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

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#### Abstract

Panisaspis n. gen. is a clade of pliomerid trilobites from the Tulean and Blackhillsian stages (Floian) of the Great Basin. It includes Protopliomerops? quattuor Hintze, 1953, and ten new species, six of which are formally named: Panisaspis millardensis (type species), P. sevierensis, P. deltaensis, P. rancherensis, P. topscityensis, and P. loganensis. Four new species are not well enough known for formal naming and are described in open nomenclature. All species are Tulean in age except for P. millardensis, which is earliest Blackhillsian. Synapomorphies of Panisaspis include a short, nearly semicircular anterior border; small L1; large genal spines; a rounded, ovoid hypostomal border; elongated third pygidial spines; and a large, triangular terminal piece with distinct pitted impressions. Phylogenetic analysis indicates that $P$. millardensis and $P$. sevierensis are sister taxa, and that $P$. deltaensis, $P$. rancherensis, $P$. topscityensis, $P$. quattuor, and $P$. loganensis are successive sister species. The group may be sister to Ibexaspis Přibyl and Vaněk in Přibyl et al., 1985.


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

## Introduction

This is the fourth paper in a series (McAdams and Adrain, 2009a, 2010a, 2011) describing and revising the systematics of members of the trilobite family Pliomeridae Raymond, 1913, from Ibexian (Tremadocian-Floian) and lower Whiterockian (Dapingian) strata in the Great Basin. Silicified trilobite faunas from sections in southeastern Idaho and northern Utah (Ross, 1951) and western Utah and eastern Nevada (Hintze, 1953) are the subject of ongoing field-based description and systematic revision (e.g., Adrain et al., 2001, 2003, 2009; Adrain and Westrop, 2007a, 2007b; McAdams and Adrain, 2009a, 2009b), and the history of their study was summarized by Adrain et al. (2009). New sampling of these sections has resulted in a great number of new species and much more complete knowledge of previously established species of pliomerids, which are typically common, well preserved, and often abundant.

Pliomeridae includes over 40 genera and nearly 200 named species, yet no cladistic analysis of any component of the family has previously been published. Absence of modern cladistic analyses of pliomerid taxa means that their phylogenetic status is uncertain (see also a brief summary in McAdams and Adrain, 2009a), and a lack of well known stratigraphically early, and potentially plesiomorphic, species compounds the problem. Species from the Great Basin have been recovered from closely spaced horizons with good biostratigraphic control, and include some of the oldest known members of the family.

Full systematic revision of Pliomeridae cannot proceed without description of new taxa, resampling (where possible) and redescription of previously named species, followed by phylogeny reconstruction using modern
methods. These are the aims of this paper, which focuses on Panisaspis, a new genus with species ranging in age from the Tulean to earliest Blackhillsian (lower to mid-Floian). The taxa assigned to Panisaspis were previously known from only a single named species, Protopliomerops? quattuor Hintze, 1953 (which included misassociated sclerites of different ages, some of which belong to Ibexaspis brevis (Young, 1973)), and a handful of sclerites figured in open nomenclature (Hintze, 1953; Demeter, 1973). In this paper we: 1) revise Panisaspis quattuor (Hintze, 1953) on the basis of new material; 2) name and describe six new species from Utah, Idaho, and Nevada, and describe four more in open nomenclature; 3) reconstruct the phylogenetic relationships of the seven named species via cladistic analysis; and 4) diagnose Panisaspis on the basis of putative synapomorphies.

## Localities and Stratigraphy

Most of the new taxa described herein are from the Fillmore Formation (Hintze, 1951), and were collected from Tulean and Blackhillsian horizons in sections G and H of Hintze (1951, 1953, 1973) in the southern Confusion Range, Ibex area, Tule Valley, Millard County, western Utah (Fig. 1.1, 1.4, 1.5). Species ranges are shown logged against stratigraphy in Figures 2 (Section G) and 3 (Section H). One species is from the Garden City Formation (Richardson, 1913) at Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho (Fig. 1.1-1.3), and one species occurs in both Section G at Ibex and in the "Yellow Hill Beds" (Westgate and Knopf, 1932) in the Ely Springs Range, Lincoln County, eastern Nevada (Fig. 1.1, 1.6). Full locality details were given by Adrain et al. (2009, pp. 544-548) and are not repeated herein. We use the new trilobite zonal scheme for the Tulean and Blackhillsian introduced by Adrain et al. (2009, fig. 3).

## Phylogenetic Analysis

Methods. Parsimony analysis was carried out using the implicit enumeration (exact search) algorithm of TNT (Goloboff et al., 2008), with branch collapsing not permitted. Group support was evaluated with Bremer decay (Bremer, 1994), in TNT, and reported as absolute support. Nonparametric bootstrapping using implicit enumeration with 10,000 pseudoreplicates in TNT was also used to evaluate group support. Bootstrap frequencies are reported as GC (Groups supported/Contradicted) values (Goloboff et al., 2003). Character optimization was explored with WinClada (Nixon, 2002).

Taxa. The ingroup is made up of all seven formally named species of Panisaspis. The four taxa reported herein in open nomenclature were excluded from the analysis via safe taxonomic reduction (STR, Wilkinson, 1995), or due to damage, the extremely small $(\mathrm{n}=1)$ sample size, or small size of the specimens (likely indicating immaturity). The cranidia of Panisaspis sp. 1 and Panisaspis sp. 3 are very morphologically similar to those of the derived species, although they seem to have smaller, blunter genal spines. They were excluded because there is only one specimen for each species, that of Panisaspis sp. 1 is fairly damaged, and that of Panisaspis sp. 3 is small and possibly sub-adult. The pygidium of Panisaspis sp. 2 was eliminated by STR with P. millardensis. The pygidia of Panisaspis n . sp. A code identically with those of $P$. deltaensis, and although its hypostome is too damaged to code, it appears to have morphology also like that of $P$. deltaensis. This species is therefore also excluded.

The outgroup taxon is Hintzeia parafirmimarginis McAdams and Adrain, 2011, from Section HC6 (equivalent to Ross's [1949, 1951] Locality 6) 165.2 m , in the lower Tulean Psalikilus spinosum Zone. The stratigraphically earliest member of Panisaspis occurs in the overlying Hintzeia celsaora Zone. The cranidium of the outgroup taxon resembles that of $P$. loganensis in possession of a relatively broad, shallowly arched anterior border; a glabella with a small frontal lobe and an L1 roughly equal in size to other lateral lobes; anteriorly positioned palpebral lobes; and wide interocular fixigenae. The taxa also share a long librigenal field with small pits, a smoothly curved outer margin of the librigenal border, and a short posterior projection of the border. The pygidia of these species also have a small, unindented terminal piece, narrow, only slightly tapered, subparallel and posteriorly directed pygidial pleural spines, and a third pair of pygidial spines equal in width and length (compared at posterior tips) to the other pairs. The hypostome of P. loganensis is unknown, but those of the other plesiomorphic species (discussed in results of the phylogenetic analysis, below) are elongate and subrectangular, with a long, spinose posterior border much like the hypostome of Hintzeia parafirmimarginis.

Characters. Twenty-two characters (eight cranidial, three hypostomal, four librigenal, and seven pygidial) were used in parsimony analysis of Panisaspis. Character 22 was ordered on the basis of ontogeny. The elongation of the third spine pair relative to the fourth during growth can be seen clearly, if subtly, in the ontogeny of Panisaspis quattuor (cf. Figs. 31.1, 31.3, 32.10, 32.31). All other characters were unordered. The taxon-character matrix is reproduced as Table 1.

## Cranidium

1. Shape of arc of anterior border: 0, shallow arch (Fig. 33.1, 33.3); 1, moderately deep semi-ellipse (Figs. 5.1, 20.1).
2. Position of palpebro-ocular ridges relative to glabella: 0 , more anteromedial, with midlength of lobe approximately even with L3 (Fig. 25.1); 1, more posterolateral, with midlength of lobe approximately even with S2 (Fig. 5.1)
3. Width of interocular fixigenae at S2: 0, moderate, about same width as L3 (Figs. 25.1, 33.2); 1, narrow, about half width of L3 (Figs. 5.1, 12.10).
4. Shape of glabella: 0, straight-sided, subparallel; 1, straight-sided, gently anteriorly tapered (Figs. 25.3, 33.1); 2, anteriorly expanded, with laterally convex sides (Figs. 5.1, 13.1, 20.1).
5. Shape of LF: 0, narrow, sub-triangular or wedge-shaped (Figs. 22.1, 25.1, 33.1); 1, wide, sub-semi-elliptical (Figs. 5.1, 12.1, 17.2, 20.1).
6. Size of L1: 0, similar to other lateral lobes (Figs. 25.1, 33.1); 1, smaller (narrower and shorter) than other lobes (Figs. 5.1, 12.1, 20.1).
7. Length of posterior fixigena (excluding posterior border) behind posterior end of palpebro-ocular ridge compared to sagittal cranidial length: 0 , medium, about $1 / 3$ (Fig. 25.1); 1, short, about $1 / 4$ (Figs. 5.1, 12.3, 17.1, 20.28).
8. Size of genal spine: 0, small nub (Figs. 22.8, 25.5); 1, large, tapered conical spine (Figs. 5.1, 12.10, 17.1).

## Hypostome

9. Shape of hypostomal margin: 0, shelf-like posteriorly, overall sub-rectangular (Figs. 17.16, 23.1, 26.3); 1, rounded oval (Figs. 8.2, 13.11, 21.6).
10. Width of hypostomal lateral border at shoulders: 0 , much narrower than length of posterior border (Figs. 23.1, 29.15); 1, approximately as wide as length of posterior border (Figs. 8.3, 13.14).
11. Size of lateral and posterior border spines: 0, small nubs (Fig. 17.16); 1, small spines (Figs. 23.1, 29.15); 2, no spines (Figs. 8.2, 13.14, 21.6).

## Librigena

12. Shape of librigenal field: 0 , long, triangular wedge (Figs. 22.10, 26.12); 1, short and squared-off (Figs. 6.3, $14.7,17.15)$.
13. Shape of librigenal field pits: 0 , small circles (Figs. 21.9, 33.18); 1, large and irregularly shaped (Figs. 7.4, 14.1, 29.4).
14. Shape of outer margin of lateral border: 0 , smooth curve (Figs. 21.9, 33.18); 1, with widened "hump" just posterior to anterior branch of facial suture (Figs. 6.3, 14.4).
15. Length of posterior projection of lateral border compared to field: 0 , short, $1 / 4-1 / 3$ length (Figs. 21.9, 26.12, 33.18); 1, long, $1 / 2$ length or more (Figs. 6.3, 14.7).

## Pygidium

16. Size of terminal piece: 0 , small, length about equal to last two axial rings (Figs. 21.15, 24.1, 27.1); 1, large, length about equal to last 3 axial rings (Figs. 10.1, 15.14, 19.1).
17. Style of terminal piece indentations: 0, absent (Figs. 24.1, 34.17); 1, linear grooves extending from anterior margin (Figs. 19.2, 21.12, 27.20); 2, deep pits at about $1 / 3$ length (Figs. 10.14, 16.1).
18. Posterior exposure of terminal piece: 0 , not exposed, surrounded by pleurae; 1 , small gap between fourth pleurae and extreme tip of TP or furrow enclosing TP exposed (Figs. 21.15, 24.2, 31.1, 34.14); 2, well exposed, without enclosing furrow (Figs. 10.14, 15.14, 19.1).
19. Orientation of pygidial spines: 0, subparallel and posteriorly directed (Figs. 21.15, 31.1, 34.14); 1, laterally splayed (Figs. 10.3, 15.14, 18.1).
20. Shape of spines: 0 , narrow and rounded, tapered only at tips (Figs. 21.12, 34.18); 1, slightly dorsoventrally flattened with pointed tips (Figs. 24.1, 31.1); 2, conical and strongly tapered, with third spine blunt (Figs. 10.3, 16.1, 18.1).
21. Width of third spine compared to fourth spine: 0, same (Figs. 21.15, 24.1, 31.1); 1, distinctly wider (Figs. $15.14,19.1$ ).
22. Relative lengths of pygidial spines: 0 , essentially equal (Figs. 21.15, 34.17); 1, third pair somewhat longer than fourth pair (Fig. 31.1); 2, third pair much longer than fourth pair (Figs. 10.1, 16.1, 18.1, 24.1).

## Results

The analysis returned a single most parsimonious tree of length 37, with a consistency index of 0.75 and a retention index of 0.80 (Fig. 4). Panisaspis millardensis, P. sevierensis, and P. deltaensis form a derived clade marked by the unique, unreversed synapomorphies of long, wide genal spines; librigenae with short, sub-square fields; and pygidia with a large, posteriorly exposed terminal piece. Panisaspis rancherensis is sister to this clade, supported by the unique, unreversed synapomorphies of laterally positioned palpebral lobes; narrow interocular fixigenae; short posterior projections; and a hypostome with lateral borders as wide as the length of the posterior border. The next successive sister taxon is $P$. topscityensis; the unique, unreversed synapomorphies of that clade include a con-vex-sided glabella with a wide, sub-semicircular LF and with L1 smaller than L2 and L3. Panisaspis quattuor is the second-most plesiomorphic taxon, with a slightly elongate third pair of pygidial spines compared to the fourth pair. Panisaspis loganensis is the most plesiomorphic species, as discussed above. The synapomorphies of the genus (transformed in derived taxa) are a straight-sided, gently anteriorly tapered glabella, and a terminal piece with a narrow gap exposing its posteromedian edge (or the median part of its enclosing furrow) between the fourth pair of pleurae.

## Systematics

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

Terminology. Morphological terms follow Whittington and Kelly (1997). The combined structure of the ocular ridge and palpebral lobe is referred to as the palpebro-ocular ridge.

## Family Pliomeridae Raymond, 1913

## Panisaspis n. gen.

Type species. Panisaspis millardensis n . sp., from the lower Blackhillsian (Strigigenalis plicolabeona Zone) of western Utah, USA.

Other species. Panisapsis deltaensis n. sp. (Tulean; Heckethornia bowiei Zone); Panisaspis loganensis n. sp. (Tulean; Hintzeia celsaora Zone); Protopliomerops? quattuor Hintze, 1953 (Tulean; Psalikilopsis cuspidicauda Zone and Psalikilus typicum Zone); Panisaspis rancherensis n. sp. (Tulean; Psalikilus pikum Zone); Panisaspis sevierensis n. sp. (Tulean; Psalikilus pikum Zone); and Panisaspis topscityensis n. sp. (Tulean; Protopliomerella contracta Zone).

Etymology. From the Latin noun panis, bread, and Greek noun aspis, shield, in reference to the long, slender pygidial spines that resemble breadsticks. Gender is feminine.

Diagnosis. Cranidium with anteriorly tapered glabella and short, wide anterior border (transformed to a subsemicircular anterior border and laterally bowed glabella in derived species). Hypostome sub-rectangular, with long posterior border, and spines at shoulders and posterolateral corners (transformed to long, broad, ovoid, with rounded margin in derived species). Pygidium with close, subparallel spines of roughly even length (transformed
in most species to shorter fourth spine pair and longer third spine pair); terminal piece with a narrow gap exposing its posteromedian edge (or the median part of its enclosing furrow) between the fourth pair of pleurae.

Discussion. Ibexaspis Přibyl and Vaněk in Přibyl et al., 1985, is the likely sister taxon of Panisaspis. A forthcoming work will revise Ibexaspis, including abundant new material of the type species and multiple new species. It is a diverse clade with an origin contemporaneous with Panisaspis. Early members of either genus are phenetically quite similar, and both groups undergo significant within-group morphological change. As explained in the results of the phylogenetic analysis, a straight-sided, gently anteriorly tapered glabella, and a terminal piece with a narrow gap exposing its posteromedian edge (or the median part of its enclosing furrow) between the fourth pair of pleurae are the basal synapomorphies of Panisaspis. Revision of Ibexaspis and description of its diversity, together with a broader analysis of pliomerid relationships, will permit a more extended comparative treatment.

