Bartonaspis new genus, a trilobite species complex from the base of the Upper Cambrian Sunwaptan Stage in North America

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Abstract: Despite being reported widely from basal Sunwaptan strata, *Dellea*? *punctata* Palmer, 1965, is known from only four figured cranidia. New material from Nevada, Utah and Oklahoma, including librigenae and pygidia, indicate that specimens assigned previously to *D*.? *punctata* are best interpreted as a complex of related species that are assigned to a new genus, ***Bartonaspis***. This genus is diagnosed by punctate sculpture, a pair of fossulae at the anterior corners of the glabella, and by a subelliptical pygidium with a short convex axis composed of three segments. Three new species, ***B. fredericksoni***, ***B. palmeri***,and ***B. wilsoni***, are described and *B. punctata* (Palmer) is restricted to its holotype. *Bartonaspis* is known only from the *Irvingella major* Zone, and its first appearance defines the base of the Sunwaptan Stage. *Dellea* Wilson, 1949, is related to *Bartonaspis* and is differentiated from it primarily by pygidial morphology. In contrast to *Bartonaspis*, the pygidium of *Dellea* has an axis composed of four, rather than three, segments and a narrow concave border.

Résumé : Bien que sa présence dans des strates sunwaptiennes basales ait été notée à maintes reprises, *Dellea*? *punctata* Palmer, 1965, n'est représenté que par quatre cranidiums figurés. Du matériel neuf du Nevada, de l'Utah et de l'Oklahoma, dont des librigènes et des pygidiums, indique qu'il serait plus exact d'interpréter des spécimens antérieurement affectés à *D*.? *punctata* comme faisant partie d'un complexe d'espèces reliées appartenant à un nouveau genre, ***Bartonaspis***. La diagnose de ce genre repose sur une sculpture ponctuée, une paire de fossules aux coins antérieurs de la glabelle et un pygidium subelliptique présentant un court axe convexe composé de trois segments. Trois nouvelles espèces, ***B. fredericksoni***, ***B. palmeri*** et ***B. wilsoni***, sont décrites et *B. punctata* (Palmer) est restreint à son holotype. *Bartonaspis* n'est connu que de la zone d'*Irvingella major* et sa première apparition définit la base de l'étage sunwaptien. *Dellea* Wilson, 1949, est relié à *Bartonaspis*, dont il se distingue principalement par sa morphologie pygidiale. À l'encontre de celui de *Bartonaspis*, le pygidium de *Dellea* présente un axe composé de quatre segments plutôt que trois, ainsi qu'une étroite bordure concave.

[Traduit par la Rédaction]

Introduction

Dellea? *punctata* was named by Palmer (1965) for a single figured cranidium from the *Irvingella major* Zone (basal Sunwaptan Stage) of Nevada. Since then, the species has been reported from coeval strata in Texas (Longacre 1970), Oklahoma (Stitt 1971), and Alberta (Westrop 1986), but only three additional cranidia were illustrated in these studies. All specimens show the prominent fossulae at the anterior corners of the glabella and the pitted sculpture of the holotype, but also display variation in, for example, glabellar proportions, strength of glabellar furrows, and frontal area proportions. This species concept, cobbled together from small samples in widely separated areas, exemplifies a common approach to Cambrian trilobite systematics (Adrain and Westrop 2005). Differences between specimens are tacitly interpreted as geographic variation within a single species but the evidence generally remains anecdotal. Our recent work with large silicified samples of Upper Cambrian and Lower Ordovician trilobites (Adrain and Westrop 2005, 2006) indicates that some widely reported species actually represent geographically arrayed groups of distinct species. The occurrence of such species complexes in the fossil record is not unexpected, given the discovery of many geographically or environmentally structured groups of cryptic or sibling species among modern animals (e.g., Knowlton et al. 1992). Although this revolution in modern species discrimination has been driven by widespread application of molecular methods, cryptic species can often be recognized by more traditional approaches. A number of recent analyses

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of a broad range of animals have shown that a variety of morphometric methods produce results that are congruent with those based on molecular analyses (e.g., Knowlton et al. 1992; Adams and Funk 1997; Martin and Bermingham 2000; Guy et al. 2003; Nicola et al. 2003; Gouws et al. 2004; Lockwood et al. 2004; Olsen et al. 2004), so that species complexes should be recognizable in the fossil record (e.g., Pandolfi et al. 2002; Holcomb et al. 2004).

Despite the confidence with which the species has been identified from different regions, the published record of *Dellea*? *punctata*, like those of many Cambrian species, is inadequate for a meaningful evaluation of variation. However, problems of inadequate documentation are not limited to paleontology. In her discussion of "pseudo-sibling species," Knowlton (1993, p. 190) argued that extensive differentiation among modern marine species goes unnoticed because of incomplete information on morphology or other characteristics, and, "in the absence of information to the contrary, considerable intraspecific variability is considered 'normal'". She also noted (p. 190) that "wide geographic ranges have been uncritically accepted as the natural consequence of potentially broad oceanic dispersal", even though the extent to which wide dispersal reduces geographic isolation and speciation in the marine realm is not well understood. Knowlton's comments mirror the conventional wisdom of marine paleontology, and there are good reasons to believe that there is considerable unrecognized species diversity in the fossil record. Although some authors have presented evidence for variable species (e.g., Hughes 1994; Labandiera and Hughes 1994) and broad geographic ranges (McCormick and Fortey 1999) among trilobites, the data from modern animals indicate that species complexes should be commonplace. Moreover, the expansive epeiric seas of the Paleozoic were not homogenous but were instead divided into distinct, salinity- and temperature-defined water masses that are expressed by differences in geochemistry, lithofacies, and biofacies (e.g., Holmden et al. 1998; Simo et al. 2003; Young et al. 2005; Panchuk et al. 2006). In tandem with the inevitable influence of current systems (e.g., Palumbi 1994, p. 550) and physical barriers (e.g., the periodically emergent Transcontinental Arch of the lower Paleozoic of Laurentia), these conditions would have been conducive to the development of geographically and environmentally segregated species complexes.

