14*l*, 14*o*) include the development of a thin eye socle; expansion of the area of the librigenal field; narrowing and incision of the lateral border furrow; inflation of the border and effacement of its tuberculate sculpture; and lengthening and thinning of the genal spine.

Pygidial growth of *H. bowiei* is known from a transitory pygidium to a large mature specimen (cf. Figs. 15*a*, 15*bb*). Notable ontogenetic changes include the release of the remaining thoracic segment from the transitory pygidium; lengthening of the pygidium – "wall" area; widening and

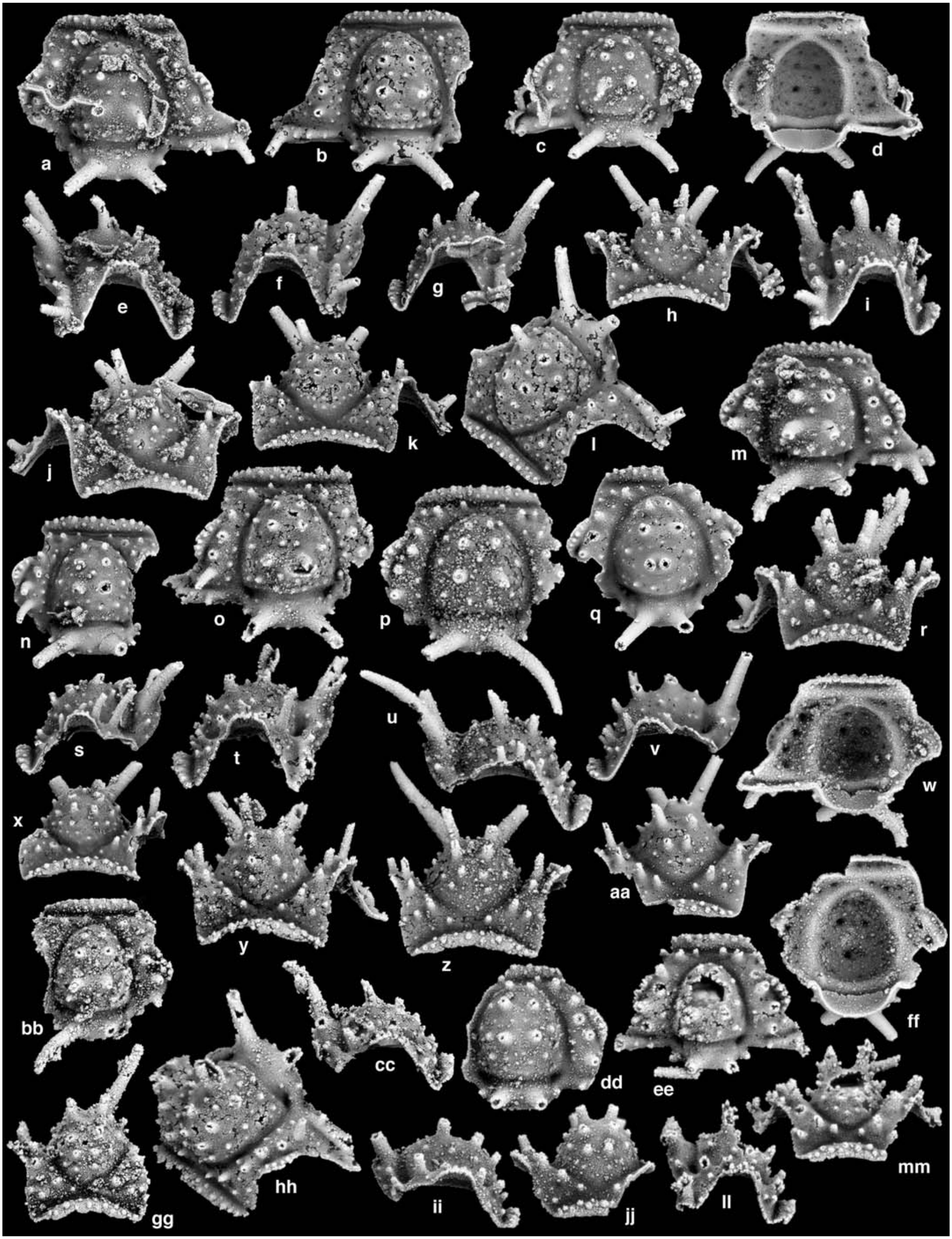
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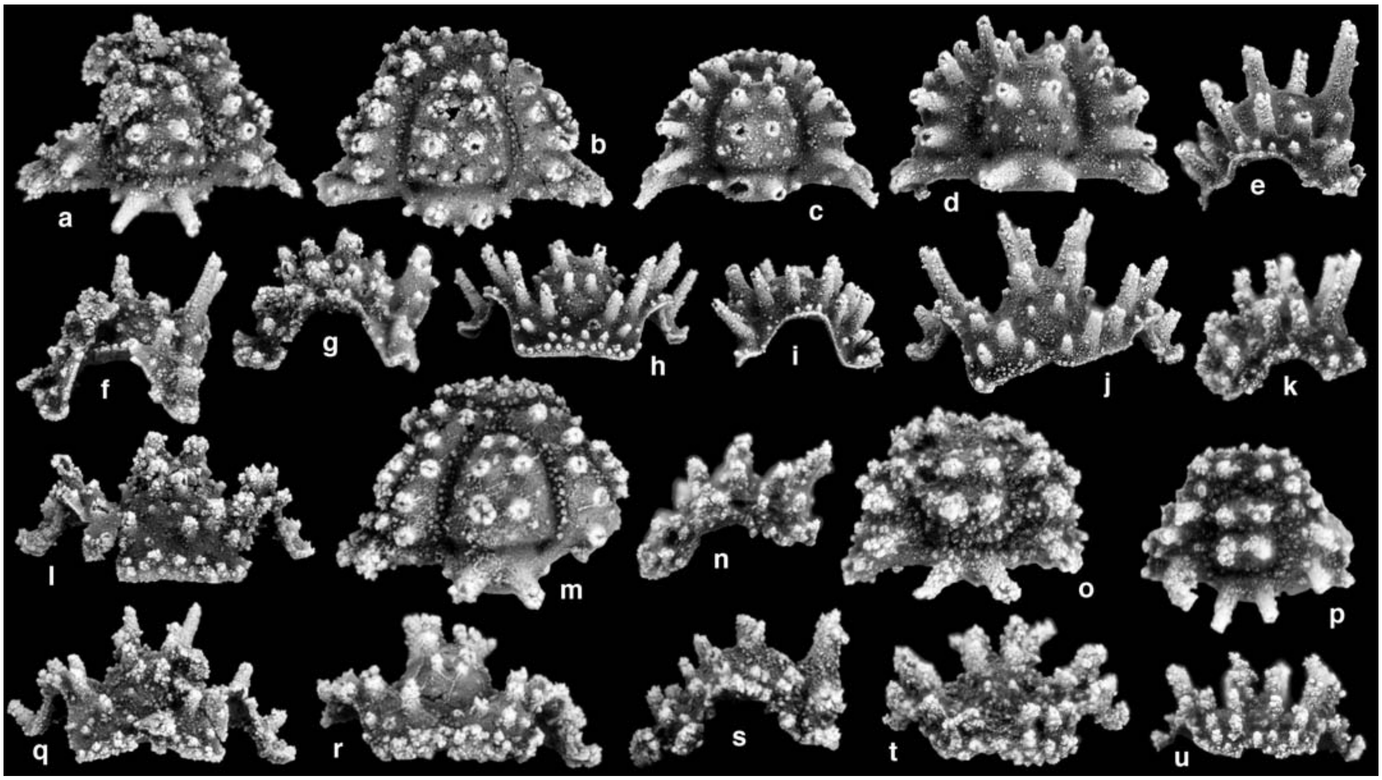
Fig. 12. *Heckethornia bowiei* n. sp., from section H 93.4–127.1 m, Fillmore Formation (Ibexian; Tulean), southern Confusion Range, Ibex area, Tule Valley, Millard County, western Utah. (*a*, *f*, *q*) Cranidium, SUI 113453, dorsal, left lateral, and anterior views, ×15 (H 127.1 m). (*b*, *g*, *l*) Cranidium, SUI 113454, dorsal, left lateral, and anterior views, ×20 (H 127.1 m). (*c*, *h*, *i*) Cranidium, SUI 113455, dorsal, anterior, and right lateral views, ×15 (H 93.4 m). (*d*, *e*, *j*) Cranidium, SUI 113456, dorsal, left lateral, and anterior views, ×25 (H 93.4 m). (*k*, *p*, *u*) Cranidium, SUI 113457, left lateral, dorsal, and anterior views, ×35 (H 93.4 m). (*m*, *r*, *s*) Cranidium, SUI 113458, dorsal, anterior, and left lateral views, ×30 (H 127.1 m). (*n*, *o*, *t*) Cranidium, SUI 113459, left lateral, dorsal, and anterior views, ×30 (H 93.4 m).



inflation of the axis; effacement of the axial furrow; growth of a prominent tubercle pair on the anteriormost fulcra; expression of the first axial ring; development of the long, slot-like inter-ring furrow; lengthening and thickening of the pygidial spines; development of tubercles between the spines; great increase in the height of the "wall"; and development of the slanted, slot-like furrows on the upper "wall."

REMARKS: *Heckethornia bowiei* is the most derived of the seven species in the genus. It possesses numerous autapomorphic features (see "Diagnosis"), some of which are coded in the cladistic analysis. These are an unusually broad anterior border (character 4(3)); LO sculpture, including a small tubercle at the anterior and posterior margins of the lobe on the sagittal axis (character 11(2)); a librigenal field arc of three tubercles (character 20(2)); and slotted furrows on the upper "wall" of the pygidium (character 35(2)).

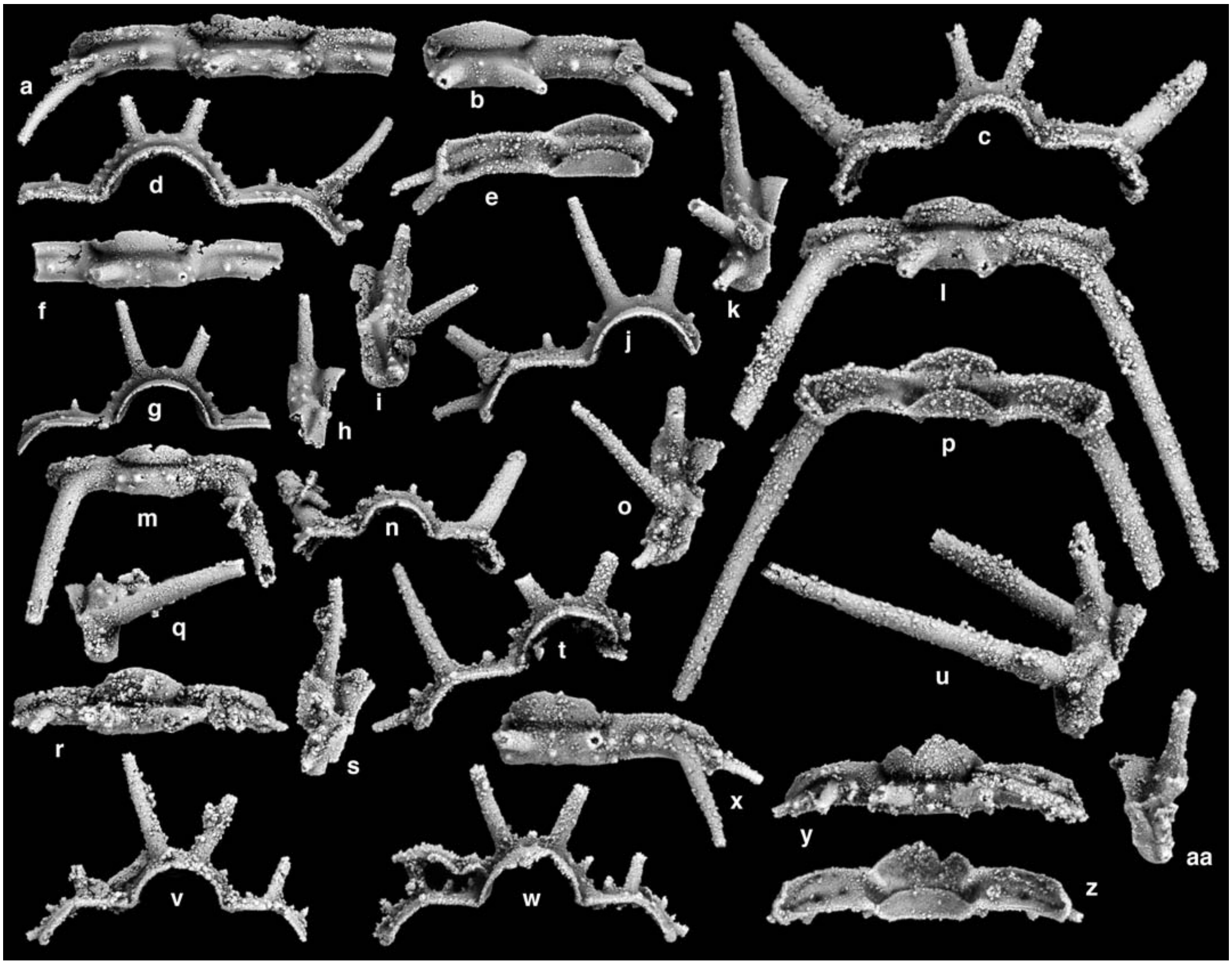
Similarly sized specimens of *Heckethornia bowiei* do not exhibit much intraspecific variation. Cranidial differences include varying expression of the small tubercles and spines (cf. Figs. 11*a*, 11*b*; 11*m*, 11*n* — sparser vs. denser glabellar sculpture); higher and lower glabellar inflation (cf. Figs. 11e, 11f); and wider and narrower spaces between the LO spine pair (cf. Figs. 11*p*, 11*q*). One specimen (Figs. 11*q*, 11*v*, 11*aa*) has an unusually close-set posteriormost pair of glabellar spines.