Hintze (1953) misassigned sclerites of two separate younger species of Ibexaspis to Panisaspis quattuor (see discussion of $P$. quattuor). Based on new field data, the earliest species of Ibexaspis occurs in the Psalikilopsis cuspidicauda Zone, and the genus ranges upward into the "Pseudocybele nasuta Zone". Ibexaspis shares potential synapomorphies with Panisaspis including a semicircular anterior border; large, semicircular LF; small L1; ovoid hypostome; short, wide librigenal field; and a kinked librigenal lateral border. The cranidia differ in that those of Ibexaspis are altogether more convex (sag., tr.), usually possess a highly vaulted glabella, and have small genal spines. Ibexaspis pygidia have four segments, like those of Panisaspis, but the spines are always short, of equal length, and splayed, and the pygidia have either a small, enclosed terminal piece or none at all. They also commonly have median axial nodes. Both pygidia and cranidia typically have coarser tuberculate sculpture than do those of Panisaspis.

Hintze (1953) originally assigned Panisaspis quattuor to Protopliomerops Kobayashi, 1934. The type species of Protopliomerops, P. seisonensis Kobayashi, 1934, is not well known; cranidia are small and irregularly oriented, no librigenae were figured, and only the ventral surface of the single pygidium was illustrated. The cranidia are somewhat similar to Panisaspis quattuor in overall shape (narrow, elongate glabella; broad triangular fixigenae; anteriorly postitioned palpebro-ocular ridge), but not in detail. Notably, the anterior border of P. seisonensis is much broader and extends over the inner portion of the palpebro-ocular ridges, the glabella is more elongate and straight-sided, and the fixigenae are much longer. The pygidium is very dissimilar; it is short and wide, with five axial rings and short, broad spines of even lengths. The broad similarity of the cranidia is likely plesiomorphic or convergent, and the two genera do not seem to be closely related.

Demeter (1973) figured a number of sclerites from Section G and the Mesa Section (Hintze, 1973) that could belong to members of Panisaspis. However, the small photographs and lack of views to supplement the standard dorsal for most specimens hinders identification. Identifiable or tentatively identifiable sclerites are included in the species synonymies herein, but some remain enigmatic. The pygidium of Demeter's pl. 3, fig. 5a-c, from Mesa Section, which he called Protopliomerops sp. III, clearly belongs to a derived species of Panisaspis, but its coarse granulose sculpture and posteriorly widened third spines are unique. The same horizon yielded a small cranidium which Demeter figured (1973, pl. 2, fig. 10) as Protopliomerops aff. P. quattuor and incorrectly associated with a cranidium and pygidium belonging to Ibexaspis; it may also represent this species. The Mesa horizon correlates roughly to Section H 131 m , so these sclerites may alternatively be specimens of Panisaspis sp. 1 (the cranidium and/or pygidium) or Panisaspis sp. 2 (the cranidium; possibly the pygidium if the third spines become less swollen through ontogeny). The range of these taxa would then be slightly extended. It is unlikely that the cranidium represents $P$. deltaensis, as it is coarsely sculptured. Demeter also figured a number of sclerites as "genus and species undetermined". The hypostomes of pl. 6, figs. 1, 4, 7 resemble those of $P$. quattuor, but diagnostic details cannot be seen in the photographs. They could also belong to other pliomerids with a similar plesiomorphic hypostome. The hypostome of pl. 6, fig. 2 is similar to that of $P$. topscityensis, but not enough detail is visible to confirm the association. Likewise, it is possible that the five-segmented pygidium of pl. 6, fig. 6 is a transitory pygidium of $P$. quattuor or another species, and that the damaged pygidium of pl. 6, fig. 11 may represent a derived species of Panisaspis with a posteriorly exposed terminal piece.

## Panisaspis millardensis n. sp.

Figs. 5-11
1953 Undetermined gen. and sp. Loc. H-20. Zone H. (not described); Hintze, pl. 21, figs. 6, 7.

Material. Holotype, pygidium, SUI 125637, from Section H 187.4 m and assigned specimens SUI 125596125636, 125638-125648, from Section H 185.6 m and 187.4 m, Fillmore Formation (Blackhillsian; Strigigenalis plicolabeona Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

Etymology. From Millard County, Utah.
Diagnosis. Hypostome with very wide and long ovoid border; thoracic segments with very long (dorsoventrally), strongly downturned pleural spines; with pair of tubercles straddling axis; and with dense granulose sculpture all over; pygidium with densely granulose axis; pleural spines effaced dorsally except for posterior half of third pair; terminal piece with pair of indentations near anterior margin and second pair at about $1 / 3$ length.

Description. Cranidium somewhat triangular in outline, short, wide posteriorly, with sagittal length $46.4 \%$ width across posterior border, moderately vaulted (anterior view), mostly due to sloping fixigenae; anterior border short, fairly wide, sub-circular in shape, ends even with S3, strongly anteroventrally curved such that doublure is expressed mainly anteriorly with only a short ventral rim, and with dense granulose sculpture; anterior border furrow short, deep, incised, strongly anteriorly bowed, longest and deepest in lateral section forming apodemal pits even with S3; glabella ovoid, long, relatively narrow, widest at S2, with width $100.0 \%$ ( $91.1-106.6 \%$ ) sagittal length excluding LO, moderately vaulted (sag., tr.), with well defined lateral lobes and furrows, and with very dense sculpture of tiny granules; L1 small, subtriangular, L2 and L3 large, subrectangular, roughly equal in area, frontal lobe very large, sub-semicircular, all lateral furrows very short, slightly longer near axial furrows and at adaxial ends, very deep, with strong projection ventrally, all directed posteromedially at about $30^{\circ}$, S 3 with slight anterior projection near abaxial end on some cranidia (e.g., Fig. 5.2, 5.11); SO short, fairly shallow medially, but deepens laterally into apodemal pits, course very gently W-shaped, gently anteriorly bowed medially, and wrapped around base of L1 laterally; LO long medially and tapered laterally, slightly narrower than base of glabella, gently dorsally inflated, with dense granulose sculpture and small but prominent median tubercle, doublure long medially, tapered laterally, lens-shaped, effaced; axial furrows narrow and deep, wider and shallower at intersections with lateral glabellar furrows, SO, and lateral branch of anterior border furrow, gently anteriorly divergent until S2, then gently convergent; palpebro-ocular ridges long, moderately wide, arcuate in shape with widest curvature posteriorly, with anterior edge defined by line of pits running dorsolaterally from intersection of axial furrow and S3, and with dense granulose sculpture; palpebro-ocular furrows narrow, moderately shallow, shallower anteriorly, gently sigmoid in course; fixigenae with moderately dense sculpture of tiny granules, and small caecal pits except near axial and posterior border furrows, interocular fixigenae long, narrow, triangular, posterior fixigenae short, wide, subrectangular, moderately ventrolaterally sloped, with gently anteriorly bowed anterior margin; posterior border furrow short, deep, incised, roughly transverse along posterior border, pointed at genal angle with short, medially directed anterior branch; posterior border short adaxially, expanded laterally to maximum length (about double) at genal angle, then strongly anteromedially tapered, with moderately thick and long, conical, gently tapered spine at genal angle, and dense granulose sculpture, doublure along posterior portions very short and rimlike, expanded rapidly to maximum length just before genal spine, then cut by facial suture at genal spine.

Rostral plate unknown.
Hypostome long, wide, with maximum width across anterior wings only slightly greater than across shoulders, width $96.2 \%$ ( $91.4-101.1 \%$ ) sagittal length; anterior suture very broad, moderately anteriorly bowed; anterior border very short medially, laterally expanded into long, wide, triangular wings with deep apodemal pits; anterior border furrow short, deep, incised; middle body very large, narrow, elongate, sub-ovoid and posteriorly tapered, with lobes ill-defined; anterior lobe sub-ovoid, strongly ventrally inflated, with dense granulose sculpture concentrated anteriorly and scattered caecal pits; middle body furrow not impressed except as narrow, deep, anterolateral branches anteriorly coincident with lateral furrows and as very slightly impressed median crescent on larger specimens (Fig. 8.1, 8.2); posterior lobe of middle body short, narrow, U- to V-shaped, effaced; lateral furrows narrow and very shallow between junctions with anterior border and middle body furrows, impressed when coincident with middle body furrows, shallow across lateral extensions of posterior lobe of middle body, then deep and slightly widened along posterolateral reaches of posterior lobe; posterior border furrow about twice as long as anterior border furrow, moderately deep; lateral and posterior borders broad and long, forming ovoid margin, gently ventrally flexed toward rims, with dense granulose sculpture; lateral notch fairly short and shallow dorsoventrally, but deeply mediolaterally impressed; posterior wing not adequately preserved; lateral doublure very wide, strongly dorsomedially raised, and posterior doublure imperfectly preserved.

Librigena overall long and wide, with width of field $43.9 \%$ (36.7-50.2\%) length along lateral border furrow and length of field $46.0 \%$ ( $42.3-49.4 \%$ ) length of border; base of visual surface arcuate, strongly elevated from librigenal field (ventrolateral views); librigenal field wide, fairly short, weakly convex, with dense sculpture of tiny granules somewhat concentrated near eye and moderately densely overlain by large caecal pits; lateral border furrow moderately short, very deep, incised, slightly curved; lateral border long and wide, about $1 / 2$ width of librigenal field and twice as long as field, moderately inflated, with broad, shallow indentation in middle of border along anterior half of librigenal field, with long, dog-legged anterior and long, straight posterior projections, and with dense granulose sculpture; anterior branch of facial suture roughly L-shaped, slightly shorter along field than along border projection; posterior branch long and sloped at about $60^{\circ}$ above horizontal along field, then short (about 3/4 length along field) and nearly transverse along border; lateral border doublure wide, with effaced and roughly crescentic inner true doublure and more inflated, granulose inner faces of anterior and posterior projections also visible, and also shown as slight triangular projection above posterior branch of facial suture in external view.

Total number of thoracic segments unknown. Thoracic segments short, broad, with axis $44.3 \%$ pleural width excluding spine, highly vaulted axially and pleurally; articulating half ring moderately short medially, semilunate and strongly laterally tapered; articulating furrow long, shallow over most of course but with large, deep apodemal pits anterolaterally, and with granulose sculpture in some specimens (Fig. 9.1); axial ring fairly short, only slightly longer and wider than articulating half ring, strongly dorsolaterally inflated, with dense granulose sculpture and pair of small tubercles straddling posterior midline; axial ring doublure long, semilunate, smooth; axial furrows wide and flared anteriorly and posteriorly, slightly constricted along posterior pleural band, moderately deep, confluent with articulating, pleural, and posterior articulating ridge furrows; inner pleurae narrow, with very steeply curved fulcrum close to distal ends; anterior pleural band very short, finely granulose, with extremely short anterior articulating ridge set off posteriorly by short, shallow furrow, and with distal tips curved dorsomedially (anterior view) into articulating device; pleural furrow moderately short, flared ventrolaterally (lateral view), moderately deep, deeper adaxially; posterior pleural band long, strongly inflated with semicircular cross-section, with long, gently tapered, strongly downturned, semi-flattened blade-like to conical spine produced from fulcrum, and with dense granulose sculpture, posterior margin of posterior pleural band forms very short articulating ridge set off from inflated band by very short, deep, incised furrow.

Pygidium of four segments each bearing long, thick spine on posterior pleurae, with medium-sized triangular terminal piece, moderately vaulted (mostly axially), moderately long and narrow with sagittal length from articulating furrow to posterior tip of terminal piece $75.9 \%$ ( $72.7-78.6 \%$ ) width across anterior pleurae; articulating half ring short, slightly narrower than first axial ring, laterally tapered, semilunate; articulating furrow short, deep (somewhat shallower medially), incised, with deep apodemal pits at lateral limits somewhat set back into anterior margin of axial ring; axis long and wide (about half maximum pygidial width), highly vaulted anteriorly and progressively less vaulted toward nearly flat terminal piece, strongly posteriorly tapered; axial rings moderately short, decrease slightly in length posteriorly, anterior rings wide, fourth ring about $3 / 4$ width of first ring, each ring independently inflated, with semicircular cross-section, and with dense sculpture of fine granules (also on terminal piece of some specimens); terminal piece subtriangular to slightly heart-shaped, long, narrow, strongly posteriorly tapered, with two pairs of indentations: one pair of small dimples close to anterior margin, and one pair of larger, more elongate impressions at about $1 / 3$ length, impressions merged or partially merged on many specimens, e.g., Fig. 10.3, 10.12, specimens of Fig. 11, and with posteromedian margin exposed; inter-ring furrows moderately long (first one longer), somewhat shallow medially, shorter and very deep laterally, producing large apodemes ventrally; axial furrows moderately wide, strongly impressed over first three segments, lightly impressed over fourth, then merged with narrow, posteriorly shallowing furrows along sides of terminal piece; only first segment with anterior and posterior pleural bands, anterior band very short, slightly longer laterally, strongly downturned at fulcrum, with slight inward curvature at tips for articulation; pleural furrow short, slightly flared laterally, deep, incised; posterior band long (3-4 times length of anterior band), narrow (about half width of first axial ring), strongly inflated, with rounded adaxial margins, and with spine produced from outer pleurae, outer pleurae strongly downturned, with ventral tips merged into rim of doublure; spine long, thick, conical, gradually tapered, mostly effaced dorsally and ventrally, but densely granulose along sides and toward tips; first interpleural furrow moderately long, slightly flared exsagittally, deep, posterolaterally directed at about $45^{\circ}$ below horizontal, with subsequent furrows shorter and more posteriorly directed, and with third furrows nearly subparallel; second through fourth posterior pleural bands like first, but more strongly posteriorly directed, and with spines lengthening to a maximum nearly equal to
the sagittal length of the pygidium on the third segment (also slightly posterodorsally upturned), then roughly half that length and almost subparallel on the fourth segment; pygidial doublure fairly short, tapered anteriorly, with rounded and slightly posteromedially peaked inner margin (anterior view; Fig. 10.10), effaced, merged with tips of pleurae to form short (lower posteriorly) raised wall with granulose exterior.

Ontogeny. Cranidia of Panisaspis millardensis (cf. Figs. 5.1 and 6.16) become wider and more vaulted overall through ontogeny. The glabella expands laterally, changing from anteriorly expanded to laterally expanded in shape, and the lateral furrows become longer, deeper, and more defined. Cranidial furrows (anterior border, axial, posterior border, palpebo-ocular, SO ) lengthen and widen. Granulose sculpture is coarser on juveniles than adults, but the fixigenal pitting is more defined on large specimens. The genal spine becomes proportionately thinner and slightly longer. The hypostome (cf. Fig. 8.1, 8.13) widens considerably through ontogeny, with the middle body becoming narrower relative to the lateral border. The middle body becomes less granulose, with finer granules remaining concentrated anteriorly, and the pits increase in size and visibility. The lateral branches of the middle body furrow deepen. The lateral and posterior borders increase in width and length, their granulose sculpture remains dense but grows finer, and the margin becomes smoother as the very tiny spines at the shoulders and posterolateral corners fade away. The librigena (cf. Figs. $6.3,7.16$ ) changes only subtly in the specimens available for study. The librigenal field increases slightly in height and overall area, and its pitting deepens slightly. The lateral border furrow is somewhat wider and deeper in larger specimens. The lateral border widens and inflates slightly, and the anterior curve (along the outer rim of the anterior projection and on toward the main part of the border) steepens. Not enough information is known about the thoracic segments to discuss their ontogenetic changes. Pygidial changes (cf. Figs. 10.1, 11.4) are also fairly subtle. The axis becomes broader, with more inflated rings and longer inter-ring furrows; the axial furrows widen; the terminal piece increases in size (length and width) and its indentations increase in complexity (one pair versus two); the degree of spinal splay increases; the spines lengthen compared to the sagittal length of the pygidium; and the ends of the third and fourth spines develop coarse granules.

Discussion. The pairs of terminal piece indentations (e.g., Fig. 10.14) may represent poorly developed interring furrows for unexpressed fifth and sixth axial rings that have been subsumed into the terminal piece. The right L1 of the cranidium of Fig. 5.2 is deformed; it is smaller than the left L1 and S 1 is longer on that side in compensation.

Panisaspis millardensis is most similar to its sister taxon, P. sevierensis, and they are compared in the differential description of the latter species. It is also compared to $P$. rancherensis in the discussion section of the latter. Panisaspis millardensis differs substantially from $P$. deltaensis, the next most similar species. The cranidium of $P$. deltaensis is not as well known, but its frontal lobe is smaller, L1 is bigger relative to the other lobes, the fixigenae are slightly narrower and longer, and the genal spine is much wider at the base. Panisaspis deltaensis has a long, narrow, rectangular plesiomorphic hypostome, with a narrow lateral border and small spines along the borders. Its librigena is wider and more elongate than that of $P$. millardensis, without a pronounced curve near the anterior projection. Pygidia of $P$. millardensis are narrower and longer than those of P. deltaensis, with a larger, more strongly and complexly impressed terminal piece; much shorter third spines and somewhat longer fourth spines (relative to each other and to pygidial length); and possess coarse granules near the ends of the third and fourth spines.