In this paper, we examine the conventional interpretation of *Dellea*? *punctata* using new collections from the Great Basin and southern Oklahoma. With a much larger sample of sclerites, we can identify significant differences between members of what we interpret as a species complex using even simple bivariate methods (Imbrie 1956; Jones 1988). Moreover, we are able to assign librigena and pygidia to species and these strengthen the case for discrete species groupings. In addition, we establish a new genus, *Bartonaspis*, for this complex of "pseudo-sibling" species.

Despite the change in species concept, *Bartonaspis* retains considerable biostratigraphic significance. The genus is confined to a narrow stratigraphic interval at the base of the Sunwaptan Stage in shelf facies of Laurentia. Most occurrences lie within the *Irvingella major* Zone (Palmer 1965; Stitt 1971, 1977; Westrop 1986), although Longacre (1970) reported that it ranges into basal strata of the overlying *Taenicephalus* Zone in central Texas. It remains a key taxon for the correlation of the Steptoean-Sunwaptan stage boundary.

Localities and stratigraphic setting

In addition to restudying the holotype of *Dellea*? *punctata*, we collected new material from four localities in Nevada, Utah, and Oklahoma (Fig. 1). In all cases, collections are from the basal Sunwaptan *Irvingella major* Zone. Full details of the stratigraphy and sedimentary facies at these localities will be presented elsewhere, and only a brief summary is provided here.

East-central Nevada

The *Irvingella major* Zone occurs at the top of the Barton Canyon Limestone (Fig. 2), a thin (11 m), cliff-forming, bioturbated wackestone–packstone unit at the base of the Windfall Formation in the Cherry Creek and northern Egan ranges, White Pine County, Nevada. We collected samples from ridges on each side of Barton Canyon, Cherry Creek Range (Fig. 1*b*), where the *I. major* Zone is a thin (8 cm), condensed interval of amalgamated packstone, grainstone, and rudstone. *Bartonaspis* is rare (<1% of sclerites recovered) and the assemblage is dominated by *Irvingella* Ulrich and Resser, in Walcott, 1924, *Comanchia* Frederickson, 1949, and agnostoids. The overlying Catlin Member of the Windfall marks a shift from shallow subtidal deposition to deeper subtidal, cherty lime mudstone, laminated calcisiltite, thin shale, and minor packstone horizons that yield faunas dominated by olenid trilobites and agnostoid arthropods.