Librigenal variation is very low. Some specimens (e.g., Figs. 14*b*, 14*m*, 14*p*) have a few stray tubercles outside the arc on the librigenal field; depth of the lateral border furrow varies (cf. Figs. 14*e*, 14*p*); as does robustness of the lateral border tubercles (cf. Figs. 14*c*, 14*n*); and also the size of the field (cf. Figs. 14*h*, 14*j*, 14*n*). One specimen (Figs. 14*r*, 14*t*, 14*u*) has an unusually large field, four tubercles in the arc, a very shallow lateral border furrow, and an extremely short genal spine.

Pygidial variation is mainly due to size differences, but among similarly sized specimens the expression of the inter-ring furrow (cf. Figs. 15*a*, 15*c*, 15*x*); thickness of the large spines (cf. Figs. 15*h*, 15*i*); expression of the pleural tubercles (cf. Figs. 15*h*, 15*l*); height of the "wall" (cf. Figs. 15*g*, 15*l*); density of the "wall" tubercles (cf. Figs. 15*h*, 15*l*); and direction of the slot-like "wall" furrows (cf. Figs. 15*v*, 15*y*) vary.

Heckethornia bowiei is differentiated from *H. numani* under the latter species. The cranidium of *H. bowiei* differs from that of *H. smithi* most pronouncedly in the possession of a wider anterior border, much more robust spinose sculpture, and denser background sculpture. More subtle differences include its thimble-shaped (vs. ovoid) glabella and longer, more laterally tapered LO. The librigena of *H. bowiei* lacks eye socle tubercles, has a wider librigenal field, an arc of three (vs. four) tubercles, and long genal spine. The pygidia of the two species are similar in overall form,

Fig. 13. *Heckethornia bowiei* n. sp., from section H 127.1 m, Fillmore Formation (Ibexian; Tulean), southern Confusion Range, Ibex area, Tule Valley, Millard County, western Utah. (*a*, *d*, *i*) Thoracic segment, SUI 113460, dorsal, anterior, and left lateral views, ×7.5. (*b*, *e*, *j*, *k*) Thoracic segment, SUI 113461, dorsal, ventral, anterior, and right lateral views, ×10. (*c*, *l*, *p*, *u*) Thoracic segment, SUI 113462, anterior, dorsal, ventral, and right dorsolateral views, ×12. (*f–h*) Thoracic segment, SUI 113463, dorsal, anterior, and right lateral views, ×7.5. (*m*, *n*, *q*) Thoracic segment, SUI 113464, dorsal, anterior, and left lateral views, ×12. (*o*, *t*, *x*) Thoracic segment, SUI 113465, right lateral, anterior, and dorsal views, ×12. (*r*, *s*, *v*) Thoracic segment, SUI 113466, dorsal, right lateral, and anterior views, ×12. (*w*, *y*, *z*, *aa*) Thoracic segment, SUI 113467, anterior, dorsal, ventral, and left lateral views, ×15.



but that of *H. bowiei* has only two segments, much more robust spines, a taller "wall," thinner posterior border, and unique slot furrows on the "wall." *Heckethornia bowiei* does share several c.i.-one synapomorphies with *H. smithi* and *H. numani*, including two occipital spines with a single pair of flanking tubercles, and equally long anterior and posterior branches of the facial suture (as measured on librigena).

Heckethornia hyndeae does not closely resemble *H. bowiei*. Prominent cranidial differences include the broad anterior border, robust paired spines, less inflated glabella, wider posterior projections, and larger LO of *H. bowiei*. The librigenae of these two species can be distinguished by the large field, arc of three tubercles, larger and less dense lateral border sculpture, and long genal spine of *H. bowiei*. Pygidia of *H. bowiei* differ from those of *H. hyndeae* in their lack of axial ring sculpture, pronounced ridge under the spine bases, very tall "wall" with slot furrows, and thinner posterior border.

Heckethornia morrisseyi n. sp.
(Figs. 16–17)

Undetermined gen. and sp. loc. H-7. Zone G-2. (Not described); Hintze, 1953, pl. 19, figs. 11, 15.

DERIVATION OF NAME: After Steven Morrissey.

HOLOTYPE: Holotype cranidium, SUI 113495, from section H 93.4 m, Fillmore Formation (Ibexian; Tulean), southern

Fig. 14. *Heckethornia bowiei* n. sp., from section H 93.4–163.3 m, Fillmore Formation (Ibexian; Tulean), southern Confusion Range, Ibex area, Tule Valley, Millard County, western Utah. (*a*, *d*) Left librigena, SUI 113468, external and ventrolateral views, ×10 (H 127.1 m). (*b*) Left librigena, SUI 113469, external view, ×15 (H 127.1 m). (*c*, *f*, *g*) Left librigena, SUI 113470, external, ventrolateral, and internal views, ×10 (H 127.1 m). (*e*) Left librigena, SUI 113471, external view, ×12 (H 127.1 m). (*h*) Left librigena, SUI 113472, external view, ×10 (H 127.1 m). (*i*, *j*) Right librigena, SUI 113473, internal and external views, ×10 (H 127.1 m). (*k*, *n*) Left librigena, SUI 113474, internal and external views, ×10 (H 127.1 m). (*l*, *q*) Right librigena, SUI 113475, external and internal views, ×15 (H 127.1 m). (*m*) Right librigena, SUI 113476, external view, ×12 (H 127.1 m). (*o*) Right librigena, SUI 113477, external view, ×20 (H 93.4 m). (*p*) Left librigena, SUI 113478, external view, ×12 (H 127.1 m). (*r*, *t*, *u*) Left librigena, SUI 113479, external, internal, and ventrolateral views, ×10 (H 93.4 m). (*s*) Left librigena, SUI 113480, external view, ×20 (H 93.4 m). (*v*) Right librigena, SUI 113481, external view, ×12 (H 93.4 m). (*w*, *x*) Left librigena, SUI 113482, ventrolateral and external views, ×12 (H 163.3 m).

Confusion Range, Ibex area, Tule Valley, Millard County, western Utah.

MATERIAL: Assigned specimens SUI 113493 – SUI 113524 from section H 93.4 m (Hintze's (1953) 190′/ H-7), Fillmore Formation (Ibexian; Tulean), southern Confusion Range, Ibex area, Tule Valley, Millard County, western Utah and section YH 175.9 m (Hintze's (1953) 577′/ YH-16), "Yellow Hill Beds" (Ibexian; Tulean), Yellow Hill, near Pioche, Lincoln County, eastern Nevada.

DIAGNOSIS: Exoskeleton highly effaced (with some effaced tubercles, small granules, and anastomosing line sculpture), except for occipital spine, genal spine, thoracic spines, and pygidial spines and granules; cranidium with very short anterior border, glabella with laterally bulging L2, and very robust occipital spine; librigena with large field and long, thick, very robust genal spine; pygidium with very broad axis and short, robust spines.

DESCRIPTION: Cranidium effaced, except for prominent occipital spine; anterior border short, tapered laterally, moderately dorsally inflated, with sculpture of fine ridges along anteroventral rim; anterior border furrow moderately long, tapered laterally, shallow medially, deeper laterally, with transverse to slightly posterolaterally curved course; anterior branches of facial suture moderately laterally bowed; preglabellar field moderately long, slightly medially depressed; frontal areas very broad, gradually tapered toward palpebral lobes, steeply sloped down to anterior border, fairly effaced, but with some granulose and anastomosing ridge sculpture; preglabellar furrow very short and shallow medially, slightly longer and deeper posterolaterally, converges to gentle point at sagittal axis; glabella moderately long and wide, tapered anteriorly, thimble-shaped, with width across L2 96.2% (93.8%–99.0%) sagittal length, with inflation highest (approximately) even with posterior margin of palpebral lobe, glabellar outline slightly waisted along L1, distinctly exsagittally curved along L2, and anteriorly tapered along L3, holaspid specimens with granulose or anastomosing ridge sculpture, with very faint traces of paired tubercles; SO long, somewhat shallow medially, deepens and lengthens laterally into apodemal pits; LO very long medially, tapered laterally, crescentic, with long, very robust, conical median spine gradually tapered to blunt point, projecting posterodorsally at about 45° above horizontal, with gently ventrally curved tip; LO doublure long, tapered laterally, crescentic, with smooth anterior margin; axial furrow moderately broad, narrower anteriorly, moderately deep, deepest and widest along L2, course follows outline of glabella (anteriorly divergent until mid-L2, then convergent), separated from SO by short ridge extension of LO; fixigenae moderately broad, moderately steeply sloped down to axial furrow, interocular fixigenae slightly inflated (Fig. 16*e*); palpebral furrow narrow, shallow, slightly sinuous in course; palpebral lobes incompletely known, fairly narrow anteriorly, dorsally inflated; posterior fixigenae, posterior branch of facial suture, posterior border and furrow all unknown from fully mature material.

Rostral plate unknown

Librigena with robust genal spine; eye elliptical, highly inflated, separated from socle by narrow, incised furrow; eye socle of smooth, narrow band, set off from librigenal field by moderately narrow, shallow furrow; anterior branch of facial suture long, steep, with short anteriorly curved section along anterior projection of lateral border; posterior branch of facial suture slightly shorter, gently posteriorly curved; librigenal field with width at midlength of eye 65.8% (63.9%–67.5%) length along lateral border, and length along eye about 1/4 length along lateral border, convex, more strongly posteriorly, effaced, but some specimens (e.g., Fig. 17*e*) with anastomosing ridges; lateral border furrow broad, very shallow, effaced posteriorly, gently curved in course anteriorly, then posteromedially diagonal from midlength rearward; lateral border wide anteriorly, wider near base of genal spine, then narrower along slight posterior projection past spine, slightly inflated, more strongly inflated near spine base, with sculpture of fine ridges and effaced tubercles; border doublure broad, broader near genal spine, tapered along anterior projection of border, with anastomosing ridge sculpture and large, shallow Panderian notch; genal spine long, very robust and thick at base, gradually tapered to narrow tip, gently posteromedially curved, with granulose and anastomosing sculpture.