## Panisaspis sevierensis n. sp.

Figs. 12-16
2009 Pliomeridae gen. nov. sp. nov. A; Adrain et al., p. 570, fig. 16Q.
Material. Holotype, pygidium, SUI 125681, from Section H 163.3 m and assigned specimens SUI 115310, 125649-125680, 125682-125695, from Section H 163.3-182.6 m, Fillmore Formation (Tulean; Psalikilus pikum Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

Etymology. From Sevier Lake, which lies to the east of the Ibex area.
Diagnosis. Librigena with very long posterior projection of lateral border; third pair of pygidial spines long and very widely splayed; terminal piece with single pair of indentations at about $1 / 3$ length.

Description. Panisaspis sevierensis is morphologically similar enough to P. millardensis that it is treated via extended comparison. Ratios are given to aid comparison with other members of the genus.

Cranidia of $P$. sevierensis are extremely similar to those of $P$. millardensis. They differ mainly in having a slightly shorter and wider glabella, with width $97.5 \%$ ( $89.7-101.1 \%$ ) length, slightly larger L1 relative to other lateral lobes, and possibly slightly larger palpebral lobes (cf. Figs. 6.1 and 6.2 with 12.3), although that comparison cannot be made with exactly equally sized specimens. The cranidial length/width ratio for $P$. sevierensis is $44.6 \%$, based on the specimen of Fig. 12.10.

Hypostomes of $P$. sevierensis and $P$. millardensis are also very similar, but those of $P$. sevierensis are narrower (width $89.4 \%$ ( $87.1-91.0 \%$ ) length), with narrower and less pronounced shoulders, narrower borders, and fewer pits on the middle body.

Librigenae of $P$. sevierensis are somewhat more elongate, with a slightly shorter field [width $43.6 \%$ (40.8$48.5 \%$ ) length along lateral border furrow and length of field $42.1 \%(40.5-43.1 \%)$ length of lateral border], with a longer posterior branch of the facial suture (measured along the lateral border), a slightly narrower lateral border with a larger amount of doublure visible externally, slightly smaller granulose sculpture on the border, and a much less pitted librigenal field.

Panisaspis sevierensis segments are not well known, but they are slightly more finely granulose than those of P. millardensis, and possibly have more small tubercles on the axis (cf. Figs. 9.1 with 13.26 ; two tubercles on a complete axial ring vs. three on a partially missing ring).

Pygidia of $P$. sevierensis are wider (length $71.9 \%$ (67.0-76.5\%) width, using same measuring points) than those of $P$. millardensis, with a slightly narrower axis, slightly narrower and shallower axial furrows, wider pleurae, much longer and thicker third pleural spines which are also more strongly posterodorsally upturned, slightly thicker and more conical spines overall, a smaller terminal piece with only one pair of indentations at about $1 / 3$ length and a more widely exposed posterior margin, more effaced sculpture overall, and a shorter, wider merged pleural wall.

Ontogeny. Panisaspis sevierensis cranidia are less well known, but ontogenetic changes seem to closely resemble those of $P$. millardensis. The smallest cranidium (Fig. 12.19) is narrower across the fixigenae, with a shorter, broader genal spine than the larger cranidia. The most complete cranidium (Fig. 12.10), compared to the largest cranidia (Figs. 12.1, 12.3, 12.16; cranidia of Fig. 13) has a shorter anterior border; slightly narrower and less laterally convex glabella; and narrower LO; and the sculpture overall is coarser. Hypostomal and thoracic changes cannot be assessed with the material available. Librigenae (cf. Fig. 14.3, 14.4) increase in the length and height of the librigenal field, and the curve underneath and posterior from the anterior projection of the lateral border increases in steepness. The pygidium (cf. Fig. 15.1, 15.14, 16.3) elongates slightly compared to its width; the interrings furrows lengthen considerably; the axial furrows widen; the spines splay further away from each other and taper more rapidly; and the sculpture decreases in coarseness.

Discussion. Cranidia of Panisaspis sevierensis differ subtly from those of P. deltaensis. The anterior border is slightly narrower; L1 is slightly smaller relative to the other lateral glabellar lobes and less rounded in outline; the lateral fixigenae are shorter; and the genal spine is narrower. Hypostomes of P. sevierensis are ovoid and possess rounded borders, unlike the sub-rectangular and spinose-bordered hypostome of $P$. deltaensis. The pygidium of $P$. sevierensis can be distinguished by its more widely splayed spines, particularly the third pair; longer fourth pair of spines; and distinct pair of indentations at about $1 / 3$ length of the terminal piece. Panisaspis sevierensis is compared with $P$. rancherensis in the discussion section of the latter.

## Panisaspis deltaensis n. sp.

Figs. 17-19

2009 Pliomeridae gen. nov. sp. nov 4; Adrain et al., p. 567, fig. 15AA, GG.
Material. Holotype, pygidium, SUI 125706, from Section H 127.1 m, and assigned specimens SUI 115289, 115290, 125696-125701, 125707-125713, from section H 93.4 m and 127.1 m , Fillmore Formation (Tulean; Heckethornia bowiei Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

Etymology. From the town of Delta, Utah.
Diagnosis. Base of genal spine very broad; terminal piece large, but narrower and more elongate than in other species; third pygidial spine very long and stout compared to other spines; third pygidial spine recurved medially at tips; fourth spine very short.

Description. Cranidium short, narrow anteriorly and wide posteriorly, with sagittal length $47.1 \%$ width across genal angle, strongly vaulted; anterior border strongly anteriorly bowed, somewhat long and narrow, highly inflated, granulose; anterior border furrow very short, slightly longer medially, deep, incised, with narrow lateral branches anterior from palpebro-ocular ridges; glabella nearly equally long as wide, with maximum width across S2 99.8\% (92.0-105.5\%) sagittal length, moderately vaulted, densely granulose, with distinct lateral lobes and furrows; L1 about $25 \%$ smaller than L2 and L3, ovoid, L2 and L3 similar, sub-rectangular, LF large, wide, long, wedge-shaped; S1-S3 all short, deep, incised, posteromedially directed at about $30^{\circ}$ above horizontal, S 1 with slightly lengthened and deepened inner end; axial furrows narrow, deep, gently laterally bowed, convergent with other cranidial furrows; SO fairly short, moderately deep medially, very deep laterally in apodemal pits; LO slightly narrower than glabella across L1, long medially and slightly tapered laterally, with very slightly anterolaterally curved ends, granulose, with small median tubercle; posterior border furrow short, deep, incised, with posterior course sub-transverse, then gentle $90^{\circ}$ curve at genal angle; posterior border short near axial furrows, flared outward to maximum length and width at genal angle, then strongly anteriorly tapered, with dense sculpture of tiny granules and moderately long, very thick, gradually tapered and blunt genal spine projecting at just past parallel; posterior fixigenae short (about half glabellar length), wide, subrectangular, interocular fixigenae short, narrow, subtriangular, fixigenae with very tiny dense granules and densely spaced small pits except along edges of axial and posterior border furrows; palpebro-ocular furrow sigmoidal, narrow, deeply incised over most of course but totally effaced near glabella; palpebo-ocular ridge not well known, extends from S3 to just short of S1, strongly angled dorsolaterally from cranidium, granulose.

Rostral plate unknown.
Hypostome long and narrow; anterior border not well known, short, flared laterally into small, approximately equilaterally triangular wings with small, deep wing process pits; anterior border furrow moderately anteriorly bowed, very short, shallow, and separated from lateral border furrow (where confluent with middle body furrow) by short effaced section; middle body ellipsoid, long, narrow, with maximum width even with lateral notch, posteriorly tapered, strongly ventrally convex anteriorly, decreasing posteriorly, with ill-defined lobes (anterior long and ovoid; posterior about $1 / 3$ length of anterior and U-shaped, with lateral sections interrupting meeting of posterior border and lateral border furrows), and with dense granules slightly coarser than those of the borders concentrated anteriorly on anterior lobe; middle body furrow narrow, deep, strongly impressed laterally where overlapped with lateral border furrows, posteriorly convergent, almost totally effaced in curved medial section; lateral border narrowest at lateral notch, expanded posterolaterally to maximum at posterolateral corners, moderately downturned, with dense granulose sculpture and rounded angles at shoulders, posterolateral corners, and slightly posteromedially from corners; posterior border furrow shallow, moderately long, somewhat indistinct ventrally (better visible in Fig. 17.21), highly posteriorly curved; posterior border about as long as widest point of lateral border, somewhat downturned, with sculpture like that of lateral border; lateral notch long and shallow, with tall, smooth doublure; other hypostomal doublure not well known.

Librigena roughly triangular in outline, wide, moderately long, with small ellipsoid eye; anterior branch of facial suture short and very steep along field, almost flat and about equal in length along anterior projection of lateral border; posterior branch of facial suture long and posteriorly sloped at about $45^{\circ}$ along field, then gently upturned along short segment of border; librigenal field fairly short and long, with width at midpoint of eye $43.3 \%$ $(43.2,43.3 \%)$ length along lateral border furrow, gently convex, with steep break in slope from ocular surface to field, and with very dense sculpture of tiny granules and small, irregularly shaped pits; lateral border furrow very narrow, deep, incised; lateral border long, wide, widest slightly behind anterior edge of field, shallowly curved, highly inflated, with dense granulose sculpture; border doublure wide, reaching about $2 / 3$ to furrow, with curved margin, smooth, slightly projected above posterior end of border in triangular shape.

Thorax unknown.
Pygidium shorter than broad (axial length from articulating furrow $62.7 \%$ (61.5-63.7\%) width across anterior pleural band), roughly subtriangular in shape, strongly vaulted axially and moderately vaulted pleurally, made of four segments, each with large spine, and large triangular terminal piece; articulating half ring very short and broad; articulating furrow long, deep, deepest in lateral apodemal pits; axis broad anteriorly, strongly tapered posteriorly to very narrow tip of terminal piece, strongly convex anteriorly decreasing to nearly flat terminal piece, with strongly independently inflated axial rings, rings short medially, slightly expanded laterally, densely granulose, with width decreasing posteriorly such that fourth ring is a little more than half width of first; inter-ring furrows
long medially, abruptly tapered laterally to short slits over apodemal pits, deep; axial furrows moderately narrow and shallow, not well impressed over fourth segment, then well impressed along terminal piece, strongly posteriorly convergent but slightly posteromedially directed over fourth segment; terminal piece triangular, longer than wide, strongly posteriorly tapered, with pair of short indentations leading from last ring furrow, and with narrow but exposed posterior point; pleurae narrow, with inner pleurae narrower than outer, with moderately steep fulcral angle (anterior view) and outer pleurae merged ventrally into short, narrow wall structure; only first segment with anterior and posterior pleural bands, anterior band short and wide, gently backturned; pleural furrow short, very slightly ventrolaterally expanded, deep, incised; posterior pleural bands long, slightly expanded laterally into base of spine, highly inflated, granulose, with spines projecting ventro-posterolaterally from tips; spines thick, rapidly tapered, conical, with third pair very thick and long (about twice saggital length of pygidium), and gently upturned toward tips, and with short fourth pair; interpleural furrows long, moderately deep, increasingly posteriorly directed, with third furrows subparallel; doublure triangular, longest posteromedially and tapered anteriorly (anterior view), smooth, connected to short, externally granulose wall made of outer pleurae.

Ontogeny. Cranidial material of $P$. deltaensis is not well represented, but it is possible to see that the glabella becomes relatively wider and more convexly sided through growth, and the cranidial furrows become longer or wider and deeper. Hypostomes, librigenae, and thoracic segments are not sufficiently known for discussion. Pygidia of $P$. deltaensis slightly increase in width; all furrows lengthen or widen and deepen; the third spine pair becomes much wider and more widely splayed; and the terminal piece indentations become more prominent.

Discussion. Panisaspis deltaensis is compared with P. millardensis, P. sevierensis, and P. rancherensis in the discussion sections of those species. One cranidium (Fig. 17.2) lacks the left L1.

## Panisaspis rancherensis n. sp.

Figs. 20-21

2009 Pliomeridae gen. nov. sp. nov. B; Adrain et al., p. 570.
Material. Holotype, cranidium, SUI 125714, from Section H 172.5 T m and assigned specimens SUI 125715125730 from Section H 172.5 m , 172.5 T m, and 173.2 m , Fillmore Formation (Tulean; Psalikilus pikum Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

Etymology. From The Rancher, a cafe and motel in Delta, Utah.
Diagnosis. L1 very small compared to other glabellar lobes; librigena narrow; pygidium narrow, with spines narrowly separated; dense sculpture of coarse granules all over pygidium.

Description. Cranidium short, narrow across glabella and very wide across posterior border (ratio not given due to breakage), highly vaulted across fixigenae (tr.), with gently vaulted (sag., tr.) glabella, and with dense sculpture of small granules and sparser small tubercles on all dorsal surfaces, with palpebro-ocular ridges, LO, and posterior border slightly effaced; anterior border moderately long, inflated, with arch-shaped cross section, broad, with gently curved anterior margin and short lateral limbs along anterior edge of palpebro-ocular ridges; anterior border furrow very short, slightly longer medially, deep, incised, gently anteriorly arched, with narrow roughly transverse lateral branches in front of palpebro-ocular ridges; palpebro-ocular ridges arc- to sigmoidally shaped, extend from S3 to approximately even with mid-L2, dorsolaterally extended; palpebro-ocular furrow very short, deep, but shallower adaxially, incised, gently sigmoidal; interocular fixigenae moderately narrow, triangular, posterior and lateral fixigenae moderately wide, short, rectangular, steeply ventrolaterally sloped; posterior border furrow short, deep, incised, sub-transverse until broadly rounded genal angle, then nearly perpendicular to slightly anteriorly convergent; posterior border slightly shorter than anterior border on average, shortest adaxially, flared to maximum length at genal angle, then strongly tapered anteriorly; axial furrows narrow, very deep, deepest in apodemal pits slightly anterolateral from S3, very gently laterally bowed, convergent with all other cranidial furrows; glabella long, moderately narrow, with maximum width across L2 or L3 (in larger specimens, e.g., Fig. 20.1, 20.19) 95.2\% (92.9\%$96.5 \%$ ) sagittal length, moderately vaulted, with distinct lateral lobes; L1 small, sub-ovoid, L2 slightly smaller than L3, both sub-rectangular, LF very large, wide, nearly semi-circular; lateral glabellar furrows short, deep, incised, reach not quite $1 / 3$ across glabella, S 2 and S 3 similar, about $30^{\circ}$ above horizontal, S 1 slightly steeper and lengthened at inner end; SO moderately short, deep, shallower medially and very deep in lateral apodemal pits, conver-
gent with axial and posterior border furrows; LO slightly longer than anterior border, slightly narrower than maximum glabellar width, sub-rectangular, with small but distinct median tubercle.

Rostral plate unknown.
Hypostome long, moderately wide, sub-ovoid, with width across shoulders $93.1 \%$ ( $88.8,97.4 \%$ ) sagittal length; hypostomal suture broadly anteriorly arched, slightly steeper along wings; anterior border vanishingly short medially, flared laterally into small subrectangular wings with large, deep wing process pits; anterior border furrow strongly anteriorly bowed, extremely short medially, slightly longer laterally, convergent with lateral branches middle body furrow and likewise lateral border furrow; middle body long, narrow, sub-ovoid, strongly ventrally convex at anterior, but deflated to nearly flat posteriorly, with large, egg-shaped anterior lobe and short, U- or V-shaped posterior lobe with lateral segments interrupting lateral border furrow, lobes densely granulose with pits on anterior lobe, except median middle body effaced on larger specimen; middle body furrow short, shallow, strongly Ushaped medially, with incised anterolateral branches (equivalent to anterior branches of lateral border furrow); lateral border furrow along posterior lobe of middle body moderately wide and deep, strongly posteriorly convergent; lateral border wide, gently downturned, densely granulose, with rounded margin; posterior border furrow short, shallow, indistinct; posterior border long, also with rounded margin; lateral notch short and deep, with tall, smooth doublure; posterior wing small, short, triangular.