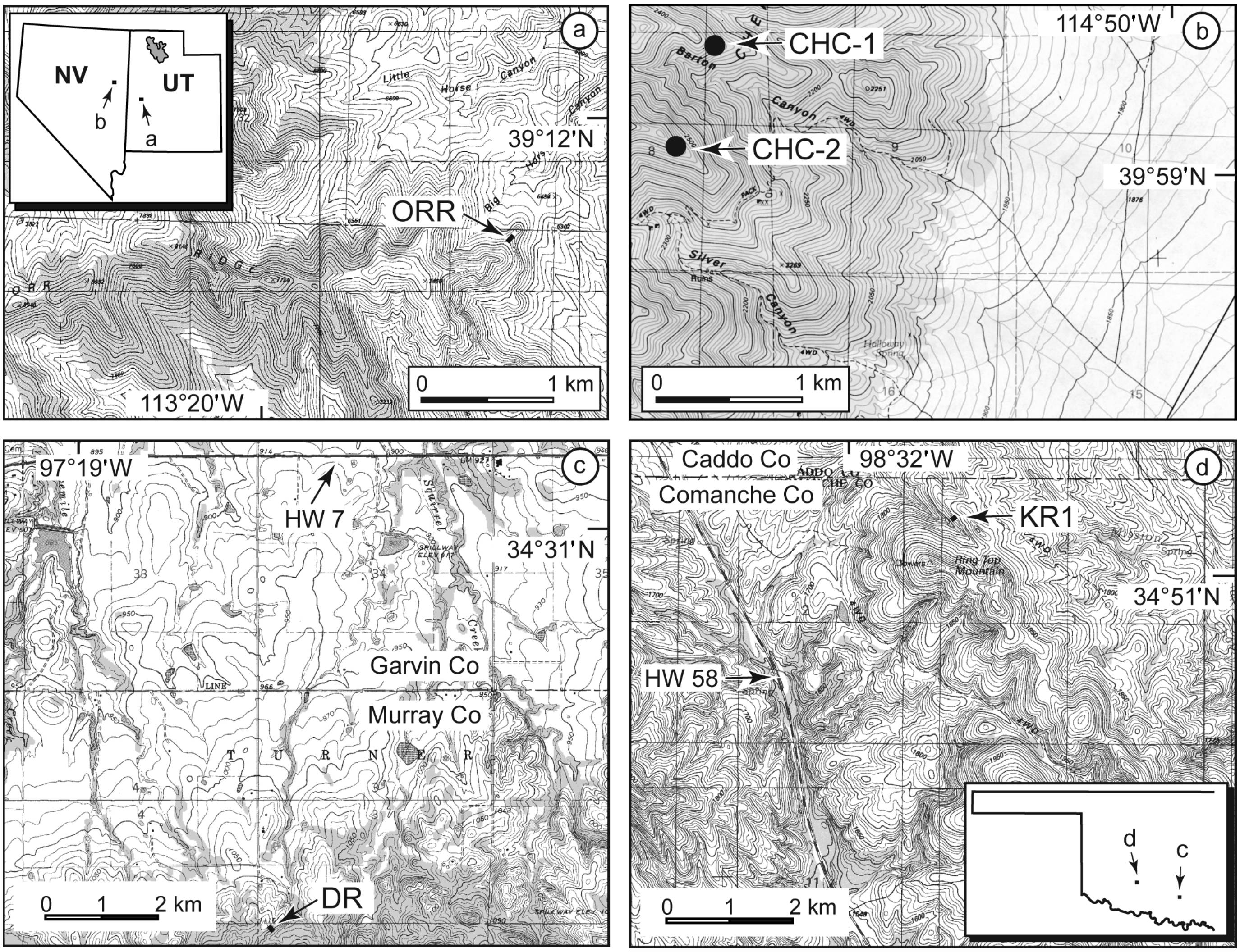
Northern House Range, Utah

The type section of the Orr Formation (Hintze and Palmer 1976, fig. 4) extends along a ridge on the north side of Big Horse Canyon, at the eastern end of Orr Ridge, northern House Range, Millard County, Utah. We measured, logged, and sampled a section on the south side of the canyon (Fig. 1*a*), which has more complete exposures of the upper two members of the formation, the Corset Spring Shale (31.8 m thick) and overlying Sneakover (49.6 m thick) members. This interval is sparsely fossiliferous, but silicified *Elvinia* Zone faunas that include *Elvinia* Walcott, 1924, *Iddingsia* Walcott, 1924, *Kindbladia* Frederickson, 1949, *Cliffia* Wilson, 1951, and *Pterocephalia* Roemer, 1849, occur 25–30 m above the base of the Corset Spring Shale. The base of the *Irvingella major* Zone lies at 60.2 m above the base of the section, 28.4 m above the gradational, somewhat arbitrarily defined boundary between the Corset Spring Shale and Sneakover members. *Bartonaspis* is relatively common in the collections, which have provided most of the information about sclerite associations. Associated genera include *Irvingella*, *Comanchia*, *Stenambon* Palmer, 1965, and several agnostoid arthropods.

Southern Oklahoma

Changes in land ownership over the years have meant that some classic localities in southern Oklahoma are no longer accessible. We measured, logged, and sampled sections at two localities that provided collections from the Honey Creek Formation (Figs. 1–2). In the Slick Hills on the north

Fig. 1. Locality maps. (*a*) Orr Ridge area, Millard County, Utah (collection ORR 60.3 – ORR 60.4). (*b*) Barton Canyon area, White Pine County, Utah (collection CHC-1-0). (*c*) Dotson Ranch area, Murray County, Oklahoma (collection DR-12.2 – DR-12.45). (*d*) Ring Top Mountain area, Wichita Mountains, Comanche County, Oklahoma (collections KR1-22.3 – KR1-22.45, KR1–24).

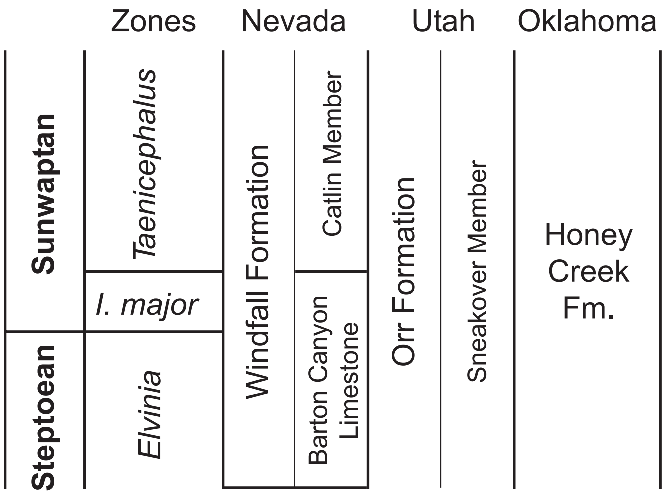


flank of the Wichita Mountains (northern Comanche County), the Kimbell Ranch section was measured on the east side of gully at the north end of Ring Top Mountain, 1.5 km east of Highway 58 (Fig. 1*d*). Here, the *Irvingella major* Zone is 2 m (22–24 m above the base of the section) thick and is characterized by decimetre-scale thick alternations of trilobite- and orthid brachiopod-rich bioclastic rudstone. The trilobite-rich horizons are dominated by *Irvingella* and *Comanchia*, whereas *Bartonaspis* and agnostoid arthropods are rare, accounting for <1% of the sclerites recovered. The Dotson Ranch Section (Fig. 1*c*) is located 5 km east of Hennepin in the Arbuckle Mountains (northern Murray County), and was measured in a south-facing slope about 200 m east of the house. The *Irvingella major* Zone is only 25 cm in thickness (12.2–12.45 m above the base of the section) at this locality and is composed of trilobite-dominated rudstone; as at the Kimbell Ranch section, *Bartonaspis* is a rare component in the *Irvingella* and *Comanchia* dominated fauna. Orthid-rich rudstones that immediately overlie the trilobite rudstone yield sclerites of the trilobite genus *Parabolinoides* Frederickson, 1949 and thus belong to the younger *Taenicephalus* Zone.