Total number of thoracic segments unknown. Thoracic segments with width of axis 36.4% (one specimen) width of segment, moderately vaulted pleurally and axially (overall highly vaulted), with strongly spinose sculpture; articulating half ring semilunate, inset from anterior pygidial margin; articulating furrow short, tapered laterally, shallow medially, deep laterally in apodemal pits, course anterolaterally curved; axial ring long, gently dorsally inflated, wrapped anterolaterally around articulating half ring, with sculpture of pair of large conical spines on top, flanked by pair of small spinose tubercles midway down side of ring; ring doublure very long medially, tapered laterally, almost semicircular; axial furrow broad, very shallow, forms parenthetical shape

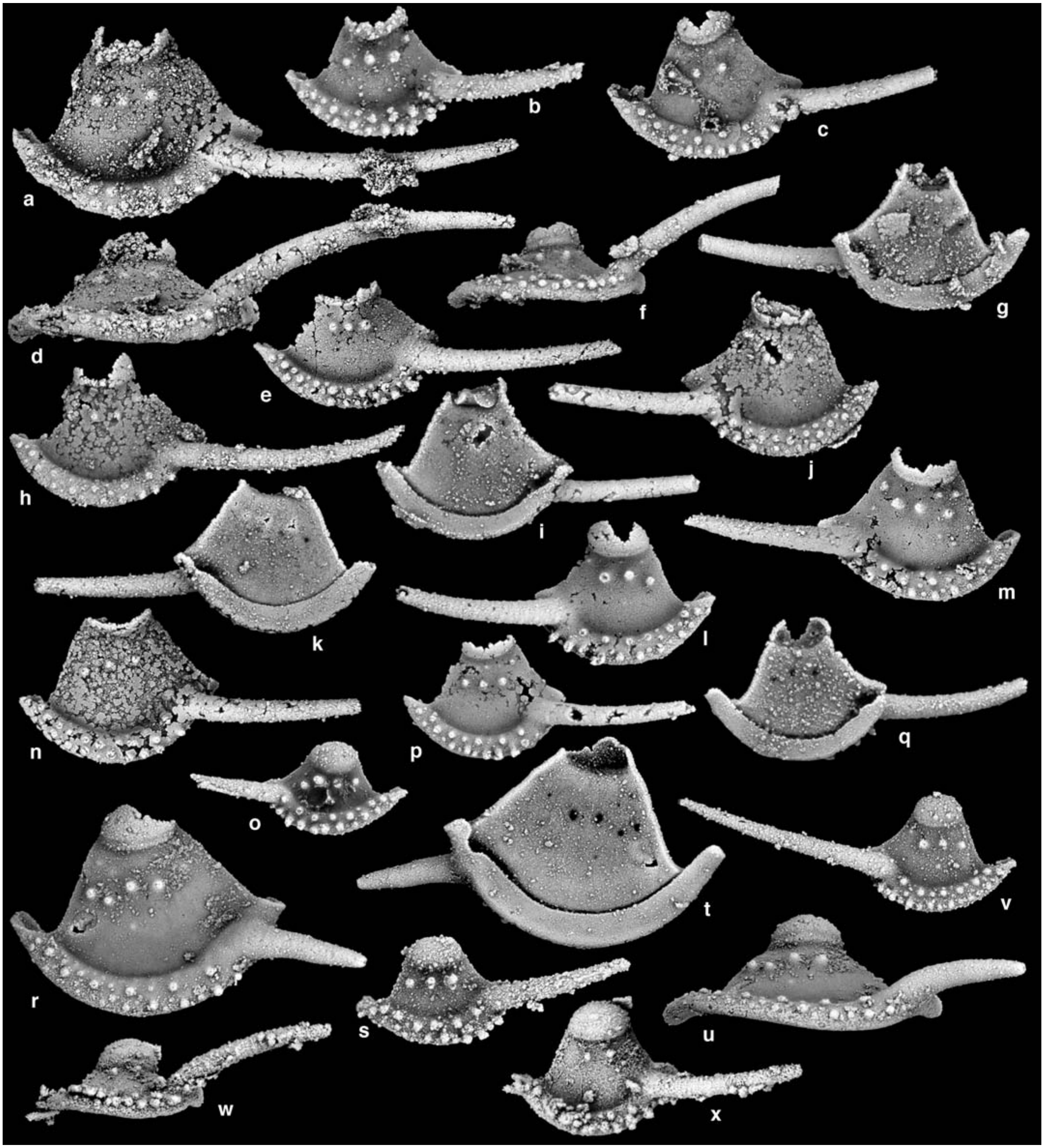

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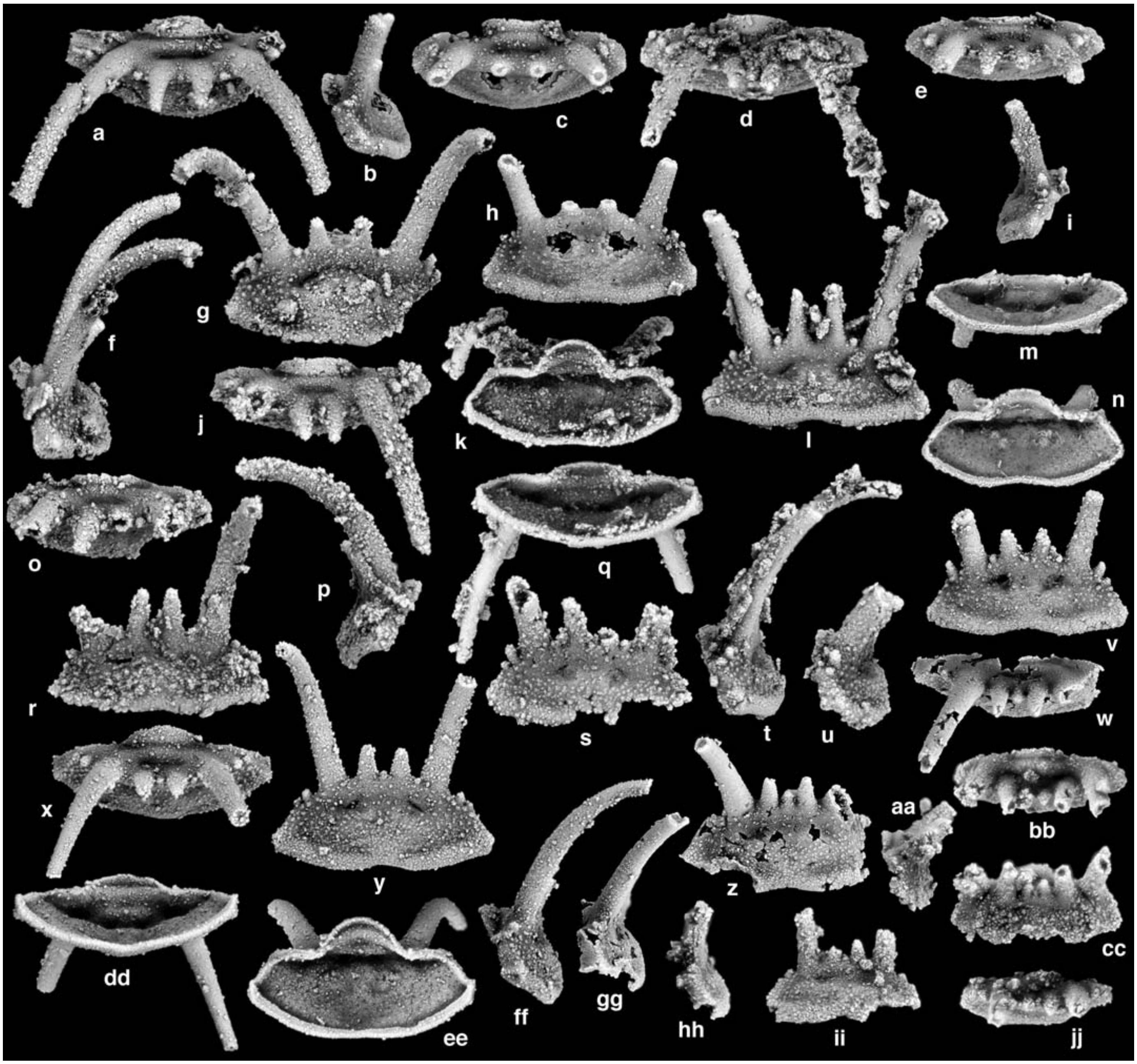
Fig. 15. *Heckethornia bowiei* n. sp., from section H 93.4–127.1 m, Fillmore Formation (Ibexian; Tulean), southern Confusion Range, Ibex area, Tule Valley, Millard County, western Utah. Specimens are from H 127.1 m, except where noted. (*a*, *f*, *g*) Pygidium, SUI 113483, dorsal, left lateral, and posterior views, ×12. (*b*, *c*, *h*) Pygidium, SUI 113484, left lateral, dorsal, and posterior views, ×12. (*d*, *k*, *l*, *q*, *t*) Pygidium, SUI 113485, dorsal, anterior, posterior, ventral, and left lateral views, ×12. (*e*, *i*, *m*, n, *v*) Pygidium, SUI 113486, dorsal, right lateral, ventral, anterior, and posterior views, ×12. (*j*, *p*, *r*) Pygidium, SUI 113487, dorsal, right lateral, and posterior views, ×20. (*o*, *s*, *u*) Pygidium, SUI 113488, dorsal, posterior, and left lateral views, ×20. (*w*, *z*, *gg*) Pygidium, SUI 113489, dorsal, left lateral, and posterior views, ×15 (H 93.4 m). (*x*, *y*, *dd*, *ee*, *ff*) Pygidium, SUI 113490, dorsal, posterior, ventral, anterior, and left lateral views, ×12 (H 93.4 m). (*aa–cc*) Pygidium, SUI 113491, left lateral, dorsal, and posterior views, ×25 (H 93.4 m). (*hh–jj*) Pygidium, SUI 113492, left lateral, posterior, and dorsal views, ×25 (H 93.4 m).



around lateral curvature of axial ring; inner pleurae broad, subhorizontal; fulcral angle very steep; outer pleurae narrow; anterior pleural band short, slightly longer ventrolaterally, with tongue-and-groove articulating structure on inner pleurae and small, triangular articulating facet on outer pleurae, effaced; pleural furrow short, very shallow on inner pleurae, deeper ventrolaterally; posterior pleural band long, slightly inflated, with sculpture of small spinose tubercle midway between axial furrow and fulcrum, and very large, conical spine projecting laterally from just below fulcrum, (partial segment, Figs. 17*r*–17*t*, with large spine at fulcrum and additional spine below fulcrum), with raised ridge on posterior edge of inner pleurae for articulation; pleural doublure only at ventral edge, narrow, with posterior notch for articulation and enrollment accommodation.

Pygidium of three segments, roughly semi-elliptical in outline; articulating half ring large, semilunate; articulating furrow short and shallow; axis broad, short, highly vaulted, with two expressed axial rings and the third obscured by spines, with granulose or anastomosing ridge sculpture; first axial ring broad, short medially due to large semi-articulating half ring of second segment, long laterally, slightly independently inflated; inter-ring furrow long and very deep in lateral slots, short and shallow along posterior of semi-articulating half ring; semi-articulating half ring large, lens shaped, slightly recessed, set off anteriorly by very short, shallow furrow; second axial ring short, narrow, slightly independently inflated, defined posteriorly by short, shallow inter-ring furrow in front of short, lens-shaped recessed area (may represent third axial ring or pseudo-articulating half ring of third axial ring; main part of third ring obscured by spines) flanked by pair of small, moderately shallow pits (lateral expression of second inter-ring furrow); axial furrow broad, shallow, deepest in intersection with lateral pits of inter-ring furrows, shallowest across spine bases, with U-shaped to nearly semicircular course; inner pleurae subhorizontal, merged into "deck" with posteriorly projecting spines; fulcral angle steep; anterior pleural band of first segment long, slightly dorsally inflated, with very large, nubby tubercle at fulcrum, slightly longer ventrolaterally, with large, subrectangular articulating facet; pleural furrow faintly impressed, angles posterolaterally about 30° below transverse; posterior pleural band very long, with a depressed wedge bounded by posterior margin of anterior band and anterior margin of large spine on posterior band; anterior and posterior bands of second and third axial rings not well defined, expressed as depressed area between spines followed by inflated base of spine, with areas shorter toward rear of pygidium; interpleural and pleural furrows merged, not discernible on dorsal surface of pygidium, but present as slightly recessed lineations on "wall"; pygidial spines stout, strongly tapered, conical, fairly short (inferred), all roughly same length, project posterodorsally from fulcrum of posterior bands of segments at about 45° above horizontal, with dense granulose sculpture (also on outer edge of inner pleurae in some specimens, e.g., Figs. 17*v*, 17*w*, 17*z*); inner pleural – spine "deck" defined posteriorly by long, shallow furrow under spine bases (Fig. 17*u*); fused outer pleural "wall" very tall, highly posteriorly convex, with dense granulose sculpture; posterior border furrow long and shallow; posterior border thick, with very dense granulose sculpture and some thin ridges ventrally; border doublure curled under, moderately long and wide, with U-shaped cross-section.