Librigena narrow and wide, subtriangular, with short, very steep anterior branch of facial suture along field, then long and nearly horizontal along anterior projection of lateral border; posterior branch of suture long and sloped about $45^{\circ}$ along field, then short along border; librigenal field roughly $30-60-90^{\circ}$ triangular, with dense granulose sculpture overlaid by dense tubercles and scattered small pits concentrated posteriorly (seen as raised impressions ventrally); lateral border furrow narrow, long, deep, slightly convex toward border; lateral border wide, tapered posteriorly, strongly inflated, with long, subrectangular anterior projection, densely tuberculate with sculpture slightly coarser than that of field; border doublure wide, reaches about halfway to furrow, smooth, slightly projected above posterior tip, and abruptly terminated just anterior from anterior branch of facial suture.

Thorax unknown.
Pygidium of four segments, each with long spine, and triangular terminal piece, triangular in shape (excluding spines), with sagittal length from articulating furrow to tip of terminal piece $71.6 \%$ (67.6-76.3\%) width measured across anterior pleural band of first segment, strongly vaulted axially and pleurally, with dense sculpture of small tubercles dorsally, and smaller granules ventrally (also visible along edges of pleural spines); articulating half ring wide but slightly narrower than first ring, short, slightly laterally tapered; articulating furrow nearly twice length of ring medially, tapered laterally, deep, deepest in lateral apodemal pits; axis wide anteriorly and strongly tapered posteriorly, strongly convex anteriorly and nearly flat across terminal piece; axial rings independently inflated, short, wide, with rounded margins, fourth ring slightly greater than half width of first ring; inter-ring furrows short (shorter posteriorly), wide, deep; terminal piece large, nearly equilaterally triangular, with pair of indentations in anterior margin and with posterior tip very nearly enclosed; axial furrows narrow deep, incised along first two or three segments (varies with size of pygidium), then shallow over third and/or fourth, with very narrow, wellimpressed furrow along sides of terminal piece; first segment only with both anterior and posterior pleural bands; inner pleurae very narrow, with steep fulcral angle; outer pleurae slightly wider, merged ventrolaterally into short wall (Figs. 21.19, 21.21); anterior band very short, slightly flared ventrolaterally, strongly backturned; posterior pleural band (applies to all segments) long, merged into long, thick, conical spine with blunt tip; pleurae and therefore spines increasingly swept backward such that fourth spines are subparallel or gently convergent, spines of lengths such that the tips form points on an even arc; doublure fairly tall (Fig. 21.24), with strong posteromedian peak and rapid anterolateral taper, smooth.

Ontogeny. Cranidia of $P$. rancherensis are too similar in size to preserve ontogenetic information. The number of hypostomal and librigenal specimens, and the lack of thoracic material prohibits their discussion. The pygidium broadens; the spines become slightly more separated from each other; the terminal piece enlarges and develops a pair of indentations; and the sculpture increases in density, but decreases slightly in coarseness.

Discussion. Panisaspis rancherensis possesses an interesting mix of plesiomorphic and derived features that necessitate comparison with all other species of Panisaspis. Compared to P. millardensis, P. sevierensis, and P. deltaensis, $P$. rancherensis cranidia are overall narrower; have much coarser sculpture; the glabella is relatively shorter and has a very small L1, even compared to the reduced L1 of the derived taxa; and the occipital tubercle is not as prominent. The librigenae are much narrower, with a longer, more wedge-shaped field, and lack the deep
pits on the field, the sharp anterior curve of the lateral border, and the long posterior projection common to the aforementioned taxa. The hypostome of $P$. rancherensis is of the derived, ovoid, smooth-bordered style shared by P. millardensis and P. sevierensis; P. deltaensis retains the plesiomorphic sub-rectangular hypostome with border spines. That of $P$. rancherensis is very similar to $P$. sevierensis, but is slightly narrower and more finely granulose. Pygidia of $P$. rancherensis are plesiomorphic. They lack the splayed spines, elongate third spine pair, and exposed terminal piece shared by the three derived taxa, and also possess much coarser tuberculate sculpture. Some of these differences, such as the plesiomorphic librigenae and pygidium, may be attributable to paedomorphosis, but more investigation of ontogenetic series would be required to examine this idea.

The group of plesiomorphic species ( $P$. loganensis, $P$. quattuor, and $P$. topscityensis) resemble $P$. rancherensis in possessing librigenae with narrower, more elongate fields, a smoothly arcuate lateral border; and a short posterior projection of the border. The cranidium of $P$. topscityensis resembles that of $P$. rancherensis in its long, densely granulose anterior border; slightly larger (of the three plesiomorphic taxa) frontal lobe; and anteriorly rounded glabella. The cranidia of $P$. quattuor and $P$. loganensis have short, medially pointed anterior borders; a strongly tapered glabella; and wide interocular fixigenae. The rounded, sub-ovoid hypostome of Panisaspis rancherensis is unique; the other three taxa under consideration possess the plesiomorphic morphology of a spinose, sub-rectangular border. The pygidium of $P$. loganensis resembles that of $P$. rancherensis in its short, narrow shape with short, subparallel spines; small terminal piece; and sparse, coarse sculpture. However, as discussed above, these similarities may be due to paedomorphosis. It differs in having sparser sculpture, slightly shorter spines compared to the sagittal length, and a relatively narrower axis. The pygidia of $P$. quattuor and $P$. topscityensis are both wider and more elongate than that of $P$. rancherensis, with relatively narrower axes, longer spines, and much finer sculpture. That of $P$. quattuor is nearly dorsally effaced, and possesses a slight differentiation in the lengths of the third and fourth pairs of spines. That of $P$. topscityensis has widely splayed spines, and the third pair is very long compared to the fourth pair.

The pygidium of Fig. 21.28 has slightly different morphology and may be assignable to Panisaspis sp. 3 Compared to the similarly sized pygidium of Fig. 21.15 , its pleural spines are much more splayed; the sculpture is coarser; and the terminal piece is smaller.

## Panisaspis topscityensis n. sp.

Figs. 22-24
? 1973 Hintzeia sp. zone G2; Demeter, pl. 3, fig. 15.
2009 Pliomeridae gen. nov. sp. nov. 2; Adrain et al., p. 563, fig. 13BB.
Material. Holotype, pygidium, SUI 115253, and assigned specimens SUI 125731-125744 from Section G 210.2 m, Fillmore Formation (Tulean; Protopliomerella contracta Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

Etymology. After Top's City Cafe in Delta, Utah, where we have eaten many breakfasts during Ibex fieldwork.

Diagnosis. Hypostome with wide and very long border; with two pairs of elongate small spines at posterolateral corners; posterior border medially pointed; librigenal border very curvy (convex outward), with large triangle of doublure visible externally over inner edge of posterior projection; large pygidia nearly effaced except for thick rim of granules near furrows and edges of spines; third pair of pygidial spines longer than fourth pair by (approximately) "inseam" measurement of fourth pair.

Description. Cranidium short, narrow anteriorly and broad posteriorly, highly vaulted by strongly downturned fixigenae; anterior border moderately short, fairly wide, inflated and anteriorly curved such that doublure is expressed as anterior face and only a rim ventrally, strongly anteriorly arched with narrow lateral sections in front of palpebro-ocular ridges, with dense granulose sculpture; anterior border furrow short, slightly longer medially, fairly shallow except along lateral segments, with deep apodemal pits near S3; palpebro-ocular ridges long, dorsolaterally raised, with steeply sloped anterior face, finely and densely granulose, with small pits on anterior face distinguishing very narrow granulose ridge (anterior view); palpebro-ocular furrow not well known, narrow, deep, incised; inner fixigenae long, narrow, finely granulose with densely spaced small pits except along axial and posterior border furrows; outer fixigenae not well known, with sculpture like inner fixigenae, strongly downturned; pos-
terior border furrow short, deep, incised, transverse along most of posterior border, but strongly anteriorly curved at genal angle; posterior border short adaxially, lengthened laterally to maximum at genal angle, then abruptly anterolaterally tapered to a point, with dense tiny granules and small spine at genal angle, doublure short adaxially, expanded laterally to maximum just adaxial from genal angle, with broad, shallow scoop as facial suture cuts genal angle; axial furrows subparallel, narrow, wider at lateral glabellar furrows and along LO, deep, convergent with all other cranidial furrows except palpebro-ocular; LO moderately long medially, gently tapered laterally, slightly narrower than maximum glabellar width, with sculpture of granules overlain by small tubercles, doublure reaches about halfway to SO, slightly tapered laterally, smooth; SO somewhat long and shallow medially, short, deep, and incised laterally, particularly in apodemal pits; glabella sub-ovoid, with maximum width across L2 104.7\% sagittal length, shallowly inflated, with distinct lateral lobes, and with very dense sculpture of small granules; L1 smallest, shorter and slightly narrower but nearly same size as L2 and L3, sub-ovoid; L2 and L3 similar, short, sub-rectangular, about $1 / 3$ total glabellar width; LF large, wedge shaped, long medially and strongly tapered laterally; lateral glabellar furrows all similar, short, deep, incised, about $30^{\circ}$ above horizontal, with S 3 slightly shallower, and S1 with elongated inner end.

Rostral plate unknown.
Hypostome long and wide, with width across wings $81.7 \%$ (78.2-85.2\%) sagittal length; hypostomal suture broad, nearly flat medially, then gradually posteriorly sloped along wings, with small flat section along apodemal pits; anterior border extremely short medially, rapidly expanded laterally into tall, strongly dorsolaterally raised, large, approximately $30-60-90^{\circ}$ triangular wings with very deep apodemal pits; anterior border furrow short, deep medially, effaced laterally with only slight connection to overlap of lateral and middle body furrows; middle body long, narrow, posteriorly tapered, with very large ovoid anterior lobe and short, small, U-shaped posterior lobe, strongly ventrally convex, with convexity highest even with lateral notch and gradually decreasing anteriorly and posteriorly, densely granulose, with larger granules anteriorly and with tiny granules toward and on posterior lobe, also with irregularly spaced small pits on anterior lobe; middle body furrow very narrow and deep anterolaterally, with anteriormost segment confluent with lateral furrows (then separated by anterolateral branch of posterior lobe of middle body), and with median segment strongly posteriorly curved and nearly effaced; lateral border furrows narrow, deeply incised, strongly anteriorly divergent, disconnected by posterior lobe of middle body; posterior border furrow very shallow and indistinct; lateral border very narrow anteriorly at junction with wings, then strongly expanded posterolaterally, moderately downturned, with broad nubby angle at shoulders, two pairs of medium sized spines at posterolateral corners, and very dense granulose sculpture; posterior border long, wide, formed into very broad median point; doublure wide along lateral notch, narrower and shorter posteriorly, strongly upturned, with long lateral notch and small triangular posterior wings.

Librigena long and narrow, subtriangular, with width of field approximately $33.1 \%$ length along lateral border furrow and length of field $50.3 \%$ length of border; anterior branch of facial suture very short and subvertical along librigenal field, then long and subhorizontal along lateral border; posterior branch of suture long and moderately sloped along field, with small change in slope about midway to border, shorter (about half length) and slightly upturned along border; ocular surface poorly known, strongly raised above field with abrupt break in slope at base of eye; librigenal field of low convexity, long, narrow, subtriangular, densely granulose (moreso on smaller specimens), with many evenly spaced, irregularly shaped small pits; lateral border furrow moderately wide, slightly tapered posteriorly, deep, gently laterally bowed; lateral border long, with anterior projection of almost $1 / 3$ total length and posterior projection slightly shorter, wide, almost width of librigenal field, with maximum width just before anterior projection, strongly inflated anteriorly, less so posteriorly, with outer margin gently convex over most of length, but flattened abruptly along outer half of anterior projection, and with very dense granulose sculpture; doublure wide, slightly over half total width of border, smooth, with inner side visible as small triangle above posterior tip of border in external view, does not extend along anterior projection.

Thorax unknown.
Pygidium of four segments each with long spines and terminal piece, strongly vaulted axially and pleurally, roughly triangular, with sagittal length of axis from articulating furrow $68.4 \%$ ( $66.1-70.1 \%$ ) width across anterior pleural band; articulating half ring very short and wide, slightly longer medially; articulating furrow long, deep, slightly tapered laterally into apodemal pits; axis moderately long, wide anteriorly and strongly tapered, triangular, highly vaulted anteriorly with vaulting progressively decreased to almost none across terminal piece; first axial ring wide, about twice length of articulating half ring, slightly shorter medially on larger specimens, strongly inde-
pendently inflated, with rounded lateral edges, and with small granules lining edges, subsequent rings slightly shorter and increasingly narrower, with fourth ring about half width of first; first inter-ring furrow long medially and tapered somewhat laterally, deep, second furrow also longer medially, subsequent furrows shorter; terminal piece about as long as last two rings, narrow, triangular, with granulose sculpture concentrated anteriorly, and with posterior point separated from pygidial margin by depression of posterior junction of axial furrows; axial furrows moderately narrow, deep, well impressed over all segments and along terminal piece; inner pleurae very narrow and increasingly so posteriorly, with steep fulcral angle (about $30^{\circ}$ from vertical; Fig. 24.8), outer pleurae slightly wider, merged into short, granulose ventral wall; first segment only with anterior and posterior pleural bands, anterior band very short, slightly flared and anteriorly directed at tips; pleural furrow short, slightly expanded ventrolaterally, deep; posterior pleural bands strongly inflated, with rounded inner margin, merged into long, somewhat laterally flattened conical spines; spines strongly posteriorly directed, with fourth pair subparallel to convergent, moderately splayed, longest on third segment and shortest (about half length of third) on fourth, very droopy with slightly upturned tips, and with margins of pleurae and spines granulose and central areas effaced; interpleural furrows moderately long (first longest), strongly backturned, deep; pygidial doublure V-shaped or triangular, longest posteromedially and tapered anterolaterally (Fig. 24.8), smooth.

Ontogeny. Cranidia are not known from enough specimens to discuss. Librigenal changes include elongation and anterior widening of the lateral border, development of the curve near the anterior projection, and refinement of the granulose sculpture; the field narrows and elongates, the pits increase in size, and the granules fade away. The hypostome increases in width overall, particularly along the posterior and lateral borders, the middle body also elongates, widens, and inflates more, the middle body granules are reduced except anteriorly, and the posterior border develops the median point. Pygidial changes are striking and well represented. The pygidial spines spread out slightly, elongate relative to the sagittal pygidial length, develop a stronger taper, and become dorsally effaced; the fourth pair of spines increases in length and the third pair dramatically increases in length; the axis widens and inflates, while the rings shorten medially and the inter-ring furrows lengthen, and the small tubercles of small specimens shrink to granules; the axial furrows widen; and the interpleural furrows lengthen.

Discussion. Panisaspis topscityensis most closely resembles P. quattuor, although some aspects of their morphology are very different. Cranidia of $P$. topscityensis are not well preserved, but they clearly possess a longer and more inflated anterior border; a laterally convex glabella; a smaller L1 relative to the other lateral lobes; a tuberculate LO ; a longer, wider genal angle with a larger spine; and they retain dense granulose sculpture on the glabella and fixigenae even at a large size. The best match for hypostomal comparison are those of Figs. 23.10 and 26.11. The hypostome of P. topscityensis is longer and wider; has larger wings; shallower middle body and lateral border furrows; larger and more evenly distributed tubercles on the anterior lobe of the middle body; larger pits on the anterior lobe; much larger posterolateral corner spines; and a longer, more medially pointed posterior border. Additionally, although exact size comparison is lacking, it seems that the anterior border is shorter and the posterolateral corner spines are longer at larger sizes in P. topscityensis. Librigenae (cf. Figs. 22.10; 26.12, 29.7 and alternate views) are highly similar, but those of $P$. topscityensis have a shorter librigenal field near the eye; slightly narrower field overall; wider and curvier lateral border; longer posterior projection of the border; and less downturned anterior projection of the border. No segments of $P$. topscityensis are known for comparison. Pygidia of the two species are also similar, but those of $P$. topscityensis are wider; with more splayed spines; longer spines compared to sagittal length; a slightly narrower axis; shorter axial rings; a shorter and narrower terminal piece with a posterior furrow and no indentations; longer third spine pair compared to fourth spine pair (at tips); longer fourth spine pair; and denser, coarser granulose sculpture, particularly on the axis. Comparison with Panisaspis rancherensis and $P$. loganensis was made in the discussion sections of those species.

Demeter (1973, pl. 3, fig. 15) illustrated a single cranidium from Mesa $1027^{\prime}(\approx \mathrm{G} 219.6 \mathrm{~m})$ as "Hintzeia sp. zone G2". This specimen appears to belong to $P$. topscityensis, and may indicate an upward extension of its range.