Systematic paleontology

Figured specimens are housed at the Oklahoma Museum of Natural History, University of Oklahoma (OU) and at the National Museum of Natural History (USNM). Localities are Barton Canyon, Cherry Creek Range (CHC); ORR Ridge, Utah (ORR); Royer Ranch, Arbuckle Mountains, Oklahoma (RR; J.H. Stitt Collection, now housed at the Oklahoma Museum of Natural History); Dotson Ranch, Arbuckle Mountains, Oklahoma (DR); Kimbell Ranch, Wichita Mountains, Oklahoma (KR). Cranidia from Nevada and Utah were assigned to species by visual inspection of digital images prior to measurement and bivariate analysis. All measurements were made on digital images to the nearest tenth of a millimetre using the Measure Tool of Adobe Photoshop ™. Proportions expressed in percentages in descriptions and diagnoses are means, with numbers in parentheses indicating the range of values. Reduced major axis

Fig. 2. Trilobite biostratigraphy and lithostratigraphy of the Steptoean-Sunwaptan boundary interval in east-central Nevada, western Utah and southern Oklahoma. All material described in this paper is from the *Irvingella major* Zone (*I. major*). Fm., Formation.



regressions were computed using PAST v.1.44 (Hammer et al. 2006); see Table 1 for regression coefficients and for pairwise comparisons between species that yielded significant differences (comparisons made using the method described by Imbrie 1956 and Jones 1988).

Family Dokimocephalidae Kobayashi, 1935

Genus ***Bartonaspis*** n. gen.

TYPE SPECIES: *Bartonaspis wilsoni* n. sp. from the Sneakover Member of the Orr Formation, Orr Ridge, northern House Range, Millard County, Utah, and the Barton Canyon Limestone, Cherry Creek Range, White Pine County, Nevada.

DERIVATION OF NAME: For Barton Canyon, Cherry Creek Range, White Pine County, Nevada, a locality that yielded some of the first known representatives of the genus.; *aspis* (greek), shield. Gender is feminine.

DIAGNOSIS: A genus with slit-like fossulae at anterior corners of glabella. Cranidia and librigena with punctate sculpture. Small palpebral lobe located opposite L2 lobe, with length (exsag., exsagittal) equal to 29% (24%–25%) of glabellar length (sag., sagittal). Pygidium transversely subelliptical in outline; axis short and convex with three segments; one well-defined axial ring present, with second ring poorly differentiated from terminal piece. Punctate sculpture developed on axis.

DISCUSSION: With the recognition of three new species, formerly autapomorphic cranidial characters of *Dellea*? *punctata*, including the slit-like fossulae at the anterior corners of the glabella, and the punctate sculpture of the external surface (e.g., Figs. 3, 4), become synapomorphies of *Bartonaspis* n. gen. Where visible, S1 furrows of *Bartonaspis* are sigmoid and bifurcate (e.g., Figs. 10*a*, 11*a*), a configuration that is also expressed on internal molds of some species of *Dellea* Wilson, 1949 (Ludvigsen and Westrop 1983, pl. 2, fig. 14), *Pseudosaratogia* Wilson, 1951 (Palmer 1965, pl. 2, fig. 18), *Kindbladia* (Palmer 1965, pl. 3, figs. 2, 3), *Lorrettina* Shergold, 1971 (Shergold 1980, pl. 15, figs. 1, 4), and *Protemnites* Whitehouse, 1939 (Paterson and Laurie 2004, figs. 10A, 10B, 10E). The pitted sculpture of the cranidia extends onto the librigenae, which are characterized by narrow, convex borders and moderately long genal spines that curve gently backward (Figs. 8*k*–*m*, 8*o*, 8*r*, 8*s*). Pygidia (e.g., Figs. 4*r*–*t*, 8a–*f*) are identified for the first time and provide additional support for monophyly. Assignment is based on the presence of punctate sculpture on the axis that is identical to the sculpture of the cranidia and librigenae. Transversely subelliptical in outline, the pygidia have short axes composed of two axial rings and a terminal piece, although the second ring is usually differentiated from the terminal piece by a shallow, ill-defined ring furrow.