ONTOGENY: Although no protaspides or early meraspid sclerites are known from *Heckethornia morrisseyi*, much can still be said about the ontogeny of this species. The most striking difference between small and large sclerites is the abundant sculpture of the former. Cranidial changes involve the loss of anterior border tubercles, three pairs of cranidial spines, the five or six spines of the fixigenal arcs (including the very large, posteriorly curved posteriormost spine), palpebral lobe tubercles; and some assorted smaller tubercles (cf. Figs. 16*c*, 16*y*; 16*v*, 16*dd*); narrowing of the anterior border; lateral expansion of the glabella and L2 in particular; broadening and lengthening of all cranidial furrows; inflation of the interocular fixigenae; and growth and thickening of the occipital spine.

Librigenal changes (cf. Figs. 17*c*, 17*g*) include definition of the eye socle; an increase in the area of the field; effacement of the lateral border furrow; deflation of the lateral border and effacement of its tuberculate sculpture; and growth and thickening of the genal spine.

The pygidium of *H. morrisseyi* undergoes complex changes, transforming from transitory and small holaspid pygidia that closely resemble the mature pygidium of *H. smithi* to mature forms that more closely resemble the pygidia of *H. alticapitis* and *H. ballionae.* The smallest transitory pygidium (Figs. 17*rr*, 17*ss*, 17*xx*) has an attached anterior segment with two large spines on its axial ring, which reduce in size (Figs. 17*qq*, 17*vv*, 17*ww*; 17*tt*, 17*yy*, 17*zz*) before the segment is released into the thorax. Other major changes within the transitory pygidia include shortening of the first pair of pygidial spines and lengthening of the second and third pairs; the growth of the "wall"; lowering of the angle of the spines; broadening of the axis; and shallowing of the axial and other furrows. The smallest holaspid pygidium (Figs. 17*oo*, 17*pp*, 17*uu*) possesses the large tubercle pair on the anteriormost fulcra; possesses a short, broad axis, but lacks defined axial rings; has six spines directed posteriorly from the fulcra of the posterior pleural bands, but they are spindly, not splayed, and their bases have not merged into the "deck" area; and it has a well defined "wall" area and thick posterior border, but the "wall" is still short. The smallest pygidium with typical morphology (Figs. 17*aa*, 17*ff*, 17*gg*) has two defined axial rings; thicker spines; and the spine bases have begun to splay outward and merge into the "deck". Further changes involve the development of semi-articulating half rings; further thickening and splaying of the spines; and increasing height of the "wall."

REMARKS: There is little variation among comparable-sized specimens of *Heckethornia morrisseyi*. The cranidium of Figs. 16*a*, 16*r*, 16*h* has a slightly narrower anterior border, longer preglabellar field, and shorter glabella than the other large cranidia. Librigena vary in the expression of the eye socle (cf. Figs. 17*a*, 17*c*); and slightly in the size of the librigenal field, width and degree of effacedness of the lateral border, and length and robustness of the genal spine. Pygidia vary in the definition of the axial rings and semi-articulating half rings, and the development of the slot-like lateral areas of the combined inter-ring and axial furrows. The pygidium of Figs. 17*i*, 17*l*, 17*m*, 17*p*, 17*q* possesses a median spine (seven spines total). That of Figs. 17*v*, 17*w*, 17*z* has a broader, more highly inflated axis; broader and longer axial furrow; and more distinctly inflated and granulose "deck" area.

Heckethornia morrisseyi is highly autapomorphic, and easily distinguished from all other known species of *Heckethornia* by its effaced cranidial and librigenal sculpture; long and highly robust genal spine; wide lateral border furrow; thick pygidial spines; and pygidial granules. It is additionally differentiated from its sister clade *H. alticapitis* + *H.*

Fig. 16. *Heckethornia morrisseyi* n. sp., from section H 93.4 m, Fillmore Formation (Ibexian; Tulean), southern Confusion Range, Ibex area, Tule Valley, Millard County, western Utah. (*a*, *f*, *h*) Cranidium, SUI 113493, dorsal, right lateral, and anterior views, ×12. (*b*, *g*, *i*) Cranidium, SUI 113494, dorsal, right lateral, and anterior views, ×12. (*c*, *d*, *j*, *o*) Cranidium, **holotype**, SUI 113495, dorsal, ventral, left lateral, and anterior views, ×10. (*e*, *k*, *l*, *p*) Cranidium, SUI 113496, dorsal, left lateral, ventral, and anterior views, ×12. (*m*, *n*, *q*) Cranidium, SUI 113497, dorsal, left lateral, and anterior views, ×15. (*r*, *v*, *w*) Cranidium, SUI 113498, left lateral, dorsal, and anterior views, ×15. (*s*, *t*) Cranidium, SUI 113499, right lateral and dorsal views, ×10. (*u*, *z*, *aa*) Cranidium, SUI 113500, dorsal, anterior, and right lateral views, ×15. (*x*, *cc*, *hh*) Cranidium, SUI 113501, dorsal, left lateral, and anterior views, ×15. (*y*, *ii*, *nn*) Cranidium, SUI 113502, dorsal, right lateral, and anterior views, ×12. (*bb*, *ff*, *gg*) Cranidium, SUI 113503, dorsal, right lateral, and anterior views, ×20. (*dd*, *ee*, *jj*) Cranidium, SUI 113504, dorsal, anterior, and left lateral views, ×25. (*kk–mm*) Cranidium, SUI 113505, dorsal, left lateral, and anterior views, ×20.

ballionae by its anteriorly tapered glabella; inflated fixigenae; low glabellar inflation; long genal spine; shallow lateral border furrow; pygidium with low axial vaulting; lack of axial tubercles; wide axis; and shallow axial furrow. These differences are discussed in more detail in the remarks sections of the latter two species described later in the text.

Heckethornia alticapitis (Young, 1973)
(Figs. 18–19)

Psalikilopsis (?) *alticapitis* Young, 1973, p. 106, pl. 4, figs. 1–8.
Ischyrotoma (?) pygidium (Not described); Young, 1973, pl. 6, fig. 1.
Unassigned librigena 4 (Not described); Young, 1973, pl. 7, fig. 8.
Dimeropygiella ? immature pygidium loc. H-20. Zone H. (Not described); Hintze, 1953, pl. 19, fig. 9.
Undetermined gen. and sp. loc. H-20. Zone H. (Not described); Hintze, 1953, pl. 19, figs. 12–13.

MATERIAL: Holotype cranidium, BYU 2102, and additional figured specimens SUI 113525 – SUI 113550 from section H 191.7 m (Hintze's (1953) 434′/ H-20), Fillmore Formation (Ibexian; Blackhillsian), southern Confusion Range, Ibex area, Tule Valley, Millard County, western Utah.

DIAGNOSIS: Cranidium with large, distinctly half-teardrop-shaped palpebral lobes, glabella with posteriormost pair of sagittal spines, much more robust than anterior pairs, and moderately robust occipital and posterior border spines; librigena with large eye socle, field with main arc of tubercles and roughly 10 or fewer scattered tubercles; thoracic segments with very large, highly inset articulating half ring; pygidium with almost perfectly semicircular outline, relatively short "wall," and very thick posterior border (relative to wall).

DESCRIPTION: *Heckethornia alticapitis* (Young, 1973) is sufficiently morphologically similar to *H. ballionae* that it is treated via extended differential description. Ratios are given to facilitate comparison with other members of the genus. *Heckethornia ballionae* is described in the following description.

Cranidia of *H. alticapitis* with sagittal length 89.0% (86.4%–91.6%) width across midlength of palpebral lobes and glabella with width at midlength 86.2% (82.3%–93.3%) sagittal length. Cranidia of the two species are highly similar, but those of *H. alticapitis* differ from those of *H. ballionae* in possessing much finer, denser base granulose sculpture, more anastomosing ridge sculpture, coarser large glabellar, LO, and fixigenal sculpture; a broader axial furrow with less glabellar overhang; slightly wider interocular and posterior fixigenae; larger, distinctly half-teardrop-shaped palpebral lobes with larger rim tubercles; a longer, more inflated LO; and more robust and steeply dorsoposteriorly directed LO and posterior border spines.

Librigenae of *H. alticapitis* with width of field at midpoint of eye 58.4% (54.2%–62.1%) length along lateral border. Librigenae of *H. alticapitis* and *H. ballionae* are very similar in overall shape, but differ in that those of *H. alticapitis* possess a longer anterior branch of the facial suture compared with the posterior branch; slightly smaller and less bulbous eyes; a thick eye socle; many fewer and larger and proximally concentrated librigenal field tubercles; a more evenly arcuate lateral border furrow; slightly more inflated lateral border; larger and less dense tubercles on the lateral border; and a slightly deeper Panderian notch.

Heckethornia alticapitis and *H. ballionae* share similar types of thoracic segments. Comparison is imperfect because we lack articulated thoracic material for any species of *Heckethornia*, but we are reasonably confident that we have recovered and illustrated specimens representative of all variation along the thorax for these two species. The axis of segments of *H. alticapitis* is 46.7% (44.8%–48.9%) total width. The "paired axial spine" segments (*H. alticapitis*: Figs. 19*q*, 19*y*, 19*z*, 19*ee*; 19*r*, 19*aa*, 19*ff*; 19*u*, 19*w*, 19*x*; *H. ballionae*: Figs. 21*cc*, 21*ee*, 21*gg*; 21*dd*, 21*hh*–21*jj*) are highly comparable, but those of *H. alticapitis* have longer, more inset articulating half rings; longer articulating furrows; slightly narrower and more highly vaulted axial rings (may be affected by position in thorax); stouter paired axial spines; and generally fewer pleural spines. The "arc of axial tubercles" segments (*H. alticapitis*: Figs. 19*k*–19*m*, 19*s*, 19*t*; *H. ballionae*: Figs. 21*s*–21*u*, 21*aa*; 21*x*, 21*y*, 21*bb*) are less similar, mainly in that the *H. alticapitis* segment lacks the very large, widely splayed fulcral spines present on the *H. ballionae* segments. The axial ring sculpture is similar, as are the laterally projecting ventralmost spines. It is, however, possible that *H. alticapitis* had similar segments that were not recovered.

Pygidia of *H. alticapitis* and *H. ballionae* are extremely similar, but those of *H. alticapitis* are slightly more perfectly semicircular in outline (longer and narrower, with sagittal length 36.0% (35.4%–36.6%) width across fulcra); with slightly narrower, longer, more tapered axes; shorter, more finely tapered spines; and a thicker posterior border.