## Panisaspis quattuor (Hintze, 1953)

Figs. 25-32
1953 Protopliomerops ? quattuor Hintze, p. 209, pl. 21, figs. 9, 12-14 [only; pl. 21, fig. $10=$ Ibexaspis n. sp.; pl. 21, fig. 11 = Ibexaspis brevis (Young, 1973)].
1973 Protopliomerops quattuor Hintze; Demeter, p. 53, pl. 3, fig 6 (only; fig. $1=$ Ibexaspis n. sp.).
? 1973 Protopliomerops aff. P. quattuor Hintze; Demeter, p. 53, pl. 3, fig. 7 (only; fig. $2=$ unknown pliomerid sp.).
? 1973 Hintzeia cf. H. insolita (Poulsen, 1927); Demeter, pl. 4, fig. 10 (only).
1985 Protopliomerops quattuor Hintze; Jell, p. 74, 80.
1985 Ibexaspis quattuor (Hintze); Přibyl et al., p. 119.
1989 Protopliomerops? quattuor Hintze; Dean, p. 13.
2009 Pliomeridae gen. nov. quattuor (Hintze, 1953); Adrain et al., pp. 559, 561, figs. 10U, Y, 11J, L.
Material. Assigned specimens SUI 115193, 115194, 115219, 115220, 125745-125815 from Section G 155.6 m, 162 T m, and 174.0 m, Fillmore Formation (Tulean; Psalikilopsis cuspidicauda Zone and Psalikilus typicum Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

Diagnosis. Glabella and occipital node effaced on large cranidia; hypostome with two pairs of small but distinct spines at posterolateral corners; axial rings of thoracic segments effaced and pleurae exceedingly finely granulose; pygidium effaced dorsally except for thin rim of granules around furrows; third pair of pygidial spines only slightly longer than fourth when compared at tips.

Description. Cranidium short, narrow anteriorly and very broad posteriorly, somewhat triangular in outline, with sagittal length $51.1 \%$ ( $44.0-55.7 \%$ ) maximum width measured across posterior border at genal angle, highly vaulted (tr.) abaxially, nearly flat (tr.) adaxially (anterior view); anterior border short, narrow but slightly wider than glabella, moderately anteriorly curved in course, with slight median point, moderately inflated and anteroventrally curved such that doublure is mainly expressed as anterior face of border (longer medially) and only a rim ventrally, with inverted-U-shaped cross-section, and with dense granulose sculpture dorsally (reduced anteriorly); anterior border furrow very short, deep, incised, anteriorly bowed medially, with narrow (tr.) anterolaterally directed lateral branches separating anterior border and palpebro-ocular ridges, and with deep apodemal pits at junction with axial furrows producing very large apodemes ventrally; palpebro-ocular ridges arcuate, much longer and wider anteriorly, strongly tapered posteriorly, strongly anteriorly downturned from maximum point of curvature roughly even with mid-L3, with line of small pits (shallow furrow in some specimens) extending slightly posterolaterally from junction of posterior border and glabellar furrows (anterior and oblique views; more prominent in larger specimens), and with fine granulose sculpture; palpebro-ocular furrows sigmoid in course, short and narrow, shallow at anteromedial and posterolateral tips, otherwise deeply incised; fixigenae wedge shaped, with inner fixigenae narrow and long, about $3 / 4$ glabellar length, outer fixigenae short, wide, and steeply ventrolaterally sloped, fixigenae with dense sculpture of small pits and sparse granules, dorsally effaced near glabellar, palpebroocular, and posterior border furrows, but with granules lining furrow margins; posterior border furrow short adaxially, longer abaxially, tapered anterolaterally, deep, course horizontal adaxially and strongly anterolaterally curved abaxially; posterior border wide, short adaxially, flared abaxially and slightly posteriorly to maximum length at genal angle, then strongly tapered anteriorly, moderately inflated, with very small, nubby spine at genal angle and overall extremely fine and mostly effaced granulose sculpture; posterior border doublure short, slightly flared laterally and longest at genal angle, with cut by facial suture just anterolateral from genal angle, and with short, wide, articulating tongue near axial furrows set off by short, deep articulating furrow; axial furrows wide, narrower anteriorly and along LO, deep, gently laterally convex in course, confluent with SO, posterior and anterior border furrows; glabella long, thimble-shaped, with maximum width across L1 $98.4 \%$ ( $87.8-109.8 \%$ ) sagittal length, gently anteriorly tapered, slightly inflated (sag., tr.), sagittal profile (lateral view) moderately anteriorly sloped, with three pairs of well-defined lateral lobes, and with dense sculpture of fine granules; L2 and L3 large, rectangular, roughly equal in size, L1 slightly smaller and subtriangular in shape, each lobe roughly $1 / 3$ total glabellar width, median lobe long, narrow, slightly tapered anteriorly, rectangular, approximately $1 / 3$ glabellar width, frontal lobe large, subtrapezoidal, with small, circular, slightly raised and effaced areas near S 3 on some larger specimens (e.g., Fig. 25.1); glabellar sulci short and deep, with S1 and S2 confluent with axial furrows, and S3 confluent on most specimens (see Fig. 28.1 for exception), S1 with slightly longer medial end, all sulci directed anterolaterally at 30-45 angles; SO moderately long, deep, shorter and deeper in smaller specimens, with very deep apodemal pits just adaxial from axial furrows, course transverse medially, slightly anterolaterally directed laterally; LO long, wide, rectangular, but with indents near anterolateral corners from SO apodemal pits, moderately inflated, with sculpture of partially effaced tiny granules; LO doublure moderately long, reaching halfway to $3 / 4$ toward SO, smooth, with slightly raised lateral margins.

Rostral plate unknown.

Hypostome long, wide, with maximum width across anterior wings $83.3 \%$ ( $79.0-88.9 \%$ ) sagittal length and width across shoulders slightly narrower on most specimens; hypostomal suture very wide, gently anteriorly bowed; anterior border wide, short medially, expanded laterally into large, sub-equilaterally triangular anterior wings, anterior border effaced; wings with deep wing process pits, and with very light granulose sculpture, heavier posteriorly; anterior border furrow moderately long and deep medially, shorter and shallower laterally toward merger with lateral border furrows; middle body long, moderately narrow, widest even with shoulders and strongly posteriorly tapered, anterior lobe large, ovoid, deeply ventrally inflated, with well-defined lateral limits set by moderately narrow, deep lateral branches of middle body furrow, median and posterior limit not well defined by short, very weakly impressed furrow, with dense sculpture of large granules or small tubercles and with scattered small pits near median furrow on most specimens, posterior lobe short, small and U-shaped, with narrow anterolateral arms defined by middle body and lateral border furrows, not well defined posteromedially by long, shallow posterior border furrow, lobe slightly ventrally inflated, with very fine granulose to effaced sculpture; lateral border furrows overlap with middle body furrow anteriorly, almost completely effaced over anterolateral branch of posterior middle body lobe, then moderately wide and deep, with strongly posteriorly convergent course along sides of posterior middle body; lateral border narrowest at lateral notch, strongly flared out to shoulders, and expanded posteriorly to posterolateral corners of hypostome but with lateral margins roughly parallel-sided, slightly ventrally downturned away from lateral border furrows, with dense granulose sculpture, and with very short, rounded triangular spine at shoulders, and small, nubby to short spines roughly even with posterior border furrow and at posterolateral corners; posterior border long, longer medially, equal in width to anterior border minus wings, with rounded posterior margin, effaced near posterior border furrow but mainly with dense granulose sculpture; lateral notch long, shallow, exposes deep doublure; posterior wing long and short, triangular (not well known due to breakage); lateral border doublure wide at notch, then tapered, and strongly dorsomedially raised, and posterior border doublure moderately short, slightly raised, with rounded anterior margin.

Librigena long and fairly wide, roughly triangular in shape, with width of field at midpoint of eye $34.8 \%$ (28.4-38.1\%) length along lateral border furrow, and length of field $53.3 \%$ (49.7-57.2\%) length of lateral border, and with long anterior and posterior projections of the lateral border; anterior branch of facial suture very narrow along field, nearly perpendicular to long, slightly ventromedially sloped branch along anterior lateral border projection; posterior branch of facial suture long, steeply obliquely sloped about $30^{\circ}$ below horizontal to lateral border, with long slightly posterodorsally directed branch along border; ocular surface unknown; eye socle or semicircular area adjacent to ocular surface narrow and effaced, site of abrupt break in slope from eye to librigenal field; librigenal field triangular, narrow anteriorly, widest at posterior edge of eye, then rapidly posteriorly tapered to a point, gently laterally convex, with dense granulose sculpture and dense, irregularly shaped pits; lateral border furrow moderately wide, long, deep in most specimens (but see Fig. 29.4, 29.14), with gently posteriorly sloped curvature; lateral border wide, slightly tapered anteriorly and strongly tapered posteriorly, strongly inflated, with dense granulose sculpture; lateral border doublure about $3 / 4$ as wide as border, absent along anterior projection of border, slightly tapered posteriorly, with triangular projection at posterior tip visible in external view.

Total number of thoracic segments unknown. Segments short, broad (varies with thoracic position), with broad axis $44.8 \%$ ( $38.9-52.5 \%$ ) total pleural width excluding spines, highly vaulted axially and pleurally with posterior segments increasingly vaulted; articulating half ring short, slightly tapered laterally, wide, and sharply raised above articulating furrow, with tiny granules on posterior rim; furrow with very broadly U-shaped course, long, deep, slightly shorter and deeper anterolaterally, with broad and moderately deep apodemal pits at anterolateral limits; axial ring moderately long, about half length of articulating half ring plus furrow, slightly broader than half ring and very shallowly anterolaterally curved, moderately dorsally inflated, slightly overhanging axial furrows (e.g., Fig. 30.18), with tiny granules lining anterior rim and concentrated at anterolateral limits (anterior view, e.g., Fig. 30.4) but dorsal surface effaced; axial furrows fairly narrow, deep, strongly impressed over posterior pleural band, then anterolaterally triangularly flared into pleural furrow and slightly shallower over anterior pleural band, with nearly subparallel course posteriorly, then strongly anteromedially convergent from pleural furrow; ring doublure fairly long, slightly tapered laterally, effaced, with outer corners connected to posterior rim of posterior pleural band; pleural bands of equal width, but anterior band appears narrower due to pleural spine on posterior band, inner pleurae slightly narrower than outer pleurae, fulcral angle strongly downturned (gentler in anterior segments); anterior pleural band short, slightly longer laterally, with very short articulating ridge on anterior edge of inner pleurae set off by very short incised furrow (left pleura of Fig. 30.1, Fig. 30.22), with ridge and furrow continuous
ventrolatererally but somewhat effaced (Fig. 30.11, 30.19), ending in very small anteriorly facing hook-like structure made from anteriormost edge of short, strongly upturned doublure (best viewed anteriorly), effaced; pleural furrow short and deep, slightly longer ventrolaterally and slightly shorter and shallower near axis; with straight to slightly posterolaterally curved course; posterior pleural band roughly twice as long as anterior band, moderately dorsally inflated, effaced dorsally, but with dense sculpture of tiny granules on other surfaces, with ventrolateral tips ending in very large, slightly laterally flattened, distally tapered, and slightly anteriorly curved pleural spine.

Pygidium highly vaulted axially and pleurally, made of four segments each with long spine, and medium sized triangular terminal piece, with sagittal length from articulating furrow to tip of terminal piece 67.0\% (61.3-73.0\%) maximum width across tips of anterior pleural band; articulating half ring short, laterally tapered, wide, slightly inflated, with tiny granules lining posterior margin; articulating furrow long and deep, tapered anterolaterally into very deep apodemal pits; axis of four axial rings and terminal piece moderately long (compared to length of pygidium including spines), broad anteriorly, strongly tapered posteriorly to very narrowly exposed tip of terminal piece, highly vaulted anteriorly with convexity decreasing posteriorly; axial rings subrectangular with rounded lateral margins, progressively narrower and slightly shorter, each strongly independently inflated, dorsally effaced, with fine granules rimming anterior and posterior margins; terminal piece triangular, subequilateral with length slightly longer than width, rapidly tapered to posterior point, moderately inflated, dorsally effaced, with granules lining all margins, and with somewhat triangular (Fig. 31.24) to irregularly shaped (Fig. 27.1) depression linking final interring furrow and anterior margin; axial furrows moderately wide, narrower posteriorly and narrowest between fourth axial ring and terminal piece, flared anteriorly and posteriorly at junctions with interpleural furrows, deepest midway along axis, slightly shallower anteriorly, and fairly shallow along posterior taper of terminal piece; pygidial pleurae with very narrow inner pleurae (narrower on posterior segments), strongly downturned fulcrum, and with outer pleurae roughly twice as wide as inner; anterior pleural band only present on first pygidial segment, short, slightly flared at distal tips into small articulating hook structure, equally broad as posterior band, with granules lining posterior margin; pleural furrow short, deep, incised; posterior pleural band of first pygidial segment double to triple length of anterior band, bands of successive segments slightly shorter, strongly independently inflated, increasingly posteriorly directed, with fourth posterior pleural bands posteriorly convergent, dorsally effaced, with fine granules lining anterior, posterior, and median margins; each segment with very large, long pleural spine much like those of thorax (tapered to point, slightly laterally compressed, more bladelike than perfectly conical, first three spines roughly equal in length from axial furrows to tip, but spines of fourth segment distinctly shorter than those of third, all dorsally effaced but with dense fine granulose sculpture on all other surfaces; interpleural furrows moderately long, slightly tapered laterally and flared posteriorly (posterior view), deep, strongly and increasingly backturned like pleurae; inner pygidial doublure very broadly triangular in anterior view (Figs. $27.9,32.5$ ), rounded medially and strongly tapered anterolaterally, outer doublure (ventral views) shelf-like, moderately inflated, and densely granulose, with broad, moderately shallow furrow running along and between bases of spines, and with triangular median inflection in posterior view.

Ontogeny. Panisaspis quattuor is the best known species of the genus, with ample material demonstrating some of its ontogenetic changes. The cranidium overall becomes wider and shorter; the coarse granulose sculpture is increasingly effaced, and the pits enlarged; the anterior border lengthens and inflates; the axial furrows widen significantly, and all other cranidial furrows lengthen; the glabella shortens, widens posteriorly, and tapers anteriorly; the occipital node almost disappears; and the small genal spine is reduced to a slightly pointed genal angle. The hypostome widens, particularly across the shoulders and posteriorly; the middle body widens anteriorly, inflates, and the granules fade away posteriorly; the lateral border increases in width, and the spines at the shoulder and posterolateral corners are reduced; and the posterior border lengthens. Librigenal changes include the widening of the field; effacement of granules on the field; enlargement and increasingly irregular shape of the pits; widening of the lateral border furrow; widening of the lateral border, particularly anteriorly; elongation of the anterior and posterior projections; and slight fining of the granulose sculpture. The thoracic segments are too large and too close in size to permit observation of ontogenetic changes. The pygidium becomes slightly more elongate and the axis narrows slightly relative to the maximum width; the terminal axial piece elongates and narrows posteriorly into a sharper taper; the pygidial spines elongate; the third spines become longer relative to the fourth spines (cf. Fig. 31.1 and 31.3); and the granulose sculpture coarsens on the lateral and ventral faces of the spines (cf. Fig. 31.5 and 31.6 with 31.8 ).

Discussion. Hintze (1953, pl. 21, figs. 9-14) figured two cranidia from Section H 191.7 m (Hintze's [1953] H-20) in the Strigigenalis plicolabeona Zone with a cranidium, a librigena, and two tails from Section G 174.0 m (Hintze's [1953] G-14) in the Psalikilus typicum Zone as Protopliomerops? quattuor n. sp.. The larger cranidium (Hintze, 1953, pl. 21, fig. 11a, 11b) from H 191.7 m is that of Ibexaspis brevis (Young, 1973). The smaller cranidium (Hintze, 1953, pl. 21, fig. 10) represents a new species of Ibexaspis Přibyl and Vaněk in Přibyl et al., 1985. The remaining four sclerites (Hintze, 1953, pl. 21, figs. 9, 12, 13, 14) represent Panisaspis quattuor (Hintze, 1953). The cranidium (Hintze, 1953, pl. 21, fig. 9) is small (cf. Fig. 25.16), possibly juvenile, and therefore much more granulose than most of the figured cranidia herein. Additionally, the small size and orientation of Hintze's photograph make the cranidium resemble new species of Ibexaspis from the P. typicum Zone, but no species of Ibexaspis is present at G 174.0 m (Adrain et al. 2009 faunal list, p. 561). Young (1973) recognized that Hintze's association was incorrect, and named Protopliomerops quattuor brevis (now Ibexaspis brevis) for one of the species from H 191.7 m ; the other is new and awaits formal naming. Ibexaspis will be treated in a forthcoming paper.