Among other dokimocephalid genera, *Bartonaspis* is most similar to *Dellea* (e.g., Wilson 1951, pl. 91, figs. 1–17, 25, 26; Westrop 1986, pl. 28, figs. 1–5) in frontal area topography, size, and position of the palpebral lobes, and glabellar outline and convexity, although the latter typically possesses a somewhat longer preglabellar field. However, *Dellea* has a smooth or finely granulose external surface, rather than punctate sculpture. The librigenae of *Bartonaspis* are not unlike those attributed to *D. suada* (Walcott 1890) by Wilson (1951, pl. 91, figs. 20, 21) and are also similar to those of *D. rogersi* Loch and Taylor (2004, fig. 5.12–5.14), differing in the depth of the border furrows, height and inflation of the librigenal fields, and sculpture. The pygidia assigned to *D. suada* by Wilson (1951, pl. 91, figs. 18, 22, 23) are relatively longer and narrower than those of *Bartonaspis* and have four segments in the axis; pygidial borders are narrow and concave.

Pygidia of *Dellea*? *landingi* Ludvigsen and Westrop (1983, pl. 1, figs. 1, 5, 6, 7, 8) differ from those of both *Bartonaspis* and *Dellea suada* in having a well-defined postaxial ridge and a broad, concave border. As noted by Ludvigsen and Westrop (1983, p. 19), the short, relatively flat anterior border of the cranidium is also distinctive, so that *D.*? *landingi* likely represents an undescribed genus. The pygidium assigned provisionally to *D. saratogensis* (Resser 1942) by (Ludvigsen and Westrop 1983, pl. 2, fig. 12) has an axis that, although relatively narrower and less convex, resembles *Bartonaspis* in having three segments. As noted by Ludvigsen and Westrop (1983, p. 18), this pygidium does not resemble those attributed to *Dellea* by Wilson (1951) and Grant (1965), and it may be misassigned.

Chalfontia Shergold, 1982, from the *Irvingella tropica* Zone (Iverian) of Australia, has an anteriorly tapered, weakly furrowed glabella similar to that of *Bartonaspis* (compare Figs. 10*a*–10*c*, 10*h*–10*j* with Shergold 1982, pl. 8, figs. 1–8), and the two genera also have broadly comparable frontal areas that are divided into relatively short preglabellar fields and convex anterior borders. *Chalfontia* differs in having much larger, strongly curved palpebral lobes (Shergold 1982, pl. 8, fig. 1), although like *Bartonaspis*, they are positioned near glabellar mid-length. The single, incomplete pygidium assigned to *Chalfontia* (Henderson 1976, pl. 51, fig. 4) has an axis with two well-defined axial rings in front of the terminal piece. Large palpebral lobes that extend from mid-point of L1 to S2 are also characteristic of *Lorrettina* Shergold, 1971 (e.g.,

Table 1. Regession coefficients (see Fig. 5 for plots).

(A) Glabellar width against glabellar length

Species	Slope (a)	Intercept (b)	r^2	Standard error (a)	Standard error (b)
fredericksoni	0.736	–0.027	0.994	0.012	0.058
palmeri	0.82	–0.144	0.996	0.010	0.039
wilsoni	0.725	–0.048	0.991	0.017	0.059

(B) Significant differences between slopes

Species pair	z	p
frederickson–palmeri	5.18	<0.01
palmeri–wilsoni	4.66	<0.01

(C) Anterior border length against glabellar length

Species	Slope (a)	Intercept (b)	r^2	Standard error (a)	Standard error (b)
fredericksoni	0.156	0.035	0.980	0.005	0.025
palmeri	0.119	0.036	0.982	0.003	0.011
wilsoni	0.132	0.001	0.964	0.005	0.017

(D) Significant differences between slopes

Species pair	z	p
frederickson–palmeri	6.35	<0.01
frederickson–wilsoni	3.39	<0.01

Shergold 1980, pl. 14, fig. 6, pl. 15, figs. 2, 4), an Australian dokimocephalid from slightly younger Iverian strata than *Chalfontia*; in other respects, cranidia of *Lorrettina* are quite similar to those of *Bartonaspis*. Librigenae (e.g., Shergold 1980, pl. 15, fig. 5) are characterized by very short genal spines that contrast with the longer spines of *Bartonaspis* (e.g., Fig. 8*l*, 8*m*, 8*s*). Pygidia of *Lorrettina* (e.g., Shergold 1980, pl. 14, fig. 9) are similar to those of *Bartonaspis* in outline and general proportions. However, the axis comprises four segments, and the pleural field is traversed by at least two pairs of firmly impressed, oblique pleural furrows.

Dokimocephalus Walcott, 1924, *Burnetiella* Lochman, 1958, and some species currently assigned to *Iddingsia* Walcott, 1924 (e.g., *Iddingsia anatina* Resser 1942), differ from *Bartonaspis* in possessing much longer anterior borders and, consequently, longer frontal areas, as well as larger, more posteriorly positioned palpebral lobes (e.g., Wilson 1949, pl. 9, figs. 1, 4; Wilson 1951, pl. 89, fig. 18, pl. 90, fig. 25; Westrop 1986, pl. 29, figs. 2–5). Pygidia of this group of genera are relatively broad with firmly impressed pleural and interpleural furrows, and at least four segments in the axis (e.g., Wilson 1949, pl. 89, figs. 14, 16; Westrop 1986, pl. 29, fig. 6; Chatterton and Ludvigsen 1998, figs. 22.1, 22.4, 22.6).