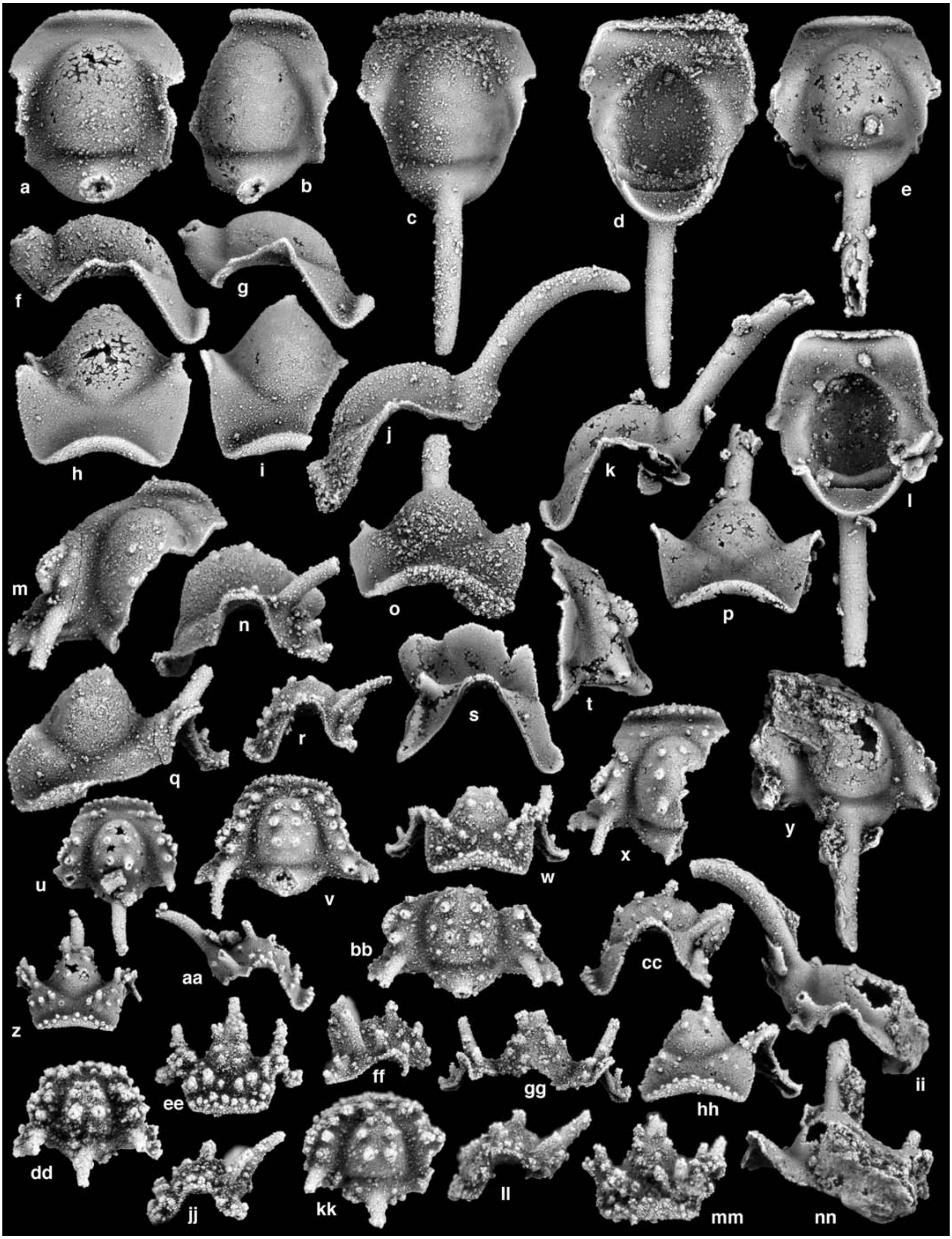

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Fig. 17. *Heckethornia morrisseyi* n. sp., from section H 93.4 m, Fillmore Formation (Ibexian; Tulean), southern Confusion Range, Ibex area, Tule Valley, Millard County, western Utah. (*a*, *b*, *d*) Left librigena, SUI 113506, external, internal, and ventrolateral views, ×10. (*c*, *f*, *j*) Left librigena, SUI 113507, external, internal, and ventrolateral views, ×10. (*e*) Right librigena, SUI 113508, external view, ×12. (*g*) Right librigena, SUI 113509, external view, ×12. (*h*, *k*, *o*, *u*, *y*) Pygidium, SUI 113510, left lateral, dorsal, ventral, posterior, and anterior views, ×15. (*i*, *l*, *m*, *p*, *q*) Pygidium, SUI 113511, dorsal, left lateral, posterior, anterior, and ventral views, ×15. (*n*) Right librigena, SUI 113512, external view, ×12. (*r–t*) Thoracic segment, SUI 113513, right lateral, dorsal, and posterior views, ×15. (*v*, *w*, *z*) Pygidium, SUI 113514, dorsal, left lateral, and posterior views, ×20. (*x*, *bb*, *cc*) Pygidium, SUI 113515, dorsal, posterior, and left lateral views, ×15. (*aa*, *ff*, *gg*) Pygidium, SUI 113516, dorsal, left lateral, and posterior views, ×20. (*dd*, *ee*, *jj*) Pygidium, SUI 113517, dorsal, posterior, and right lateral views, ×20. (*hh*, *ii*, *nn*) Pygidium, SUI 113518, dorsal, left lateral, and posterior views, ×20. (*kk–mm*) Pygidium, SUI 113519, posterior, dorsal, and left lateral views, ×20. (*oo*, *uu*, *vv*) Pygidium, SUI 113520, dorsal, posterior, and left lateral views, ×25. (*pp*, *qq*, *ww*) Pygidium, SUI 113521, left lateral, dorsal, and posterior views, ×25. (*rr*, *ss*, *xx*) Pygidium, SUI 113522, dorsal, left lateral, and posterior views, ×25. (*tt*, *yy*, *zz*) Pygidium, SUI 113523, dorsal, left lateral, and posterior views, ×25. (*aaa–ddd*) Thoracic segment, SUI 113524, right lateral, dorsal, ventral, and anterior views, ×10.

ONTOGENY: Little ontogenetic material of *Heckethornia alticapitis* has been recovered. However, the smallest cranidium (Figs. 18v, 18aa, 18bb) is proportionately much shorter and broader than the larger specimens, slightly less vaulted overall, with a relatively shorter anterior branch of the facial suture, also with a rounder, more highly vaulted glabella, less vaulted and more arcuate (not half-teardrop) palpebral lobes, and coarser and less variably sized sculpture, with less prominent fixigenal spines, and lacking small tubercles outlining the axial furrow. Librigenal trends (cf. Figs. 19*o*, 19*a*) include a rounder, more highly inflated eye, development of a thick eye socle and its defining furrows, significant broadening of the librigenal field, growth of more and larger field tubercles, loss of anteroventral tubercles on lateral border, and tapering of the spine. The smallest pygidia (Figs. 19*v*, 9*tt*) differ from the larger pygidia only subtly, but they are more perfectly semicircular in outline, with larger articulating half rings, less prominent semi-articulating half rings, narrower, more highly vaulted axes, more delicate spines, thinner posterior borders compared with overall "wall" height, and denser granulose sculpture.

REMARKS: Similarly sized cranidia of *H. alticapitis* vary little in most aspects, with main differences occurring in the density of smaller tubercles outlining the axial furrow and among the major spine arc on the fixigenae (cf. Figs. 18*a*, 18*b*), the depth of the axial furrow (cf. Figs. 18*a*, 18*c*), the width of the preglabellar field (cf. Figs. 18*i*, 18*o*), and the expression of tubercles on the anterior border (cf. Figs. 18*a*, 18*b*, with 18*c*, 18*d*). The cranidium of Figs. 18*a*, 18*e*, 18*f*, 18*j*, 18*n*, 18*o* has a longer, flatter, almost uninflated anterior border, and very close-set posteriormost pair of major cranidial spines. The cranidium of Figs. 18*c*, 18*g*, 18*l* has a broader axial furrow, less steeply sloped fixigenae, and more arcuate, less half-teardrop-shaped palpebral lobes than other large specimens.

Likewise, librigenae of *H. alticapitis* are very similar, with some minor variation in the size of the librigenal field, amount of tubercles on field, thickness of eye socle, width and tuberculation of border, and size of genal spine. The librigena of Figs. 19*d*, 19*h* has a weakly expressed eye socle, spinose field tubercles (cf. Figs. 19*h*, 19*i*), and a stouter, less tapered genal spine with tubercles near the base. The librigena of Fig. 19*j* lacks an eye socle. Variation in thoracic segments is likely due to the position of the segment in the thorax and need not be discussed.

Pygidial variation in *H. alticapitis* mainly depends on size and is discussed under ontogeny. However, there is also variation in the number of tubercles on each axial ring, with one tail (Fig. 19*v*) having four on the first and two on the second, one tail (Fig. 19*dd*) having six on the first and two on the second, one (Fig. 19*kk*) with five on the first and two on the second, and one (Fig. 19*tt*) with five on the first and four on the second.

Heckethornia alticapitis is compared with its sister taxon, *H. ballionae*, in extended differential description under that taxon. It differs from *H. morrisseyi* most notably in its robust spinose–tuberculate sculpture, but also in its longer, wider anterior border; deeper, more incised axial furrow; long, narrow, highly inflated ovoid glabella; more steeply sloped fixigenae; shorter (relative to anterior branch) posterior branch of the facial suture; W-shaped LO doublure; thicker and more distinct eye socle; smaller librigenal field; deeper lateral border furrow; more highly inflated lateral border; much shorter and less robust genal spine; much narrower pygidium with narrower, more strongly posteriorly tapered axis; longer, more delicate pygidial spines; and less inflated posterior border.

Heckethornia ballionae n. sp.
(Figs. 20–21)

DERIVATION OF NAME: After Susan Ballion.

HOLOTYPE: Holotype SUI 113553 from section H 222.1 m, Fillmore Formation (Ibexian; Blackhillsian), southern Confusion Range, Ibex area, Tule Valley, Millard County, western Utah.

MATERIAL: Assigned specimens SUI 113551 – SUI 113587 from section H 208.2–222.1 m (Hintze's (1953) 483′/ H-23–525′/ H-24), Fillmore Formation (Ibexian; Blackhillsian), southern Confusion Range, Ibex area, Tule Valley, Millard County, western Utah.

DIAGNOSIS: Cranidium with very narrow preglabellar field, short, steeply posterodorsally raked paired spines and slender occipital and posterior border spines; librigenae with very effaced socle or no socle, librigenal field with very dense granulose background sculpture topped with many tubercles, such that characteristic arc is obscured on most specimens; (some) thoracic segments with arc of tubercles on axial ring and very long, low-angle posterolaterally projecting spines on fulcra; pygidium with very dense granulose

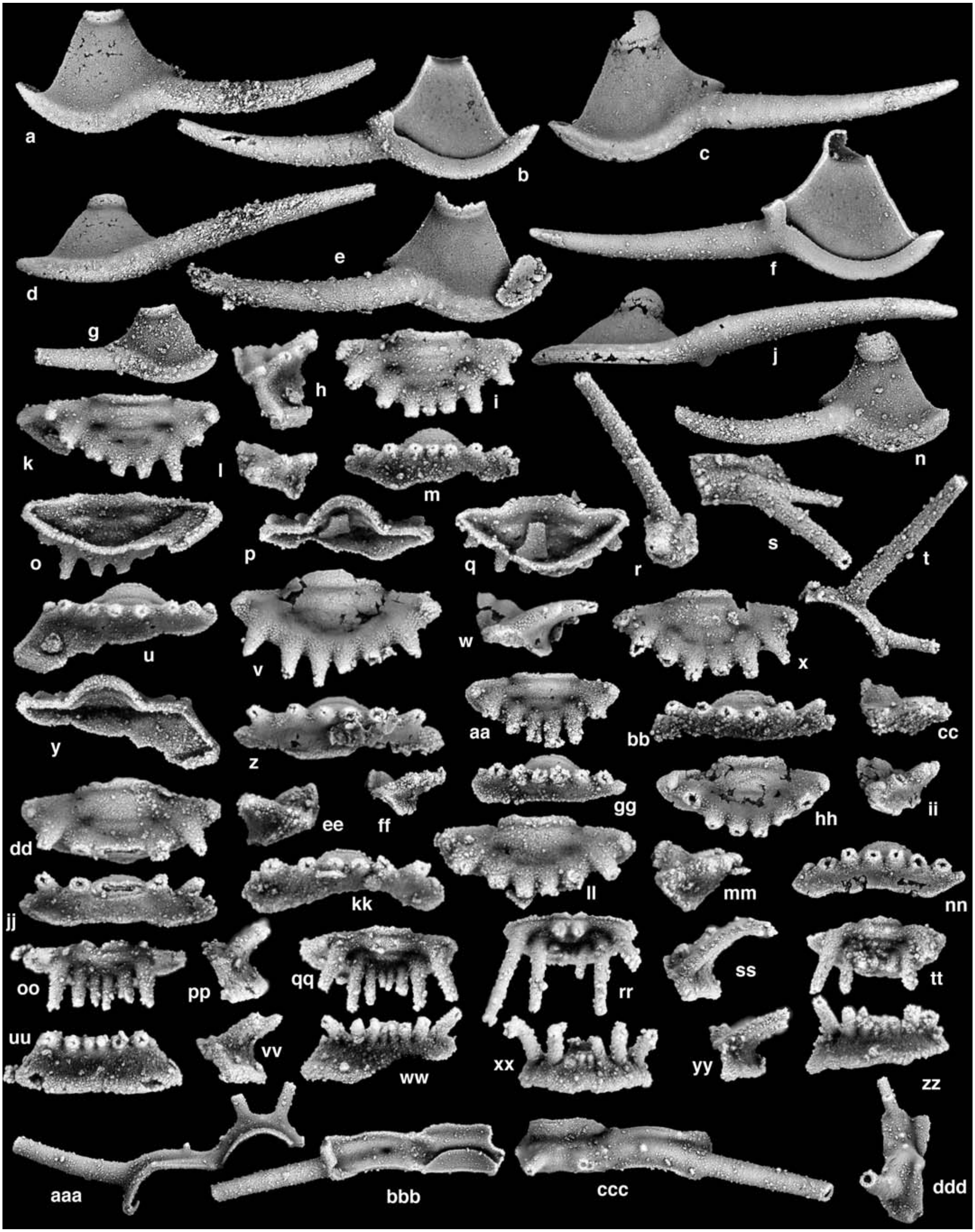
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Fig. 18. *Heckethornia alticapitis* (Young, 1973), from section H 191.7 m, Fillmore Formation (Ibexian; Blackhillsian), southern Confusion Range, Ibex area, Tule Valley, Millard County, western Utah. (*a*, *e*, *j*, *n*, *o*) Cranidium, SUI 113525, dorsal, ventral, right lateral, oblique, and anterior views, ×12. (*b*, *f*, *k*) Cranidium, SUI 113526, dorsal, right lateral, and anterior views, ×12. (*c*, *g*, *l*) Cranidium, SUI 113527, dorsal, right lateral, and anterior views, ×12. (*d*, *h*, *i*, *m*) Cranidium, SUI 113528, dorsal, left lateral, anterior, and ventral views, ×12. (*p*, *q*, *u*) Cranidium, SUI 113529, dorsal, right lateral, and anterior views, ×15. (*r*, *s*, *x*) Cranidium, SUI 113530, dorsal, anterior, and left lateral views, ×12. (*t*, *y*, *z*) Cranidium, SUI 113531, right lateral, anterior, and dorsal views, ×15. (*v*, *aa*, *bb*) Cranidium, SUI 113532, dorsal, anterior, and right lateral views, ×15. (*w*, *cc*, *dd*) Cranidium, SUI 113533, dorsal, left lateral, and anterior views, ×15.

background sculpture, long and slender spines and short, coarsely granulose "wall."