Demeter (1973) figured three pygidia (pl. 3, figs. 6, 7, 10 only) from sections $G$ and Mesa which are assignable to $P$. quattuor. That of pl. 3, fig. 6 was correctly identified, but the associated cranidium (pl. 3, fig. 1) belongs to a species of Ibexaspis. Demeter assigned the pygidium of pl. 3, fig. 7 to Protopliomerops aff. P. quattuor, but the associated pygidium of pl. 3, fig. 2 has five segments and clearly is not conspecific. The pygidium of pl. 3, fig. 10 was incorrectly assigned to Hintzeia celsaora and associated with four other pygidia and a cranidium, some of which belong to H. celsaora, but some of which represent a new species of Protopliomerella Harrington, 1957.

Panisaspis quattuor is compared to $P$. topscityensis and $P$. rancherensis in the discussion sections of those species. It is compared to $P$. loganensis through differential description of that species.

## Panisaspis loganensis n. sp.

Figs. 33-34

2009 Pliomeridae gen. nov. sp. nov. 1; Adrain et al., p. 559, fig. 9B, F.
Material. Holotype, pygidium, SUI 125827, and assigned specimens SUI 115144, 115145, 125816-125826, 185828, from Section HC5 185.6 m, Garden City Formation (Tulean; Hintzea celsaora Zone), Bear River Range, Franklin County, southeastern Idaho, USA.

Etymology. From the town of Logan, Utah.
Diagnosis. Anterior border short and broadly arched; glabella strongly anteriorly tapered; linear (across rings and onto inner pleurae; outer pleurae effaced) sculpture of coarse granules on thoracic segments and pygidium.

Description. Description of $P$. loganensis is given as an extended comparison with $P$. quattuor due to the close morphological similarity of these species. Ratios are given for comparison with other members of the genus.

Cranidia of $P$. loganensis are imperfectly known, but the anterior border is wider, particularly along the anterolateral limbs, gently medially pointed, and the sculpture is of dense granules. The glabella is slightly narrower, with width across L1 $94.4 \%$ (93.5, 95.2\%) length, slightly shorter lateral furrows, smaller LF, and has densely granulose sculpture with less densely distributed small tubercles. LO is slightly shorter, narrower, and laterally tapered and rounded, with sculpture of small tubercles, and a more prominent median tubercle. The fixigenae have smaller pits, as well as dense granules, particularly along the edges near the axial and posterior border furrows, which are effaced in $P$. quattuor.

The hypostome is not known.
The librigenae of P. loganensis are smaller than all of those of P. quattuor except that of Fig. 26.24. They differ only slightly, mainly in sculpture, in the coarser lateral border granulation, granulose librigenal field, and longer anterior branch of the border of P. loganensis. The librigenal field may also be wider (Fig. 33.18), but it seems to vary within the species (cf. Fig. 33.19). The width of the librigenal field is $46.5 \%$ ( $41.6-51.8 \%$ ) its length.

The known segments of $P$. loganensis are somewhat smaller than those of $P$. quattuor. They differ most notably in possessing a tuberculate axial ring and posterior pleurae.

Pygidia of $P$. loganensis are tuberculate on the axis, inner pleurae, and lateral margins of the spines, and lack the dense ventral granules that those of $P$. quattuor possess. The axis is slightly wider, the spines are somewhat shorter relative to the axis, and the third spine is not well differentiated when compared to P. quattuor. The sagittal
length from the articulating furrow to the tip of the terminal piece is $66.9 \%(62.8,70.9 \%)$ the width across the fulcra.

Ontogeny. The cranidial anterior border broadens, particularly the lateral sections across the palepebro-ocular ridges, and develops a slight median point; the glabella tapers anteriorly; LF narrows; the axial furrows broaden; and sculpture becomes slightly finer. Librigenae elongate slightly; the field widens and its pits enlarge; and the lateral border furrow deepens. The thorax is not sufficiently well known to discuss segments ontogeny. Pygidial changes are not well represented in the available specimens. However, the pygidium overall elongates, the terminal piece becomes narrower and longer, and the tubercles on the pleurae near the axis disappear.

Discussion. Cranidia of P. loganensis differ from those of $P$. topscityensis most notably in having a much shorter, wider, and medially pointed anterior border; narrower, anteriorly tapered glabella with a smaller LF and larger L1; wider axial furrows; a shorter LO; a shorter posterior border; and coarser sculpture all over. The hypostome is not known for comparison. Librigenae of P. loganensis are wider altogether, with a shorter, wider field; shorter lateral border furrow; and shorter, narrower, less curved lateral border with a much shorter posterior projection. The larger librigenae also have coarser granulose sculpture on the field and border, but librigenae of Figs. 22.13 and 33.20 are closer in size, and that of $P$. topscityensis has much coarser lateral border sculpture; sculptural comparison may be affected by ontogeny. Thoracic segments are not known for P. topscityensis. Pygidia of these species are dissimilar. That of P. loganensis is plesiomorphic, with short, closely spaced, posteriorly directed spines and coarse sculpture; that of $P$. topscityensis has splayed spines, differentiated third and fourth spines, and is mostly effaced with a finely granulose axis.

## Panisaspis n. sp. A

Fig. 35
2009 Pliomeridae gen. nov. sp. nov. 3; Adrain et al., p. 567.
Material. Assigned specimens SUI 125829-125834, from Section YH 128.9-129.5 m, "Yellow Hill Beds", near Pioche, Lincoln County, eastern Nevada, USA, and Section G 258.2 m, southern Confusion Range, Ibex area, Millard County, western Utah, USA, all Tulean, Heckethornia hyndeae Zone.

Discussion. A hypostome and three pygidia from the Yellow Hill locality and a pygidium from G 258.2 m clearly represent a new species of Panisaspis, which must remain unnamed until cranidia are found. The hypostome, although incomplete, is very similar to that of P. quattuor (e.g., Fig. 29.18) in the shape of the anterior wings, middle body, shoulders, and the lateral border. It differs in having a shorter anterior border with a shallower furrow; more posteriorlsy inflated middle body; shallower middle body and lateral border furrows; more pitted anterior lobe and less granulose posterior lobe of the middle body; a shallower lateral notch; and slightly larger lateral border spines. The specimen is somewhat larger than the hypostome of $P$. deltaensis, making comparison less precise, but it is distinguished by having a wider middle body with dense granules and small pits on the anterior lobe and a much shorter posterior lobe; a shallower middle body furrow; a wider lateral border; and much larger lateral border spines. Compared to the hypostome of P. topscityensis (e.g., Fig. 23.10), the specimen possesses a shorter, wider middle body with a shallower median middle body furrow, shallower pits; and slightly finer granulose sculpture; a narrower lateral border; and smaller lateral border spines.

The pygidia are distinguished from those of $P$. deltaensis (cf. Figs. 19.2 and 35.3 ) by their overall finer granulose sculpture; longer axial rings; deeper axial furrows; shorter and wider terminal piece; centered, longer, and deeper terminal piece impression; much shorter and narrower third pygidial spine pair; and relatively longer fourth spine pair. Compared with pygidia of P. topcityensis, those of Panisaspis n. sp. A are slightly wider; the sculpture is finer, but denser, without effaced stripes along the dorsal and ventral surface of the pleural spines; the axis is narrower and less inflated, with shorter rings; the terminal piece is wider, with a distinct impression; the spines are more conical; the third spine pair is longer; and the fourth pair is shorter. The pygidium representing Panisaspis sp. 2 is similar, but has very dense granulose sculpture all over, and particularly concentrated toward the tips of the third spines; longer axial rings; a longer, narrower terminal axial piece with a weak impression; slightly wider spines overall; and shorter third and fourth spines.

The smallest pygidium (Fig. 35.11) is much more densely and coarsely granulose, with a more strongly inflated axis and some median tubercles on the axial rings. It also possesses a less tapered terminal axial piece with a small impression and well-exposed posterior margin. These features, particularly the shape and exposure of the terminal piece, suggest a possible paedomorphic origin for the terminal piece morphology of the younger species $P$. sevierensis and $P$. millardensis.

## Panisaspis sp. 1

Fig. 36.1, 36.2, 36.5, 36.8

Material. Assigned specimen SUI 125835, from Section H 127.1 m, Fillmore Formation (Tulean; Heckethornia bowiei Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

Discussion. A single cranidium from Section H 127.1 m provides evidence of a new species of Panisaspis which must remain in open nomenclature due to lack of other material. It differs from the co-occuring species Panisaspis deltaensis most notably in its extremely dense granulose sculpture. Panisaspis sp. 1 also possesses a more elongate glabella with a longer frontal lobe and relatively larger L1; a wider and longer LO; a narrower genal angle; and a shorter, narrower genal spine. It resembles the cranidia of the younger species $P$. rancherensis, with very similar sculpture, but its glabella is narrower and more elongate, with a larger L 1 ; LO is wider and laterally tapered; the palpebral lobes are longer, with a narrower interocular fixigena; and the posterior fixigenae are much wider. The cranidial sculpture is also similar to that of P. loganensis, but the glabella of Panisaspis sp. 1 is anteriorly rounded instead of tapered, with a much longer and wider frontal lobe and a smaller L1 and LO is longer, with wider and more strongly laterally tapered sections. This species most closely resembles Panisaspis sp. 3, as discussed below.

## Panisaspis sp. 2

Fig. 36.4, 36.7, 36.10
Material. Assigned specimen SUI 125837, from Section H 127.1 m, Fillmore Formation (Tulean; Heckethornia bowiei Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

Discussion. A pygidium from Section H 127.1 m represents a distinct new species of Panisaspis, but does not provide enough material to allow formal naming. It differs from the pygidia of the co-occurring species Panisaspis deltaensis (cf. Figs. 19.2 and 36.4) in its denser and coarser granulose sculpture; longer, narrower axis; wider terminal piece; more conical spines; and much narrower and shorter third spine pair. It is most similar to the pygidium of Panisaspis n. sp. A, but its sculpture is denser and coarser; the terminal piece is longer and narrower, with a shallower impression; and both the third and fourth spine pairs are shorter. Compared to the pygidia of the younger species $P$. sevierensis and $P$. millardensis, that of Panisaspis sp. 2 possesses denser granulose sculpture which is coarser overall than that of $P$. sevierensis, and coarser than that of $P$. millardensis except near the tips of the third and fourth spine pairs; a slightly wider axis; a terminal piece with less distinct and more anteriorly located impressions and a less exposed posterior border; less widely splayed spines; and a relatively shorter fourth spine pair. However, the pygidium of the younger species $P$. rancherensis, which closely resembles that of the oldest species, P. loganensis, is narrower overall; possesses much coarser and sparser granulose sculpture; has a shorter and narrower terminal piece; and lacks the elongate third spine pair. Pygidia of the older species $P$. topscityensis and $P$. quattuor are not very similar. That of P. topscityensis possesses finer sculpture except for larger axial granules; strongly tapered, more elongate spines overall, with the fourth pair relatively much longer; and lacks terminal piece impressions. Panisaspis quattuor pygidia differ in being dorsally nearly effaced; possessing less splayed, narrower, more tapered spines; lacking the length differentiation between the third and fourth spine pairs; and possessing a narrower, strongly tapered terminal piece with a less exposed terminus.

Although the single cranidium representing Panisaspis sp. 1 co-occurs at this horizon, its coarser, sparser sculpture suggests that it is unlikely that they represent a single species. The other members of Panisaspis possess pygidia with similar sculpture as the cranidia, e.g., Panisaspis quattuor; or slightly coarser sculpture, e.g., $P$. rancherensis.

## Panisaspis sp. 3

Fig. 36.3, 36.6, 36.9

Material. Assigned specimen SUI 125836, from Section H 172.5T m, Fillmore Formation (Tulean; Psalikilus pikum Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA.

Discussion. A single cranidium from Section H 172.5 T m clearly belongs to a new species of Panisaspis which lacks sufficient material for naming. It differs from the cranidia of all other member of the genus, including the co-occurring species $P$. rancherensis and $P$. sevierensis, most obviously in its much sparser and coarser tuberculate sculpture. It also possesses a narrower, more elongate and more anteriorly tapered glabella (especially compared to $P$. rancherensis); a slightly more inflated glabella; and a narrower anterior border than both co-occurring species. Both its fixigenae and genal spines are shorter and narrower than those of P. sevierensis. Panisaspis sp. 3 most closely resembles the older Panisaspis sp. 1 from Section H 127.1 m. The cranidia are similar in the size and shape of the glabella and fixigenae, and they are both coarsely tuberculate. However, Panisaspis sp. 3 possesses much sparser and slightly coarser sculpture; the glabella is narrower relative to total cranidial width; the frontal lobe of the glabella is more semicircular due to only slightly inclined S3; S1 is smaller relative to the other glabellar lobes; the palpebral lobe is located further forward; the interocular fixigena is wider; LO is shorter and more posteriorly rounded; and the genal angle is narrower.

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TABLE 1. Taxon-character matrix for phylogenetic analysis of Panisaspis. The outgroup is Hintzeia parafirmimarginis McAdams and Adrain, 2011, from the early Tulean Psalikilus spinosum Zone.

| Characters |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 2 |
|  | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 0 | 1 | 2 |
| Taxa |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Hintzeia parafirmimarginis | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| P. loganensis | 0 | 0 | 0 | 1 | 0 | 0 | ? | ? | ? | ? | ? | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| $P$. rancherensis | 1 | 1 | 1 | 2 | 1 | 1 | 1 | ? | 1 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| P. quattuor | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 |
| P. topscityensis | 1 | 0 | 0 | 2 | 0 | 1 | ? | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 2 |
| P. deltaensis | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 2 | 1 | 2 | 1 | 2 |
| P. millardensis | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 2 | 0 | 2 |
| P. sevierensis | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 2 | 1 | 2 |



FIGURE 1. 1. General area map of the locations of Section HC5 in the Bear River Range, Franklin County, southeastern Idaho; Section YH near Yellow Hill, Pioche Mining District, Lincoln County, eastern Nevada; and sections G and H in the southern Confusion Range, Ibex area, Tule Valley, Millard County, western Utah. 2. Road map showing the location of Section HC5. 3. Topographical map showing the line of section for HC5 on a portion of U.S. Geological Survey 1: 24000 Egan Basin 7.5' quadrangle map (2005); portion of Mapleton U.S.G.S. quadrangle map shown directly to left of line of section. 4. Road map depicting location of sections G and H in the Tule Valley. 5. Topographical map (portion of U.S. Geological Survey 1: 24000 Warm Point provisional 7.5' quadrangle map [1991]) with the lines of section of G and H. 6. Topographical map showing line of Section YH on portion of U.S. Geological Survey 1:24000 Ely Springs 7.5' quadrangle map (1970).


FIGURE 2. Stratigraphic occurrence of Panisaspis species at Section G (Hintze 1951, 1953), Ibex area, Millard County, western Utah. Measurements are in metres, from our remeasurement of the section, and Hintze's original $(1951,1953)$ sampling horizons are indicated. A legend of lithological symbols is included on the lower right.


FIGURE 3. Stratigraphic occurrence of species of Panisaspis at Section H (Hintze, 1951, 1953, 1973), Ibex area, Millard County, western Utah. Measurements are given in metres, from our remeasurement of the section. Hintze's original collecting horizons are also marked. A full stratigraphic column of sections G and H is available in Adrain et al., 2009. A legend of lithological symbols is provided on Figure 2.


FIGURE 4. Single most parsimonious cladogram derived by implicit enumeration from the taxon-character matrix of Table 1. Length, consistency index (c.i.), and retention index (r.i.) are shown in the shadowed box. Characters with a c.i. of 1.0 are shown as black boxes; homoplasious characters (c.i. <1.0) are shown as white boxes. 1. Character-state transformations are optimized under the accelerated transformation (ACCTRAN) criterion. 2. Character-state transformations are optimized under the delayed transformation (DELTRAN) criterion. Bold numbers at the nodes are (upper) nonparametric bootstrap values, reported as GC values, from 10,000 pseudoreplicates and (lower) Bremer support values.