Fossulae are developed at the anterior corners of the glabella of *Olentella* Ivshin, 1956 (e.g., Shergold et al. 1976, pl. 42, figs. 1, 2) and *Protemnites* Whitehouse, 1939 (as revised by Shergold 1982; e.g., Shergold and Webers 1992, pl. 6, figs. 8, 10, 11; Paterson and Laurie 2004, fig. 10), two genera of uncertain affinities that have been variously assigned to the Elviniidae, Dokimocephalidae, or Aphelaspidae (e.g., see Shergold and Webers 1992; Jell, in Jell and Adrain 2003). *Olentella* has much larger palpebral lobes than *Bartonaspis*, and the pygidia assigned to the genus by Shergold (in Shergold et al. 1976, pl. 42, figs. 9–10) have much longer axes that have three axial rings in front of the terminal piece, and a wide, flattened border that expands anteriorly. In addition to larger palpebral lobes, *Protemnites* differs from *Bartonaspis* in having an inflated preglabellar field. Paterson and Laurie (2004, figs. 10K, 10L, 10O) illustrated librigenae of *Protemnites magnificans* Shergold and Webbers, 1992, and these are characterized by short, very slender genal spines. Pygidia attributed to *Protemnites* (Henderson 1976; Paterson and Laurie 2004) have relatively long axes with three axial rings and a terminal piece, but vary in the expression of pleural and interpleural furrows. *Protemnites brownensis* (Henderson 1976, pl. 50, figs. 14, 15, 19) has convex, well-furrowed pleural fields that slope down to a flat border, whereas the pleural field of *P. magnificans* is weakly furrowed and the pygidial border narrows conspicuously towards the rear.

Conspicuous glabellar fossulae are also present in the early Sunwaptan genera *Taenicephalus* Ulrich and Resser, in Walcott, 1924 (e.g., Westrop 1986, pl. 21, figs. 5, 6, pl. 22, figs. 14, 16), and *Croixana* Nelson, 1951 (e.g., Westrop 1986, pl. 23, figs. 3, 5, 12, 16), both of which currently languish in the almost certainly paraphyletic family Parabolinoididae. Both genera typically possess small, anteriorly positioned palpebral lobes that are located opposite the S2 glabellar furrow, and inflated preglabellar fields. External surfaces of the cranidia may appear irregularly pitted, but this effect is produced by a network of fine anastomosing ridges, and is unlike the sculpture in *Bartonaspis*. *Taenicephalus* has a transversely subelliptical pygidium (e.g., Bell and Ellinwood 1962, pl. 57, figs. 8, 19, 20; Westrop 1986, pl. 21, figs. 7, 15, pl. 22, figs. 6, 9) with well-incised pleural and interpleural furrows, an axis with two or three well-defined rings in front of the terminal piece, and a narrow, rim-like border. The pygidium of *Croixana* is known from only two small but distinctive specimens (Westrop 1986, pl. 23, figs. 8–9) that are strongly effaced with a long, narrow axis that shows no trace of axial rings, and an unfurrowed pleural field; external surface carries a network of fine, anastomosing ridges.

Bartonaspis punctata (Palmer, 1965)
Fig. 3*j*–3*l*

Dellea? *punctata* Palmer, 1965, p. 84, pl. 3, fig. 8.
non Dellea? *punctata* Palmer; Longacre, 1970 p. 56, pl. 1, fig. 1 (= *Bartonaspis* sp. indet.).
non Dellea? *punctata* Palmer; Stitt, 1971, p. 48, pl. 1, fig. 6 (= *Bartonaspis fredericksoni*, n. sp.).
non Dellea? *punctata* Palmer; Westrop 1986, p. 59, pl. 28, fig. 10 (= *Bartonaspis* sp. indet.).

DISCUSSION: The holotype cranidium of *Bartonaspis punctata* (Palmer; Figs. 3*j*–3*l*) is from a section through the Catlin Member of the Windfall Formation in the Eureka District, Nevada, that is now covered completely by talus from mining activities, so that additional material cannot be collected. Palmer (1965, p. 84) also recorded this species from the Cherry Creek section but did not figure any specimens; new material from this locality, illustrated in Fig. 3, is assigned to *B. wilsoni* n. sp. The holotype of *B. punctata* has a relatively narrow glabella (glabellar width/length = 0.73) that falls within the range of variation of *B. wilsoni* (glabellar width/length = 0.67–0.75). However, this cranidium has a more firmly impressed anterior border furrow and a larger palpebral lobe than cranidia of *B. wilsoni* from Nevada (Figs. 3*a*–3*i*) and Utah (Figs. 4*a*–4*n*, 4*u*–4*w*), but in the absence of additional material from the type locality, the significance of these differences cannot be evaluated. Accordingly, we recommend that *B. punctata* be restricted to the holotype.

Among other reported occurrences of *B. punctata*, the cranidium from Oklahoma illustrated by Stitt (1971, pl. 1, fig. 6) is transferred to *B. fredericksoni*, n. sp., but a decision on the status of cranidia from Texas (Longacre 1970, pl. 1, fig. 1) and Alberta (Westrop 1986, pl. 28, fig. 12) must await the discovery of additional material.

Bartonaspis wilsoni n. sp.
Figs. 3*a*–*i*; 4*a*–4*w*; 5*a*

DERIVATION OF NAME: For James Lee Wilson

HOLOTYPE: A cranidium (OU 12161) from the Sneakover Member of the Orr Formation, Orr Ridge, northern House Range, Utah (Figs. 4*a*–4*c*).