DESCRIPTION: Cranidium with sagittal length 93.2% (87.1%–98.6%) width across palpebral lobes, with distinctive tuberculospinose sculpture over background sculpture of very dense tiny granules; anterior branches of facial suture subparallel to gently anteriorly convergent, slightly laterally bowed; anterior border broad, short, longest medially, tapered and slightly curved posterolaterally, inflated with C-shaped cross-section, tall medially, tapered laterally in anterior view, with dense sculpture of tiny granules; anterior border furrow moderately short, deep, incised, transverse medially, very gently posterolaterally curved distally; preglabellar field very narrow, moderately short, slightly recessed, effaced except for background granules in most specimens; frontal areas moderately broad, strongly tapered toward palpebral lobes, steeply declined (about 20°–30° from vertical), with linear sculpture of spines (discussed on fixigena) and dense anterolateral sculpture of small tubercles, and spinose tubercles arranged in diagonal lines reflecting fixigenal tubercle lineation; preglabellar furrow short, fairly deep (shallow medially), strongly anteriorly convergent to point on sagittal axis; glabella long, slightly narrow, anteriorly tapered, ovoid, with width 87.0% (82.8%–92.3%) length, highly inflated with point of highest inflation even with posteriormost pair of glabellar spines over palpebral lobes, without well-defined lateral furrows or lobes, but widest at L2, with sculpture of three pairs of small but prominent, conical, posteriorly raked spines (Figs. 20*dd*, 20*kk*–20*nn*) across axis, and dense, evenly spaced sculpture of small tubercles; SO long, moderately deep, with very deep lateral apodemal pits, and gently anterolaterally arcuate course; LO long medially, tapered laterally, well inflated, with sculpture of long, slender, posterodorsally curved median spine flanked by one or two pairs of small spines, and with two or three pairs of small tubercles flanking axis on anterior margin; LO doublure very long medially, scalloped laterally, with W-shaped anterior margin, and with sculpture of fine ridges; axial furrow narrow, deep, incised, deepest along midlength of glabella, anteriorly divergent until mid-L2, then anteriorly convergent; fixigenae somewhat narrow, highly elevated, with steep slope down to axial furrow, with sculpture of linear arc of five prominent spines extending forward onto frontal areas and backward onto posterior fixigenae, and with small tubercles limning axial furrow; palpebral furrow diagonal, narrow and shallow, stronger along posterior part of lobe; palpebral lobes vaulted, with rectangular space underneath (lateral view), medium sized, arcuate to slightly half-teardrop shaped, very narrow anteriorly and slightly wider posteriorly, with slightly inflated rim with sculpture of about five small tubercles; posterior fixigenae only slightly wider than interocular fixigenae, triangular, with a few scattered tubercles; posterior border furrow short, shallow (especially proximally), with transverse to slightly anterolaterally curved course; posterior border wedge shaped, very short adaxially, expanded abaxially, mildly inflated, with sculpture of large, posteriorly curved spine near axial furrow, flanked by two pairs of smaller spines near exsagittal margin of posterior projections, with some interspersed tubercles on some specimens; posterior border doublure mainly expressed as posterior face, with short rim curled under.

Rostral plate unknown.

Librigena with width under midlength of eye 63.3% (58.7–65.1) length along lateral border furrow, with dense granulose sculpture topped with tubercles; anterior branch of facial suture very long, slightly posteriorly bowed or sinuous, steeply sloped; posterior branch of facial suture long, with steep posterolaterally diagonal course; eye very large, ovoid, highly inflated; eye socle narrow and very effaced (Figs. 21*i*, 21*j*, 21*p*) or not present (Figs. 21*c*, 21*q*); circumocular furrow narrow, shallow, strongly arced around base of eye; librigenal field significantly narrower posteriorly than anteriorly, gently convex, with typical arc of five tubercles obscured by many other large and small tubercles on most specimens; lateral border furrow narrow, moderately deep and effaced, with shallower "shadow" reaching inward on field, evenly arcuate anteriorly, then diagonal near genal spine; lateral border wide, widens posteriorly, then abruptly narrow on short section posterior of genal spine, highly inflated, cross-section like flattened cylinder, with short, tapered anterior projection, and with dense granulose sculpture overlain by arc of small tubercles (larger near base of spine) right along lateral border furrow and less complete arcs distally, and linear ridge sculpture ventrolaterally (Figs. 21*g*, 21*h*, 21*k*); lateral border doublure fairly broad, reaches not quite to border furrow, with small, shallow Panderian notch; genal spine large, slightly longer than librigenal field, conical, strongly tapered from broad base to blunt point, with sculpture of granules and fine ridges.

Total number of thoracic segments unknown. Thorax with great anterior–posterior variation in segment appearance, segments moderately to highly pleurally vaulted, with highly vaulted axis, and with width of axis 46.6% (41.9%–51.4%) total segment width; articulating half ring long medially, strongly tapered laterally, broad, inset into anterior margin of segment; articulating furrow long along axis, strongly tapered to narrow incised furrow anterolaterally along inset margin, course broadly U-shaped; axial ring as long as posterior pleural band of segment, U-shaped and anteriorly

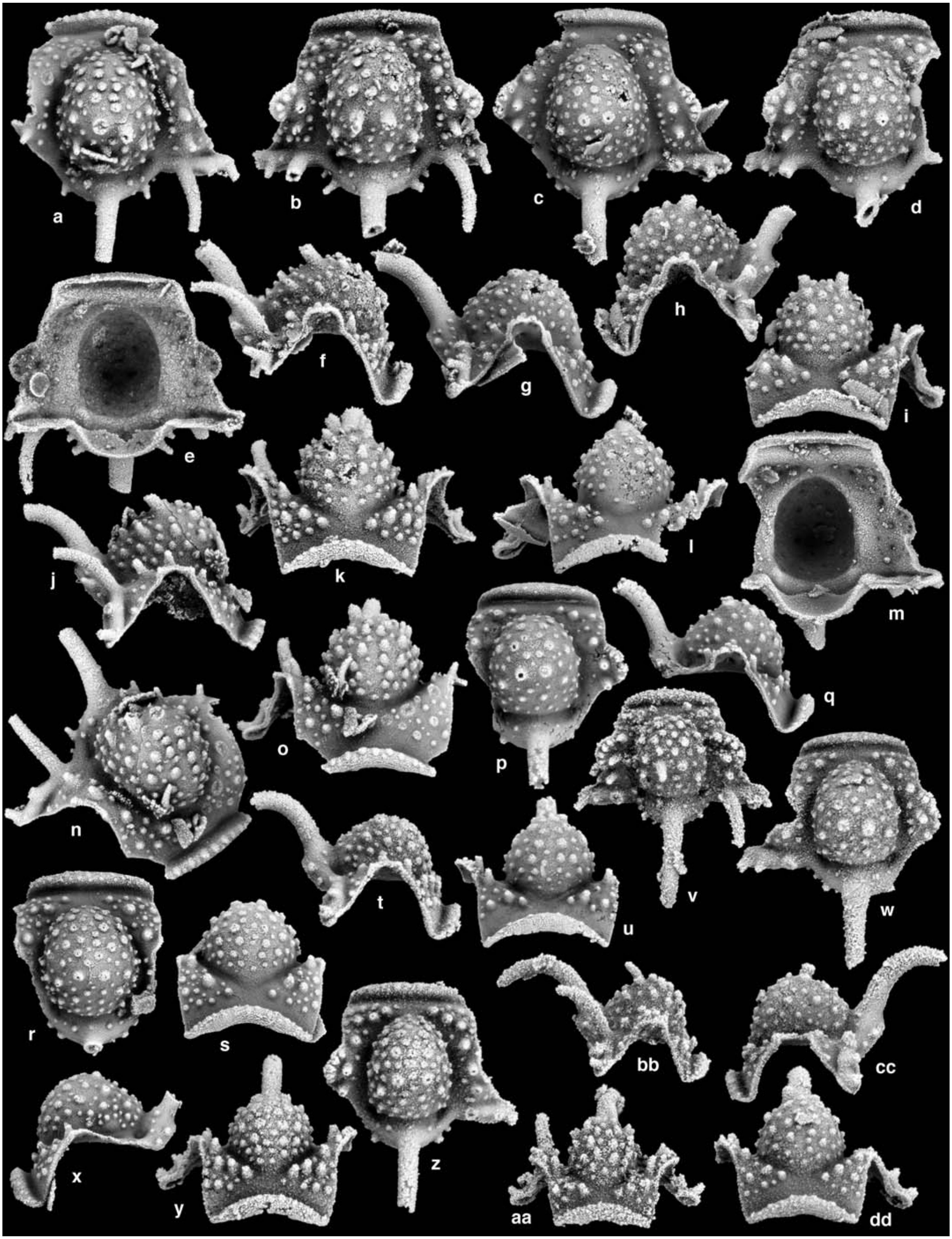
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Fig. 19. *Heckethornia alticapitis* (Young, 1973), from section H 191.7 m, Fillmore Formation (Ibexian; Blackhillsian), southern Confusion Range, Ibex area, Tule Valley, Millard County, western Utah. (*a*, *e*, *i*) Left librigena, SUI 113534, external, internal, and ventrolateral views, ×12. (*b*, *f*) Left librigena, SUI 113535, external and internal views, ×12. (*c*, *g*) Right librigena, SUI 113536, external and internal views, ×12. (*d*, *h*) Right librigena, SUI 113537, external and ventrolateral views, ×12. (*j*) Right librigena, SUI 113538, external view, ×12. (*k–m*, *s*, *t*) Thoracic segment, SUI 113539, left lateral, ventral, dorsal, posterior, and anterior views, ×15. (*n*) Left librigena, SUI 113540, external view, ×12. (*o*) Left librigena, SUI 113541, external view, ×15. (*p*) Right librigena, SUI 113542, external view, ×12. (*q*, *y*, *z*, *ee*) Thoracic segment, SUI 113543, right lateral, ventral, dorsal, and anterior views, ×12. (*r*, *aa*, *ff*) Thoracic segment, SUI 113544, left lateral, dorsal, and anterior views, ×12. (*u*, *w*, *x*) Thoracic segment, SUI 113545, dorsal, left lateral, and anterior views, ×15. (*v*, *bb*, *cc*, *gg*, *rr*) Pygidium, SUI 113546, dorsal, posterior, right lateral, anterior, and ventral views,×15. (*dd*, *hh*, *ii*) Pygidium, SUI 113547, dorsal, left lateral, and posterior views, ×15. (*jj*, *qq*, *ss*, *tt*, *uu*) Pygidium, SUI 113548, right lateral, anterior, posterior, dorsal, and ventral views, ×15. (*kk–mm*) Pygidium, SUI 113549, dorsal, right lateral, and posterior views, ×15. (*nn–pp*) Pygidium, SUI 113550, right lateral, dorsal, and posterior views, ×15.

wrapped around articulating half ring on some segments (Figs. 21*cc*, 21*dd*), more centralized on others (Figs. 21*s*, 21*y*), weakly inflated, with anteriorly convex arc of five to seven tubercles (prominent sculpture on Figs. 21*s*, 21*y*; appears as small tubercles along anterior margin of Figs. 21*cc*, 21*dd*) and (more) prominent pair of median spines on some segments (Figs. 21*cc*, 21*dd*); axial ring doublure very long medially and sharply tapered laterally, with W-shaped margin like that of LO doublure; axial furrow narrow, highly effaced, parallel-sided to anteriorly convergent around anterior projections of axial ring; inner pleurae subhorizontal; pleural angle very steep; outer pleurae steeply sloped (Fig. 21*ii*, about 45° downward) to subvertical (Figs. 21*t*, 21*bb*, 21*ee*); anterior pleural band with very short tab on anterior margin inner pleurae set off by very fine, incised furrow for articulation with short ridge structure on posterior margin of posterior pleural band; anterior pleural band very short medially, gradually expanded laterally and then ventrolaterally tapered, with small triangular articulating facet (Fig. 21*jj*); pleural furrow very short, shallow near axis, then deeper and more incised near fulcrum, then effaced along outer pleurae, with gently posterolaterally curved course; posterior pleural band slightly longer than anterior band, of even length, very weakly dorsally inflated, with sculpture of one very large, posterolaterally projected spine at fulcrum (Figs. 21*s*, 21*y*), one specimen with additional smaller spine just below fulcrum (Fig. 21*t*), or with sculpture of four pairs of spines evenly spaced along inner and outer pleurae of posterior band, with those closest to axis and lowermost most robust (Figs. 21*ee*, 21*ii*).