FIGURE 5. Panisaspis millardensis n. sp., from Section H, 185.6 m and 187.4 m , Fillmore Formation (Blackhillsian; Strigigenalis plicolabeona Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. 1, 4, 7, 10, 15. Cranidium, SUI 125596, dorsal, right lateral, oblique, anterior, and ventral views, x7.5 (H 187.4 m$)$. 2, 5, 8. Cranidium, SUI 125597, dorsal, left lateral, and anterior views, x15 (H 185.6 m ). 3, 6, 9. Cranidium, SUI 125598, dorsal, left lateral, and anterior views, x15 (H 185.6 m ). 11, 13, 14. Cranidium, SUI 125599 , dorsal, left lateral, and anterior views, x12 (H 187.4 m ). 12, 14, 17. Cranidium, SUI 125600, dorsal, left lateral, and anterior views, x12 (H 185.6 m). 18, 21-23. Cranidium, SUI 125601, dorsal, left lateral, anterior, and ventral views, x12 (H 187.4 m). 19, 20, 24. Cranidium, SUI 125602, right lateral, dorsal, and anterior views, x12 (H 187.4 m ).

FIGURE 6. Panisaspis millardensis n. sp., from Section H, 185.6 m and 187.4 m , Fillmore Formation (Blackhillsian; Strigigenalis plicolabeona Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. 1, 4, 7. Cranidium, SUI 125603, dorsal, left lateral, and anterior views, x12 (H 187.4 m). 2, 5, 8. Cranidium, SUI 125604, dorsal, left lateral, and anterior views, x12 (H 187.4 m). 3, 6. Left librigena, SUI 125605, external and ventrolateral views, x12 (H 187.4 m ). 9. Right librigena, SUI 125606, external view, x10 (H 187.4 m ). 10, 13. Cranidium, SUI 125607, dorsal and left lateral views, x12 (H 187.4 m ). 11, 14, 17, 20. Cranidium, SUI 125608, dorsal, ventral, anterior, and left lateral views, x15 (H 185.6 m ). 12, 15. Right librigena, SUI 125609, external and ventrolateral views, x10 (H 187.4 m). 16, 19, 22. Cranidium, SUI 125610, dorsal, anterior, and left lateral views, x20 (H 185.6 m ). 18, 21, 24. Right librigena, SUI 125611, external, internal, and ventrolateral views, x12 (H 187.4 m). 23. Left librigena, SUI 125612, external view, x10 (H 187.4 m).



FIGURE 7. Panisaspis millardensis n. sp., from Section H 187.4 m, Fillmore Formation (Blackhillsian; Strigigenalis plicolabeona Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. 1. Right librigena, SUI 125613, external view, x12. 2, 5. Right librigena, SUI 125614, external and ventrolateral views, x15. 3. Right librigena, SUI 125615, external view, x12. 4. Right librigena, SUI 125616, external view, x12. 6. Right librigena, SUI 125617, external view, x15. 7, 10. Right librigena, SUI 125618, external and ventrolateral views, x15. 8, 11. Right librigena, SUI 125619, external and internal views, x15. 9. Left librigena, SUI 125620, external view, x15. 12. Right librigena, SUI 125621, external view, x15. 13. Right librigena, SUI 125622, external view, x12. 14. Left librigena, SUI 125623, external view, x12. 15. Right librigena, SUI 125624, external view, x15. 16. Left librigena, SUI 125625, external view, x20.


FIGURE 8. Panisaspis millardensis n. sp., from Section H, 185.6 m and 187.4 m, Fillmore Formation (Blackhillsian; Strigigenalis plicolabeona Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. 1, 5, 9. Hypostome, SUI 125626, ventral, left lateral, and posterior views, x12 (H 185.6 m ). 2, 6, 10, 14. Hypostome, SUI 125627, ventral, left lateral, posterior, and dorsal views, x 12 (H 187.4 m ). 3, 7, 11. Hypostome, SUI 125628, ventral, left lateral, and posterior views, x12 (H 187.4 m ). 4, 8, 12. Hypostome, SUI 125629, ventral, left lateral, and posterior views, x15. 13, 17, 20. Hypostome, SUI 125630, ventral, left lateral, and posterior views, x20 (H 187.4 m ). 15, 18, 21. Hypostome, SUI 125631, ventral, posterior, and left lateral views, x15 (H 187.4 m ). 16, 19, 22, 23. Hypostome, SUI 125632, ventral, left lateral, dorsal, and posterior views, x12 (H 187.4 m).


FIGURE 9. Panisaspis millardensis n. sp., from Section H, 185.6 m and 187.4 m , Fillmore Formation (Blackhillsian; Strigigenalis plicolabeona Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. 1, 2, 5, 6. Thoracic segment, SUI 125633, dorsal, left lateral, anterior, and posterior views, x 12 (H 187.4 m ). 3, 4, 6, 8, 9. Thoracic segment, SUI 125634, right lateral, dorsal, ventral, anterior, and posterior views, x12 (H 185.6 m$) .10,12,14$. Thoracic segment, SUI 125635, anterior, right lateral, and dorsal views, x12 (H 187.4 m ). 11, 13, 15-17. Thoracic segment, SUI 125636, dorsal, anterior, left lateral, posterior, and ventral views, x12 (H 187.4 m ).

FIGURE 10. Panisaspis millardensis n. sp., from Section H, 185.6 m and 187.4 m, Fillmore Formation (Blackhillsian; Strigigenalis plicolabeona Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. 1, 4, 8, 10, 11. Pygidium, holotype, SUI 125637, dorsal, ventral, posterior, anterior, and left lateral views, x10 (H 187.4 m$) .2,5,6$. Pygidium, SUI 125638, dorsal, left lateral, and posterior views, x10 (H 185.6 m ). 3, 7, 9, 13. Pygidium, SUI 125639, dorsal, ventral, right lateral, and posterior views, x12 (H 187.4 m). 12, 15, 16. Pygidium, SUI 125640, dorsal, posterior, and left lateral views, x12 (H 187.4 m ). 14, 18, 21. Pygidium, SUI 125641, dorsal, posterior, and right lateral views, x12 (H 187.4 m). 17, 20, 24. Pygidium, SUI 125642, dorsal, posterior, and left lateral views, x12 (H 187.4 m). $19,22,23$. Pygidium, SUI 125643, dorsal, right lateral, and posterior views, x12 (H 185.6 m ).



FIGURE 11. Panisaspis millardensis n. sp., from Section H 187.4 m, Fillmore Formation (Blackhillsian; Strigigenalis plicolabeona Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. 1, 5, 12. Pygidium, SUI 125644, dorsal, posterior, and left lateral views, x12. 2, 6, 9. Pygidium, SUI 125645, dorsal, posterior, and left lateral views, x12. 3, 7, 10. Pygidium, SUI 125646, dorsal, left lateral, and posterior views, x15. 4, 8, 11. Pygidium, SUI 125647, dorsal, left lateral, and posterior views, x15. 13-15. Pygidium, SUI 125648, right lateral, posterior, and dorsal views, x 15 .

FIGURE 12. Panisaspis sevierensis n. sp., from Section H 163.3-173.2 m, Fillmore Formation (Tulean; Psalikilus pikum Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. 1, 4, 8. Cranidium, SUI 125649, dorsal, left lateral, and anterior views, x10 (H 173.2 m ). 2, 5, 6. Cranidium, SUI 125650, dorsal, right lateral, and anterior views, x 10 (H 163.3 m ). 3, 7, 9, 12, 15. Cranidium, SUI 125651, dorsal, right lateral, anterior, oblique, and ventral views, x12 (H 166.2 m ). 10, 11, 13, 14. Cranidium, SUI 125652, dorsal, ventral, anterior, and right lateral views, x15 (H 163.3 m ). 16-18. Cranidium, SUI 125653, dorsal, anterior, and left lateral views, x 10 (H 163.3 m ). 19, 22, 26. Cranidium, SUI 125654, dorsal, left lateral, and anterior views, x20 (H 173.2 m ). 20, 21. Cranidium, SUI 125655, right lateral and dorsal views, x10 (H 166.2 m). 23-25. Cranidium, SUI 125656, anterior, right lateral, and dorsal views, x15 (H 163.3 m ).



FIGURE 13. Panisaspis sevierensis n. sp., from Section H 163.3-173.2 m, Fillmore Formation (Tulean; Psalikilus pikum Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. 1, 4, 7. Cranidium, SUI 125657, dorsal, right lateral, and anterior views, x 10 (H 163.3 m ). 2, 5, 8. Cranidium, SUI 125658, dorsal, right lateral, and anterior views, x 10 (H 163.3 m ). 3, 6, 9. Cranidium, SUI 125659, dorsal, right lateral, and anterior views, x10(H163.3 m). 10, 15, 19. Hypostome, SUI 125660, ventral, left lateral, and posterior views, x12 (H 172.5 T m ). 11, 12, 16, 20. Hypostome, SUI 125661, ventral, dorsal, right lateral, and posterior views, x12 (H 172.5T m). 13, 17, 23. Hypostome, SUI 125662, ventral, left lateral, and posterior views, x12 (H 172.5T m). 14, 18, 24. Hypostome, SUI 125663, ventral, left lateral, and posterior views, x10 (H 173.2 m ). 21, 22, 25. Hypostome, SUI 125664, left lateral, ventral, and posterior views, x12 (H 169.8 m ). $26,27,30,32,33$. Thoracic segment, SUI 125665, dorsal, left lateral, posterior, anterior, and ventral views, x12 (H 163.3 m). 28, 29, 31, 34. Thoracic segment, SUI 125666, dorsal, right lateral, anterior, and posterior views, x12 (H 163.3 m ).


FIGURE 14. Panisaspis sevierensis n. sp., from Section H 163.3-173.2 m, Fillmore Formation (Tulean; Psalikilus pikum Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. 1. Right librigena, SUI 125667, external view, x10 (H 173.2 m ). 2, $4,5$. Left librigena, SUI 125668, ventrolateral, external, and internal views, x10 (H 172.5 m ). 3, 6. Right librigena, SUI 125669, external and ventrolateral views, x15 (H 172.5T m). 7, 8, 10. Left librigena, SUI 125670, external, internal, and ventrolateral views, x10 (H 163.3 m). 9. Left librigena, SUI 125671, external view, x10 (H 163.3 m ). 11, 14. Left librigena, SUI 125672, external and ventrolateral views, x10 (H 163.3 m). 12. Right librigena, SUI 125673, external view, x10 (H 163.3 m ). 13. Right librigena, SUI 125674, external view, x10 (H 163.3 m ). 15. Right librigena, SUI 125675, external view, x10 (H 163.3 m). 16. Left librigena, SUI 125676, external view, x10 (H 163.3 m). 17. Left librigena, SUI 125677, external view, x15 (H 163.3 m). 18. Left librigena, SUI 125678, external view, x10 (H 163.3 m). 19. Right librigena, SUI 125679, external view, x12 (H 172.5T m). 20. Left librigena, SUI 125680, external view, x12 (H 163.3 m ).


FIGURE 15. Panisaspis sevierensis n. sp., from Section H 163.3 m, Fillmore Formation (Tulean; Psalikilus pikum Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. All magnifications are x10. 1, 6, 9, 13. Pygidium, holotype, SUI 125681, dorsal, left lateral, ventral, and posterior views. 2, 4, 7. Pygidium, SUI 125682, dorsal, left lateral, and posterior views. 3, 5, 8. Pygidium, SUI 125683, dorsal, right lateral, and posterior views. 10-12. Pygidium, SUI 125684, left lateral, posterior, and dorsal views. 14, 17, 18. Pygidium, SUI 125685, dorsal, right lateral, and posterior views. 15, Pygidium, SUI 125686, ventral view. 16, 19, 20. Pygidium, SUI 125687, dorsal, right lateral, and posterior views.

FIGURE 16. Panisaspis sevierensis n. sp., from Section H 163.3-182.6 m, Fillmore Formation (Tulean; Psalikilus pikum Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. 1, 4, 7, 10, 14. Pygidium, SUI 115310, dorsal, posterior, ventral, anterior, and left lateral views, x12 (H 182.6 m ). 2, 5, 8. Pygidium, SUI 125688, dorsal, posterior, and right lateral views, x10 (H 173.2 m ). $3,6,9$. Pygidium, SUI 125689, dorsal, posterior, and right lateral views, x20 (H 173.2 m ). 11, 15, 19. Pygidium, SUI 125690, dorsal, posterior, and left lateral views, x15 (H 172.5T m). 12, 20. Pygidium, SUI 125691, dorsal and right lateral views, x 10 (H 169.8 m ). 13, 16, 21. Pygidium, SUI 125692, dorsal, posterior, and left lateral views, x10 (H 172.5 m$) .17,18,23$. Pygidium, SUI 125693, dorsal, posterior, and left lateral views, x15 (H 172.5T m). 22, 24, 27. Pygidium, SUI 125694, dorsal, posterior, and left lateral views, x15 (H 173.2 m). 25, 26, 28. Pygidium, SUI 125695, posterior, dorsal, and left lateral views, x15 (H 163.3 m ).



FIGURE 17. Panisaspis deltaensis n. sp., from Section H 93.4 and 127.1 m, Fillmore Formation (Tulean; Heckethornia bowiei Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. 1, 6, 8, 11. Cranidium, SUI 115289, dorsal, right lateral, anterior, and oblique views, x10 (H 93.4 m ). 2, 7, 9, 13. Cranidium, SUI 125696, dorsal, right lateral, anterior, and ventral views, x12 (H 93.4 m). 3-5. Cranidium, SUI 125697, anterior, right lateral, and dorsal views, x20 (H127.1 m). 10, 12, 14. Cranidium, SUI 125698, dorsal, right lateral, and anterior views, x12 (H 127.1 m ). 15, 18, 20. Right librigena, SUI 125699, external, ventrolateral, and internal views, x10 (H 93.4 m ). 16 , 21-23. Hypostome, SUI 125700, ventral, dorsal, left lateral, and posterior views, x12 (H 127.1 m ). 17, 19. Right librigena, SUI 125701, external and internal views, x10 (H 93.4 m).


FIGURE 18. Panisaspis deltaensis n. sp., from Section H 127.1 m, Fillmore Formation (Tulean; Heckethornia bowiei Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. 1, 2, 6. Pygidium, holotype, SUI 125706, dorsal, posterior, and right lateral views, x15. 3-5. Pygidium, SUI 125707, dorsal, posterior, and left lateral views, x15.

FIGURE 19. Panisaspis deltaensis n. sp., from Section H 93.4 and 127.1 m, Fillmore Formation (Tulean; Heckethornia bowiei Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. 1, 4, 7, 10. Pygidium, SUI 115290, dorsal, posterior, ventral, and right lateral views, x10 (H 93.4 m). 2, 5, 8, 11, 12. Pygidium, SUI 125708, dorsal, ventral, anterior, posterior, and left lateral views, x 10 (H 127.1 m). 3, 6, 9, 13. Pygidium, SUI 125709, dorsal, ventral, posterior, and left lateral views, x12 (H 93.4 m). 14, 19, 23. Pygidium, holotype, SUI 125710, dorsal, posterior, and left lateral views, x12 (H 93.4 m$) .15,16,24$. Pygidium, SUI 125711, posterior, dorsal, and left lateral views, x12 (H 127.1 m ). 17, 20. Pygidium, SUI 125712, dorsal and right lateral views, x15 (H 93.4 m ). 18, 21, 22. Pygidium, SUI 125713, dorsal, right lateral, and posterior views, x15 (H 127.1 m ).



FIGURE 20. Panisaspis rancherensis n. sp., from Section H 172.5, 172.5T, and 173.2 m, Fillmore Formation (Tulean; Psalikilus pikum Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. All magnifications are x12. 1, 6, 9, 12. Cranidium, holotype, SUI 125714, dorsal, left lateral, anterior, and ventral views (H 172.5T m). 2-4. Cranidium, SUI 125715, dorsal, right lateral, and anterior views (H 172.5T m). 5, 8, 11, 14. Cranidium, SUI 125716, dorsal, left lateral, anterior, and ventral views, x12 (H 172.5T m). 7, 10, 13, 15. Cranidium, SUI 125717, right lateral, dorsal, ventral, and anterior views, (H 172.5 T m). 16, 18, 21. Cranidium, SUI 125718, left lateral, dorsal, and anterior views, (H 172.5T m). 17, 19, 20. Cranidium, SUI 125719, anterior, dorsal, and right lateral views (H 172.5 m). 22, 23, 26. Cranidium, SUI 125720, dorsal, right lateral, and anterior views (H 173.2 m ). 24, 25, 27, 28. Cranidium, SUI 125721, left lateral, anterior, oblique, and dorsal views (H 173.2 m ).