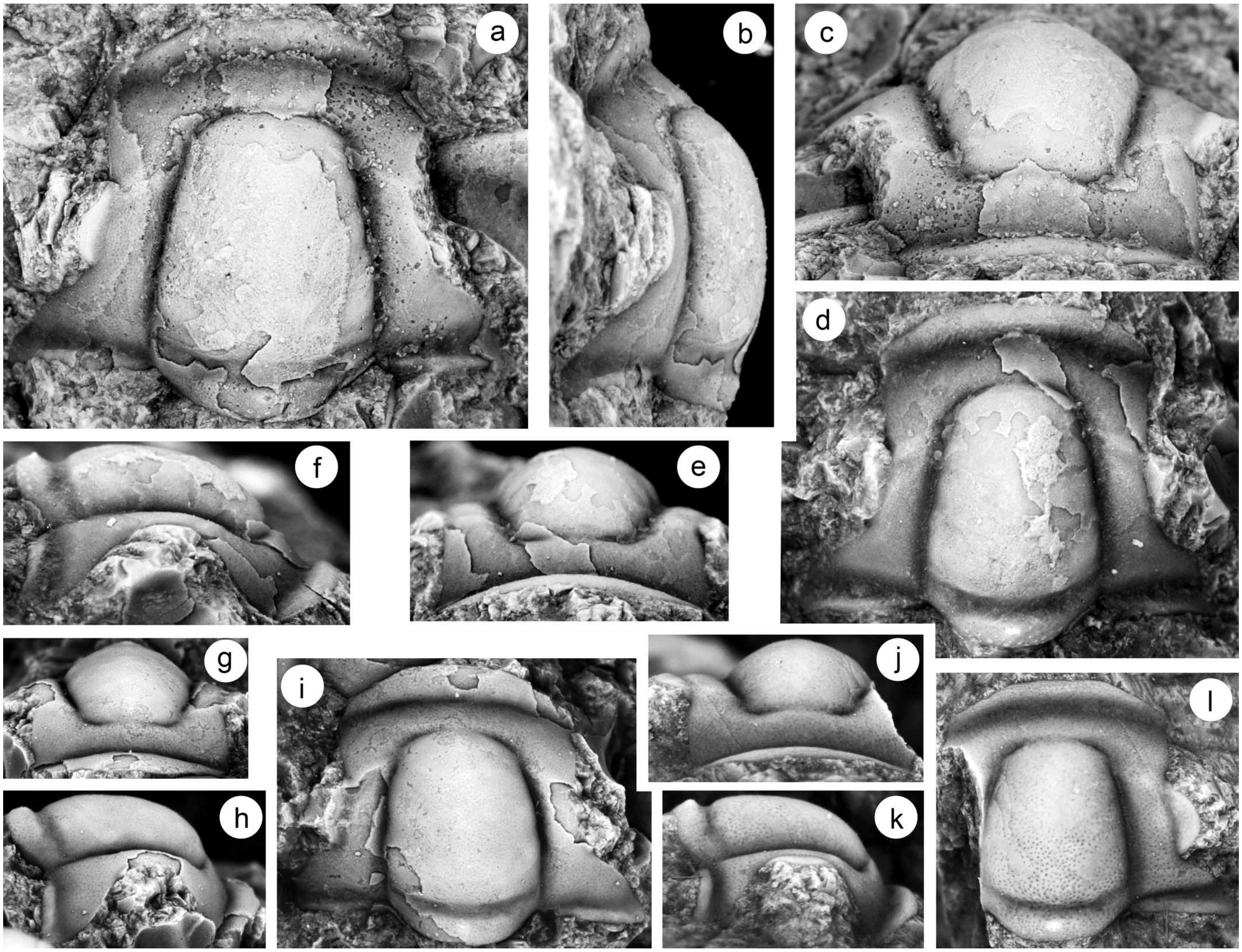
DIAGNOSIS: A species with short anterior border that occupies 11% (10%–12%) of cranidial length. Glabella relatively long and narrow, with width at occipital furrow in larger individuals (cranidial length (sag.) > 3 mm) equal to 72% (67%–75%) of glabellar length (sag.). Pygidium with relatively short axis that accounts for 72% of pygidial length.