Largest pygidial specimen (Figs. 21*ff*, 21*kk*, 21*qq*) described; smaller specimens vary in having shorter and narrower furrows, and less well-expressed semi-articulating half rings. Pygidium of three segments (two expressed, third obscured), highly vaulted, with nearly semicircular outline (sagittal length 37.6% (single specimen, Figs. 21*nn*, 21*ss*, 21*uu*) width across fulcra) and prominent tuberculate and spinose sculpture over dense granules; articulating half ring very wide; articulating furrow long, shallow, with granulose sculpture medially, slightly deeper and effaced laterally, deepest at intersection with axial furrow; axis barrel-shaped, very wide and short, U-shaped in outline, only slightly tapered posteriorly, somewhat highly vaulted (moreso anteriorly); first axial ring very broad, long, shaped like gentle convex-anteriorly arc, slightly independently inflated, with dorsal arc of large tubercles like on axial segments; first semi-articulating half ring lens-shaped, narrow, well defined anteriorly by long and shallow arcuate furrow (causing arc shape of first axial ring), truncated posteriorly by inter-ring furrow; inter-ring furrow very shallow medially, slightly deeper laterally, with very deep triangular pits intersecting with axial furrow; second axial ring slightly shorter than first, a little more than half as wide, very slightly independently inflated, with pair of prominent tubercles at midlength; second inter-ring furrow long, shallow, ill-defined, followed by very short and narrow oblong raised area and triangular depressed area, which together may be second semi-articulating half ring and furrow or third segment; main part of third segment obscured by its pair of spines; axial furrow narrow, deep along furrows, very shallow along segments and over spine bases, U-shaped, strongly anteriorly divergent posteriorly, parallel-sided anteriorly; inner pleurae merged into "deck," without well-defined anterior and posterior bands on most segments, wide anteriorly, highly tapered posteriorly to just spine base, subhorizontal; fulcral angle very steep, all segments with very large spine projecting like rays from fulcrum; outer pleurae merged into subvertical "wall" area; anterior pleural band distinguishable on first pygidial segment, very short near axis, slightly longer laterally, with raised bump at fulcrum, and short, tapered articulating facet, also with very short articulating tab on inner pleurae, followed by very short incised furrow; pleural furrow very long, slightly expanded laterally, shallow, filled with granules, carries down onto "wall" as depressed stripe; posterior pleural band of first segment distinctly dorsally inflated, entirely obscured by spine base and spine, carried onto "wall" as raised stripe; subsequent segments without distinct pleural bands, with depressed area like first pleural furrow followed by spine base and projecting spine; spines very long, all roughly same length, conical, gradually tapered to blunt point, with very dense granulose sculpture, project mainly posterolaterally, just above horizontal, distal areas curve slightly ventrally; "deck" area of axis, inner pleurae, and spines defined posteromedially by short, deep furrow under spine bases (posterior view); "wall" short compared with congeners, shortest posteromedially, with dense granulose sculpture, posterior border furrow completely effaced; posterior border thick, distinctly inflated, with very gentle dorsal median curvature; border doublure short ventrally, with U-shaped cross-section.

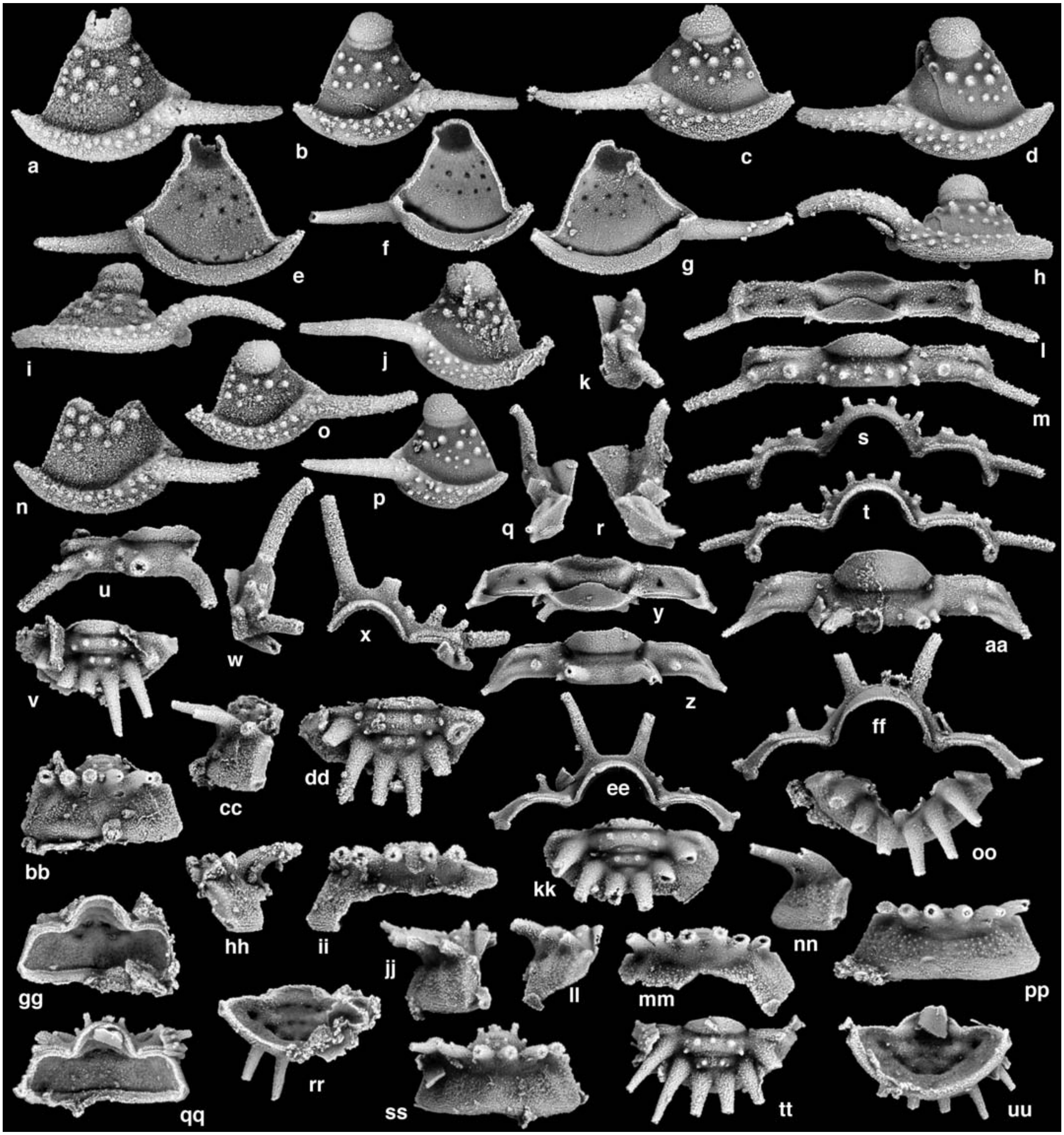
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Fig. 20. *Heckethornia ballionae* n. sp., from section H 222.1 m, Fillmore Formation (Ibexian; Blackhillsian), southern Confusion Range, Ibex area, Tule Valley, Millard County, western Utah. (*a*, *f*, *m*) Cranidium, SUI 113551, doral, right lateral, and anterior views, ×12. (*b*, *g*, *n*) Cranidium, SUI 113552, dorsal, left lateral, and anterior views, ×12. (*c*, *d*, *i*, *h*, *j*) Cranidium, **holotype**, SUI 113553, dorsal, ventral, anterior, left lateral, and oblique views, ×12. (*e*, *k*, *l*) Cranidium, SUI 113554, dorsal, left lateral, and anterior views, ×15. (*o*, *v*, *y*) Cranidium, SUI 113555, dorsal, left lateral, and anterior views, ×12. (*p*, *z*, *ee*) Cranidium, SUI 113556, dorsal, left lateral, and anterior views, ×12. (*q*–*s*) Cranidium, SUI 113557, dorsal, left lateral, and anterior views, ×12. (*t*, *bb*, *gg*, *hh*) Cranidium, SUI 113558, dorsal, right lateral, anterior, and ventral views, ×12. (*u*, *x*, *cc*) Cranidium, SUI 113559, dorsal, left lateral, and anterior views, ×12. (*w*, *aa*, *ff*) Cranidium, SUI 113560, right lateral, dorsal, and anterior views, ×15. (*dd*, *kk*–*nn*) Cranidium, SUI 113561, dorsal, ventral, oblique, left lateral, and anterior views, ×12. (*ii*, *jj*, *oo*) Cranidium, SUI 113562, dorsal, right lateral, and anterior views, ×12.

ONTOGENY: *Heckethornia ballionae* is known from very little ontogenetic material, but some growth patterns are represented. Comparison between the larger cranidia (those of Fig. 20) and the smallest cranidium (Fig. 21*xx*–21*zz*) shows that cranidial vaulting increases (with corresponding increase in length of facial sutures), the anterior border shortens and develops a higher median dorsal inflection, the preglabellar field loses its granulose sculpture and overall granulose sculpture decreases in prominence (but remains dense), glabellar inflation increases, the glabella becomes longer and more ovoid, glabellar and fixigenal spinose tubercles become more prominent and spinose, small tubercles framing the axial furrow develop, the palpebral lobes grow larger, and the occipital spine becomes less robust compared with the overall cranidial dimensions. Differences between the smallest librigenae (Figs. 21*w*, 21*z*) and the mature librigenae (e.g., Figs. 21*a*, 21*c*, 21*l*) include a smaller field with main arc of four tubercles unobscured by other tubercles (although some in Fig. 21*w*), coarser granulose sculpture than in larger specimens, a smaller, less inflated eye, denser lateral border tuberculation, and a longer spine relative to field length. Variation among thoracic segments is probably a function of the position on the thorax and is not discussed here. Small pygidia (Figs. 21*nn*, 21*vv*) differ from larger pygidia mainly in possessing a narrower, shorter axis; shorter, more inflated and more transverse axial rings without prominent pseudoarticulating half rings; deeper inter-ring furrows; a narrower, slightly deeper axial furrow; longer, thinner, less splayed spines, and more prominent granulose sculpture.

REMARKS: Variation in large cranidia of *Heckethornia ballionae* is mild and includes subtle differences in length, inflation, and dorsal median inflection of the anterior border; size and shape (arcuate vs. more half-teardrop shaped) of the palpebral lobes; degree of development of the fixigenal spine arc (cf. Figs. 20*c*, 20*o*); steepness of fixigenae (cf. Figs. 21*m*, 21*y*, 21*cc*); level of cranidial inflation (cf. Figs. 20*f*, 20*h*); size and shape of glabella (large and ovoid, e.g., Fig. 21*c* vs. smaller and more rounded, e.g., Fig. 21*u*); and prominence of cranidial spinose sculpture, including variation in the number of small tubercles on LO. The cranidium of Fig. 20*i* has a tuberculate, rather than effaced, preglabellar field.