FIGURE 21. Panisaspis rancherensis n. sp., from Section H 172.5, 172.5T, and 173.2 m , Fillmore Formation (Tulean; Psalikilus pikum Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. 1-3, 5. Hypostome, SUI 125722, ventral, dorsal, right lateral, and posterior views, x15 (H 173.2 m ). 4, 6-8. Hypostome, SUI 125723, posterior, ventral, right lateral, and dorsal views, x12 (H 172.5 T m). 9-11. Right librigena, SUI 125724, external, internal, and ventrolateral views, x12 (H 172.5 m ). 12, 17, 26. Pygidium, SUI 125725, dorsal, left lateral, and posterior views, x12 (H 172.5 m ). 13, 18, 22. Pygidium, SUI 125726, dorsal, right lateral, and posterior views, x 12 (H 172.5 m ). 14, 19, 24. Pygidium, SUI 125727, dorsal, left lateral, and posterior views, x 12 (H 172.5 m ). 15, 20, 24, 29, 32. Pygidium, SUI 125728, dorsal, left lateral, posterior, ventral, and anterior views, x15 (H 172.5T m). 16, 21, 25. Pygidium, SUI 125729, dorsal, right lateral, and posterior views, x20 (H 172.5T m). 27, 28, 30, 31. Pygidium, SUI 125730, ventral, dorsal, left lateral, and posterior views, x15 (H 172.5 Tm ).


FIGURE 22. Panisaspis topscityensis n. sp., from Section G 210.2 m, Fillmore Formation (Tulean; Protopliomerella contracta Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. 1, 2, 4, 7. Cranidium, SUI 125731, dorsal, ventral, right lateral, and anterior views, x7.5. 3, 5, 6, 8. Cranidium, SUI 125732, dorsal, ventral, anterior, and left lateral views, x7.5. 9, 11. Left librigena, SUI 125733, external and internal views, x7.5. 10, 12, 15. Right librigena, SUI 125734, external, internal, and ventrolateral views, x10. $13,14$. Left librigena, SUI 125735, external and ventrolateral views, x20.


FIGURE 23. Panisaspis topscityensis n. sp., from Section G 210.2 m, Fillmore Formation (Tulean; Protopliomerella contracta Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. 1, 2, 4, 7. Hypostome, SUI 125736, ventral, dorsal, right lateral, and posterior views, x12. 3, 5, 6. Hypostome, SUI 125737, ventral, left lateral, and posterior views, x10. 8, 12, 16. Hypostome, SUI 125738, ventral, right lateral, and posterior views, x12.9, 13, 17. Hypostome, SUI 125739, ventral, right lateral, and posterior views, x10. 10, 11, 14, 15. Hypostome, SUI 125740, ventral, dorsal, right lateral, and posterior views, x15.


FIGURE 24. Panisaspis topscityensis n. sp., from Section G 210.2 m, Fillmore Formation (Tulean; Protopliomerella contracta Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. 1, 4, 8, 12, 18. Pygidium, holotype, SUI 115253, dorsal, ventral, anterior, posterior, and left lateral views, x10. 2, 5, 6. Pygidium, SUI 125741, dorsal, posterior, and left lateral views, x10. 3, 7, $10,11$. Pygidium, SUI 125742, dorsal, ventral, posterior, and left lateral views, x20.9,13, 14. Pygidium, SUI 125743, dorsal, posterior, and left lateral views, x7.5. 15-17. Pygidium, SUI 125744, dorsal, right lateral, and posterior views, x20.


FIGURE 25. Panisaspis quattuor (Hintze, 1953), from Section G 162.0T m, Fillmore Formation (Tulean; Psalikilopsis cuspidicauda Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. 1, 4, 9, 12, 14. Cranidium, SUI 125745, dorsal, left lateral, anterior, oblique, and ventral views, x7.5. 2, 5, 10, 13. Cranidium, SUI 125746, dorsal, left lateral, anterior, and ventral views, x10. 3, 6, 7,8 . Cranidium, SUI 125747, dorsal, right lateral, anterior, and oblique views, x12. 11, 16, 17. Cranidium, SUI 125748, dorsal, anterior, and left lateral views, x12. 15, 18, 20. Cranidium, SUI 125749, dorsal, right lateral, and anterior views, x12. 19, 22, 23. Cranidium, SUI 115193, dorsal, anterior, and right lateral views, x6. 21, 24, 25. Cranidium, SUI 125750, dorsal, anterior, and right lateral views, x20.


FIGURE 26. Panisaspis quattuor (Hintze, 1953), from Section G 162.0 T m, Fillmore Formation (Tulean; Psalikilopsis cuspidicauda Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. 1, 5, 9. Cranidium, SUI 125751, dorsal, right lateral, and anterior views, x7.5. 2, 6, 10. Cranidium, SUI 125752, dorsal, right lateral, and anterior views, x12. 3, 4, 7, 8. Hypostome, SUI 125753, ventral, dorsal, left lateral, and posterior views, x12. 11, 15, 19, 23. Hypostome, SUI 125754, ventral, dorsal, posterior, and left lateral views, x12. 12, 16, 20. Right librigena, SUI 125755, external, internal, and ventrolateral views, x10. 13, 17, 21. Hypostome, SUI 125756, ventral, left lateral, and posterior views, x12. 14, 18, 22. Hypostome, SUI 125757, ventral, right lateral, and posterior views, x10. 24. Right librigena, SUI 125758, external view, x15. 25, 26. Right librigena, SUI 125759, external and internal views, x10. 27, 28, 30. Cranidium, SUI 125760, dorsal, right lateral, and anterior views, x10 (G 155.6 m ). 29, 32. Left librigena, SUI 125761, external and ventrolateral views, x10 (G 155.6 m ). 31. Right librigena, SUI 125762, external view, x 10 (G 155.6 m ).


FIGURE 27. Panisaspis quattuor (Hintze, 1953), from Section G 162.0 T m, Fillmore Formation (Tulean; Psalikilopsis cuspidicauda Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. 1, 8, 9, 12, 13. Pygidium, SUI 125763, dorsal, ventral, anterior, left lateral, and posterior views, x12. 2, 3, 5, 6. Pygidium, SUI 115194, dorsal, right lateral, ventral, and posterior views, x15. 4, 7,10 . Pygidium, SUI 125764, dorsal, right lateral, and posterior views, x15. 11, 14, 15. Pygidium, SUI 125765, posterior, dorsal, and right lateral views, x15. 16, 21, 22. Pygidium, SUI 125766, dorsal, posterior, and left lateral views, x12 (G 155.6 m$)$. 17, 19, 23. Pygidium, SUI 125767, dorsal, left lateral, and posterior views, x12 (G 155.6 m ). 18, 20, 24. Pygidium, SUI 125768, left lateral, dorsal, and posterior views, x 15 (G 155.6 m ).

FIGURE 28. Panisaspis quattuor (Hintze, 1953), from Section G 174.0 m , Fillmore Formation (Tulean; Psalikilus typicum Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. 1, 4, 7, 10, 13. Cranidium, SUI 125769, dorsal, ventral, anterior, oblique, and left lateral views, x7.5. 2, 5, 8. Cranidium, SUI 125770, dorsal, right lateral, and anterior views, x7.5. 3, 6, 9, 12. Cranidium, SUI 125771, dorsal, left lateral, anterior, and ventral views, x10. 11, 14, 15. Cranidium, SUI 125772, dorsal, anterior, and left lateral views, x7.5. $16,19,20,22,23$. Cranidium, SUI 115219, dorsal, right lateral, ventral, oblique, and anterior views, x10. 17, 18, 21. Cranidium, SUI 125773, dorsal, left lateral, and anterior views, x12.



FIGURE 29. Panisaspis quattuor (Hintze, 1953), from Section G 174.0 m , Fillmore Formation (Tulean; Psalikilus typicum Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. 1. Right librigena, SUI 125774, external view, x7.5. 2, 3. Right librigena, SUI 125775, internal and external views, x7.5. 4. Left librigena, SUI 125776, external view, x7.5. 5. Right librigena, SUI 125777, external view, x10. 6. Left librigena, SUI 125778, external view, x10. 7, 10. Left librigena, SUI 125779, external and ventrolateral views, x10. 8. Right librigena, SUI 125780, external view, x12. 9, 11. Left librigena, SUI 125781, internal and external views, x10. 12. Right librigena, SUI 125782, external view, x10. 13. Left librigena, SUI 125783, external view, x10. 14. Left librigena, SUI 125784, external view, x10. 15 , 16, 19, 20. Hypostome, SUI 125785, ventral, dorsal, left lateral, and posterior views, x12. 17, 18, 23, 24. Hypostome, SUI 125786, dorsal, ventral, left lateral, and posterior views, x12. 21, 25, 26. Hypostome, SUI 125787, ventral, left lateral, and posterior views, x15. $22,27,28$. Hypostome, SUI 125788, ventral, posterior, and right lateral views, x12.


FIGURE 30. Panisaspis quattuor (Hintze, 1953), from Section G 174.0 m, Fillmore Formation (Tulean; Psalikilus typicum Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. All magnifications are x10. 1, 2, 4, 6. Thoracic segment, SUI 125789, dorsal, right lateral, anterior, and posterior views. 3, 5, 7, 9, 12. Thoracic segment, SUI 125790, dorsal, ventral, anterior, posterior, and right lateral views. 8, 10, 11, 14. Thoracic segment, SUI 125791, anterior, dorsal, left lateral, and ventral views. 13, 17, 20, 25, 27. Thoracic segment, SUI 125792, right lateral, dorsal, ventral, anterior, and posterior views. 15, 16, 18. Thoracic segment, SUI 125793, dorsal, right lateral, and anterior views. 19, 21, 22. Thoracic segment, SUI 125794, left lateral, anterior, and dorsal views. 23, 24, 26. Thoracic segment, SUI 125795, anterior, right lateral, and dorsal views.


FIGURE 31. Panisaspis quattuor (Hintze, 1953), from Section G 174.0 m, Fillmore Formation (Tulean; Psalikilus typicum Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. 1, 5, 12. Pygidium, SUI 125796, dorsal, right lateral, and posterior views, x10. 2, 6, 9. Pygidium, SUI 115220, dorsal, left lateral, and posterior views, x10. 3, 7, 10. Pygidium, SUI 125797, dorsal, right lateral, and posterior views, x15. 4, 8, 11. Pygidium, SUI 125798, dorsal, right lateral, and posterior views, x15. 13, 17, 22. Pygidium, SUI 125799, left lateral, dorsal, and posterior views, x10. 14, 18, 23. Pygidium, SUI 125800, right lateral, dorsal, and posterior views, x10. 15, 19, 20. Pygidium, SUI 125801, right lateral, dorsal, and posterior views, x10. 16, 21, 26. Pygidium, SUI 125802, dorsal, left lateral, and posterior views, x10. 24, 29, 30. Pygidium, SUI 125803, dorsal, right lateral, and posterior views, x12. 25, 27, 28. Pygidium, SUI 125804, left lateral, posterior, and dorsal views, x 12 .

FIGURE 32. Panisaspis quattuor (Hintze, 1953), from Section G 174.0 m, Fillmore Formation (Tulean; Psalikilus typicum Zone), southern Confusion Range, Ibex area, Millard County, western Utah, USA. 1, 2, 5, 6, 9. Pygidium, SUI 125805, dorsal, ventral, anterior, posterior, and left lateral views, x12. 3, 7, 11. Pygidium, SUI 125806, dorsal, right lateral, and posterior views, x12. 4, 8, 12. Pygidium, SUI 125807, dorsal, left lateral, and posterior views, x12. 10, 13, 17. Pygidium, SUI 125808, dorsal, right lateral, and posterior views, x12. 14, 18, 22. Pygidium, SUI 125809, dorsal, right lateral, and posterior views, x12. 15, 16, 20, 21. Pygidium, SUI 125810, ventral, dorsal, left lateral, and posterior views, x12.19, 25, 26. Pygidium, SUI 125811, dorsal, posterior, and left lateral views, x12. 23, 28, 29. Pygidium, SUI 125812, left lateral, dorsal, and posterior views, x12. 24, 30, 34. Pygidium, SUI 125813, dorsal, right lateral, and posterior views, x12. 27, 32, 33. Pygidium, SUI 125814, dorsal, posterior, and right lateral views, x15. 31, 35, 36. Pygidium, SUI 125815, dorsal, left lateral, and posterior views, x 12 .



FIGURE 33. Panisaspis loganensis n. sp., from Section HC5 186.5 m , Garden City Formation (Tulean; Hintzea celsaora Zone), Bear River Range, Franklin County, southeastern Idaho, USA. 1, 5, 9, 13. Cranidium, SUI 125816, dorsal, left lateral, anterior, and ventral views, x10. $2,6,10,14$. Cranidium, SUI 115144, dorsal, left lateral, anterior, and ventral views, x12. 3, 7, 11. Cranidium, SUI 125817, dorsal, left lateral, anterior views, x12. 4, 8, 12. Cranidium, SUI 125818, dorsal, right lateral, and anterior views, x12. 15-17. Cranidium, SUI 125819, dorsal, left lateral, and anterior views, x15. 18, 21, 24. Left librigena, SUI 125820, external, ventrolateral, and internal views, x15. $19,22$. Right librigena, SUI 125821, external and internal views, x15. 20. Right librigena, SUI 125822, external view, x15. 23. Left librigena, SUI 125823, external view, x15.


FIGURE 34. Panisaspis loganensis n. sp., from Section HC5 186.5 m, Garden City Formation (Tulean; Hintzea celsaora Zone), Bear River Range, Franklin County, southeastern Idaho, USA. 1, 2, 5, 6, 8 . Thoracic segment, SUI 125824, dorsal, left lateral, ventral, anterior, and posterior views, x12. 3, 4, 7, 9, 10. Thoracic segment, SUI 125825, dorsal, left lateral, ventral, anterior, and posterior views, x15. 11-13, $15,16$. Thoracic segment, SUI 125826, dorsal, ventral, left lateral, posterior, and anterior views, x12. 14, 19, 24-26. Pygidium, holotype, SUI 125827, dorsal, ventral, right lateral, posterior, and anterior views, x15. 17, 20-22. Pygidium, SUI 125828, dorsal, ventral, right lateral, and posterior views, x15. 18, 23, 27. Pygidium, SUI 115145, dorsal, left lateral, and posterior views, x20.


FIGURE 35. Panisaspis n. sp. A, from Section YH 128.9-129.5 m, "Yellow Hill Beds", near Pioche, Lincoln County, eastern Nevada, and G 258.2 m, Fillmore Formation, southern Confusion Range, Ibex area, Millard County, western Utah, USA, both Ibexian, Tulean, Heckethornia hyndeae Zone. 1, 5, 6. Hypostome, SUI 125829, ventral, left lateral, and posterior views, x12 (YH 128.9 m). 2, 7, 9. Pygidium, SUI 125830, dorsal, right lateral, and posterior views, x12 (YH 128.9 m). 3, 4, 8, 10, 13. Pygidium, SUI 125831, dorsal, ventral, left lateral, anterior, and posterior views, x10 (YH 128.9 m ). 11, 12, 15, 19. Pygidium, SUI 125832, dorsal, right lateral, posterior, and ventral views, x15 (YH 128.9 m ). 14, 17, 18. Pygidium, SUI 125833, dorsal, posterior, and right lateral views, x12 (YH 128.9 m). 16, 20, 21. Pygidium, SUI 125834, dorsal, right lateral, and posterior views, x10 (G 258.2 m ).


FIGURE 36. All specimens from Section H, Fillmore Formation, southern Confusion Range, Ibex area, Millard County, western Utah, USA. 1, 2, 5, 8. Panisaspis sp. 1, from Section H 127.1 m (Tulean; Heckethornia bowiei Zone), cranidium, SUI 125835, dorsal, left lateral, anterior, and oblique views, x12. 3, 6, 9. Panisaspis sp. 3, from Section H 172.5T m (Tulean; Psalikilus pikum Zone), cranidium, SUI 125836, left lateral, anterior, and dorsal views, x15. 4, 7, 10. Panisaspis sp. 2, from Section H 127.1 m (Tulean; Heckethornia bowiei Zone), pygidium, SUI 125837, dorsal, posterior, and left lateral views, x12.