Librigenal variation is also slight and mainly includes the size of field (cf. Figs. 21*a*, 21*c*), density and amount of field sculpture (cf. Figs. 21*a*, 21*c*, with 21*d*, 21*l*), lateral border width and sculpture density, and expression of the eye socle (Fig. 21*i*, weak vs. Fig. 21*c*, unexpressed). One librigena (Fig. 21*f*) has an unusually wide lateral border and very short spine compared with other librigenae of the same size. Thoracic variation occurs due to position of a given segment along the thorax and cannot be discussed without articulated material.

Pygidial variation not attributable to ontogenetic patterns is mainly expressed in the number of tubercles on the axial rings. Pygidia of Fig. 21*kk*, 21*nn* have an arc of five evenly spaced tubercles on the first axial ring and a pair on the second ring; the pygidium of Fig. 21*ll* has six tubercles forming anteriorly convergent diagonal lines on the first ring and a pair on the second; and the smallest pygidium (Fig. 21*vv*) has a pair on each ring (anterior ring may have several more effaced tubercles). The pygidium of Figs. 21*nn*, 21*oo*, 21*ss*, 21*uu* has coarsely granulose sculpture on the "wall" area, instead of dense granules.

Heckethornia ballionae is compared with its sister taxon and most phenetically similar congener, *H. alticapitis*, in the differential description of the latter. The sister taxa share c.i.-one synapomorphies of posteriorly directed cranidial sculpture, two pairs of tubercles flanking the median occipital spine, W-shaped occipital doublure, dense librigenal field sculpture, and a moderately thick pygidial border.

H. ballionae differs from *H. morrisseyi* very obviously in its spinotuberculate sculpture, but also in the possession of a wider anterior border; longer, narrower, more highly inflated glabella; deeper, more incised axial furrow; shorter LO; W-shaped LO doublure; much thinner, lower occipital spine; weakly expressed or absent eye socle; wider, more inflated lateral librigenal border; much shorter and more delicate genal spine; smaller Panderian notch; pygidium with longer, narrower axis; slightly more incised inter-ring and axial furrows; much longer, thinner spines; and thinner, less inflated posterior border.

Heckethornia ballionae and *H. alticapitis* possibly share several c.i.-one synapomorphies with *H. morrisseyi*, but the morphology is not preserved in specimens of *H. morrisseyi*. These include half-teardrop shaped and highly elevated palpebral lobes, a narrow posterior fixigena with a wide border, a semicircular pygidium, and visible furrows in the pygidial "wall." These synapomorphies optimize differently in ACCTRAN and DELTRAN (Fig. 3) due to the ambiguity of coding *H. morrisseyi*.

Acknowledgements

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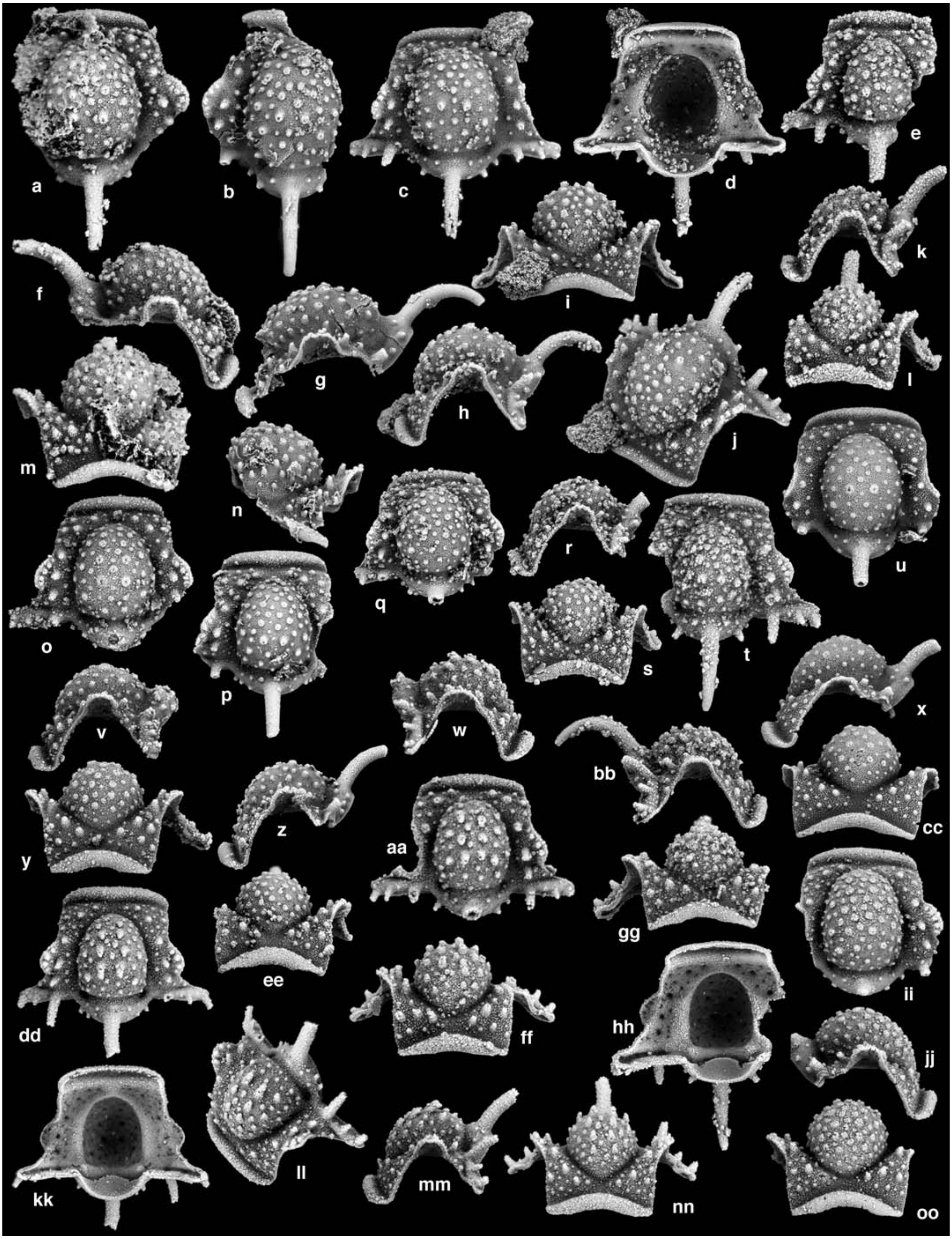
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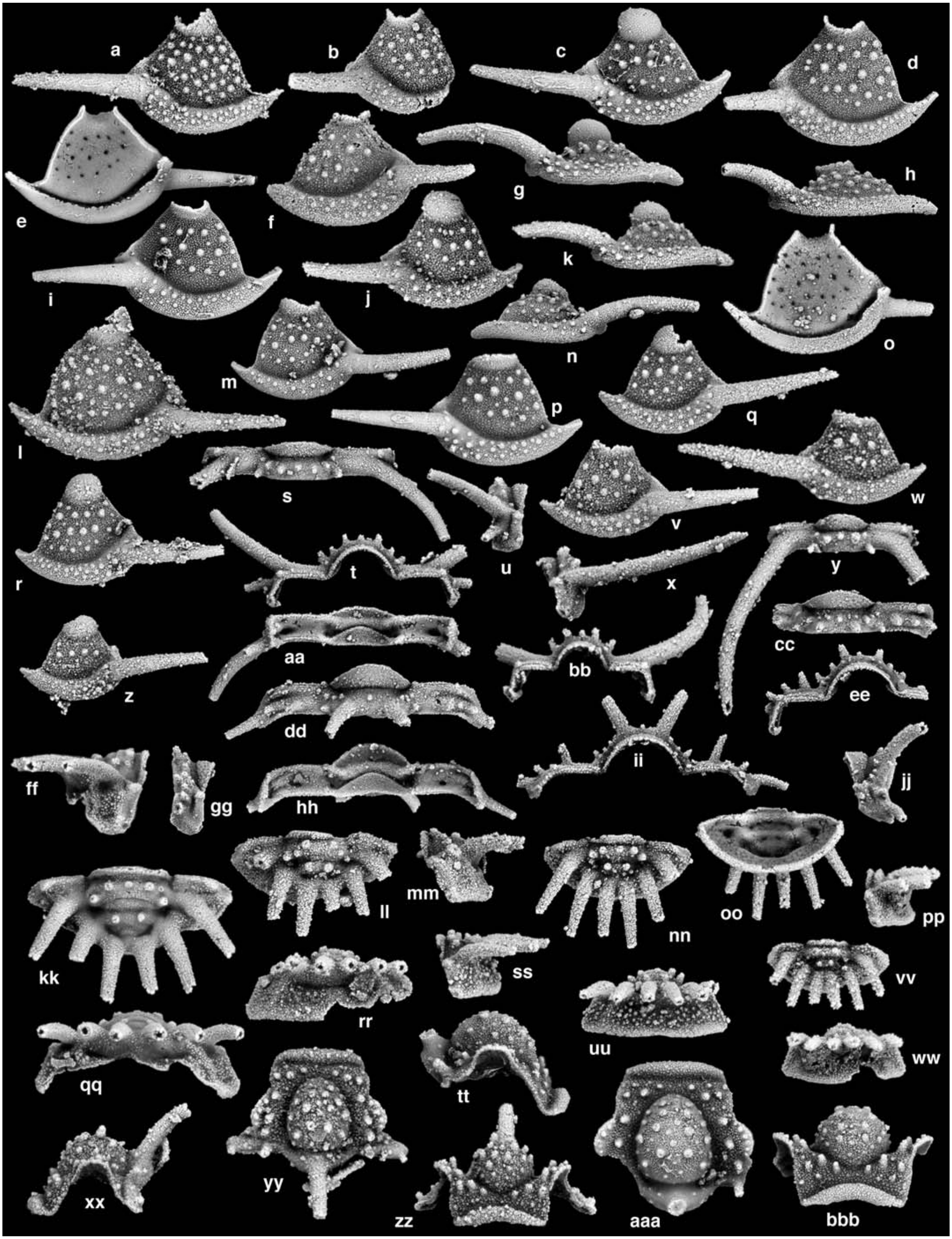
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Fig. 21. *Heckethornia ballionae* n. sp., from section H 222.1 m, Fillmore Formation (Ibexian; Blackhillsian), southern Confusion Range, Ibex area, Tule Valley, Millard County, western Utah. (*a*) Right librigena, SUI 113563, external view, ×12. (*b*) Right librigena, SUI 113564, external view, ×12. (*c*, *g*) Right librigena, SUI 113565, external and ventrolateral views, ×15. (*d*, *h*, *o*) Right librigena, SUI 113566, external, ventrolateral, and internal views, ×12. (*e*, *i*) Right librigena, SUI 113567, internal and external views, ×12. (*f*) Left librigena, SUI 113568, external view, ×15. (*j*, *k*) Right librigena, SUI 113569, external and ventrolateral views, ×15. (*l*) Left librigena, SUI 113570, external view, ×12. (*m*, *n*) Left librigena, SUI 113571, external and ventrolateral views, ×12. (*p*) Right librigena, SUI 113572, external view, ×15. (*q*) Left librigena, SUI 113573, external view, ×15. (*r*) Left librigena, SUI 113574, external view, ×12. (*s–u*, *aa*) Thoracic segment, SUI 113575, dorsal, anterior, right lateral, and ventral views, ×12. (*v*) Left librigena, SUI 113576, external view, ×15. (*w*) Right librigena, SUI 113577, external view, ×20. (*x*, *y*, *bb*) Thoracic segment, SUI 113578, left lateral, dorsal, and anterior views, ×15. (*z*) Left librigena, SUI 113579, external view, ×15. (*cc*, *ee*, *gg*) Thoracic segment, SUI 113580, dorsal, anterior, and right lateral views, ×12. (*dd*, *hh–jj*) Thoracic segment, SUI 113581, dorsal, ventral, anterior, and left lateral views, ×12. (*ff*, *kk*, *qq*) Pygidium, SUI 113582, right lateral, dorsal, and posterior views, ×15. (*ll*, *mm*, *rr*) Pygidium, SUI 113583, dorsal, left lateral, and posterior views, ×15. (*nn*, *oo*, *ss*, *uu*) Pygidium, SUI 113584, dorsal, ventral, left lateral, and posterior views, ×15. (*pp*, *vv*, *ww*) Pygidium, SUI 113585, left lateral, dorsal, and posterior views, ×20. (*tt*, *aaa*, *bbb*) Cranidium, SUI 113586, right lateral, dorsal, and anterior views, ×20. (*xx–zz*) Cranidium, SUI 113587, left lateral, dorsal, and anterior views, ×20.

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