DESCRIPTION: Cranidium exclusive of posterior projection subrectangular in outline, with width between palpebral furrows 84% (75%–93%) of cranidial length. Glabella tapers forward and bluntly rounded anteriorly, width at occipital furrow equal to 72% (67%–75%) of glabella length (sag.); occupies 80% (77%–82%) of cranidial length; convex and raised well above fixigenae; longitudinal profile arched gently upward in front of occipital ring, but curves downward anteriorly. Preglabellar furrow lightly impressed medially but deepens laterally into slit-like fossulae at anterior corners of glabella; axial furrows shallow but well-defined grooves. Occipital ring with median node and weakly inflated lateral lobe; occupies 15% (14%–18%) of glabellar length. Occipital furrow transverse and well incised medially but bifurcates at lateral lobe into very short (tr., transverse) posterior branch and longer, finely etched anterior branch that curves forward. Faint S1 and S2 curve obliquely backward; expressed on external surface largely by absence of pitted sculpture. Small cranidia (Figs. 4*q*, 5*a*) with three pairs of well-defined lateral furrows; S2 nearly transverse and S3 directed forward. Frontal area divided into steeply downsloping, weakly inflated preglabellar field and shorter, convex anterior border by forwardly curved anterior border furrow; anterior border accounts for 11% (10%–12%) of cranidial length. Posterior border furrow broad (exsag.) and firmly impressed; widens somewhat distally. Posterior border convex and widens laterally to reach maximum length (exsag.) at posterior corners of cranidium. Palpebral area of fixigenae weakly inflated and equal to 28% (24%–31%) of glabellar width at occipital furrow. Palpebral lobe is gently upsloping flap centered opposite L2 glabellar lobe and with length equal to 29% (26%–35%) of glabellar length; palpebral furrow shallow and nearly straight. Palpebral ridge weakly convex and extends obliquely forward to intersect axial furrow near anterior corner of glabella. Anterior branches of facial sutures diverge slightly between palpebral lobe and anterior border furrow, then curve sharply inward along anterior cranidial margin; posterior branches diverge backward, following a weakly sigmoid path. Sculpture of closely spaced punctae over entire cranidial surface, except furrows; augmented by anastomosing terrace ridges on anterior border. Internal molds are smooth, except for small tubercles on occipital ring (e.g., Fig. 3*d*).

Small cranidia (Figs. 4*q*, 5*a*) differ from larger individuals in having relatively narrower, parallel-sided glabellae, shorter preglabellar fields, and firmly impressed glabellar furrows. Punctae are absent, but scattered, faint tubercles present on fixigenae and glabella. Tubercles not evident on associated early meraspids (Figs. 5*b*, 5*c*).

Pygidium subelliptical in outline, with maximum width (tr.) opposite terminal piece; length 43% (42%–44%) of maximum width; convex, with height in posterior view about 30% of pygidial width. Posterior margin flexed upward medially in posterior view. Articulating facet at anterior corner with width (tr.) about half width of pleural field. Axis tapers gently backward, length 96% (94%–98%) of width at first axial ring; relatively short occupying 72% of pygidial length; width at first axial ring is 33% (32%–33%) of maximum pygidial width. Axis composed of three segments, although second axial ring indistinct ; articulating half-ring semielliptical in outline and slightly shorter than first axial ring; one well-defined, transverse ring furrow and additional faint furrow present; axis moderately convex and accounts for about half of pygidial height in posterior view. Pleural field flexed downward and separated from gently sloping border by shallow border furrow. One well-defined pleural furrow present at anterior; remaining pleural and interpleural

Fig. 3. *Bartonaspis* n. gen., all Barton Canyon Limestone, Barton Canyon, Cherry Creek Range, Nevada, collection CHC-1-0, except *j–l* (Catlin Member, Windfall Formation, Eureka District, Nevada). ***(a–i)*** *Bartonaspis wilsoni* n. sp. (*a–c*) cranidium, OU 12158, dorsal, anterior, and lateral views, ×8. (*d–f*) cranidium, OU 12159, dorsal, lateral, and anterior views, ×9. (*g–i*) cranidium, OU 12160, dorsal, anterior, and lateral views, ×10. ***(j–l)*** *Bartonaspis punctata* (Palmer, 1965). (*j–l*) cranidium, USNM 141543 (**holotype**) ×15.



furrows indistinct. Border relatively long and accounts for 14% (13%–15%) of pygidial length. External surface of axis with sculpture of punctae; remainder of surface is smooth, as are internal molds.

DISCUSSION: Two distinct cranidial morphotypes of *Bartonaspis* co-occur in the Sneakover Member of the Orr Formation at Orr Ridge, Utah, differing significantly in the relative width of the glabella (Fig. 6*a*). A similar distinction is also apparent at the top of the Barton Canyon Limestone in the Cherry Creek Range, Nevada. *Bartonaspis wilsoni* n. sp. is named for one of these morphs, and differs from the other, *B. palmeri* n.sp., in having a relatively longer, narrower glabella, whose width at the occipital furrow averages 72% of length (this proportion is 78% in *B. palmeri*). Pygidia were not recovered from the Barton Canyon Limestone, but two pygidial morphs that possess pitted sculpture on the axis are present in the Sneakover Member. These were assigned to each species on the basis of relative abundance, so that the most common pygidial morph was assumed to belong to the most abundant cranidial morph. The pygidium attributed to *B. wilsoni* is relatively longer than that of *B. palmeri* and has a proportionally shorter axis (= 72%, rather than 84%, of cranidial length). *Bartonaspis fredericksoni* n. sp. (Figs. 10, 11), from the Honey Creek Formation of Oklahoma, is indistinguishable from *B. wilsoni* in glabellar proportions (Fig. 6*a*), but has a significantly longer anterior border (Fig. 6*b*). Like *B. palmeri*, the pygidium of *B. fredericksoni* (Figs. 11*m*, 11*n*) is relatively shorter than the morph attributed to *B. wilsoni*, and the axis is relatively longer.

Bartonaspis palmeri n. sp.

Figs. ?5*b*, ?5*c*, 5*d*; 7*a*–7*s*; 8*a*–8*j*, 8*n*, 8*p*, 8*q*

DERIVATION OF NAME: For Allison R. Palmer

HOLOTYPE: A cranidium (OU 12177) from the Sneakover Member of the Orr Formation, Orr Ridge, northern House Range, Utah (Fig.7*a*–7*c*).

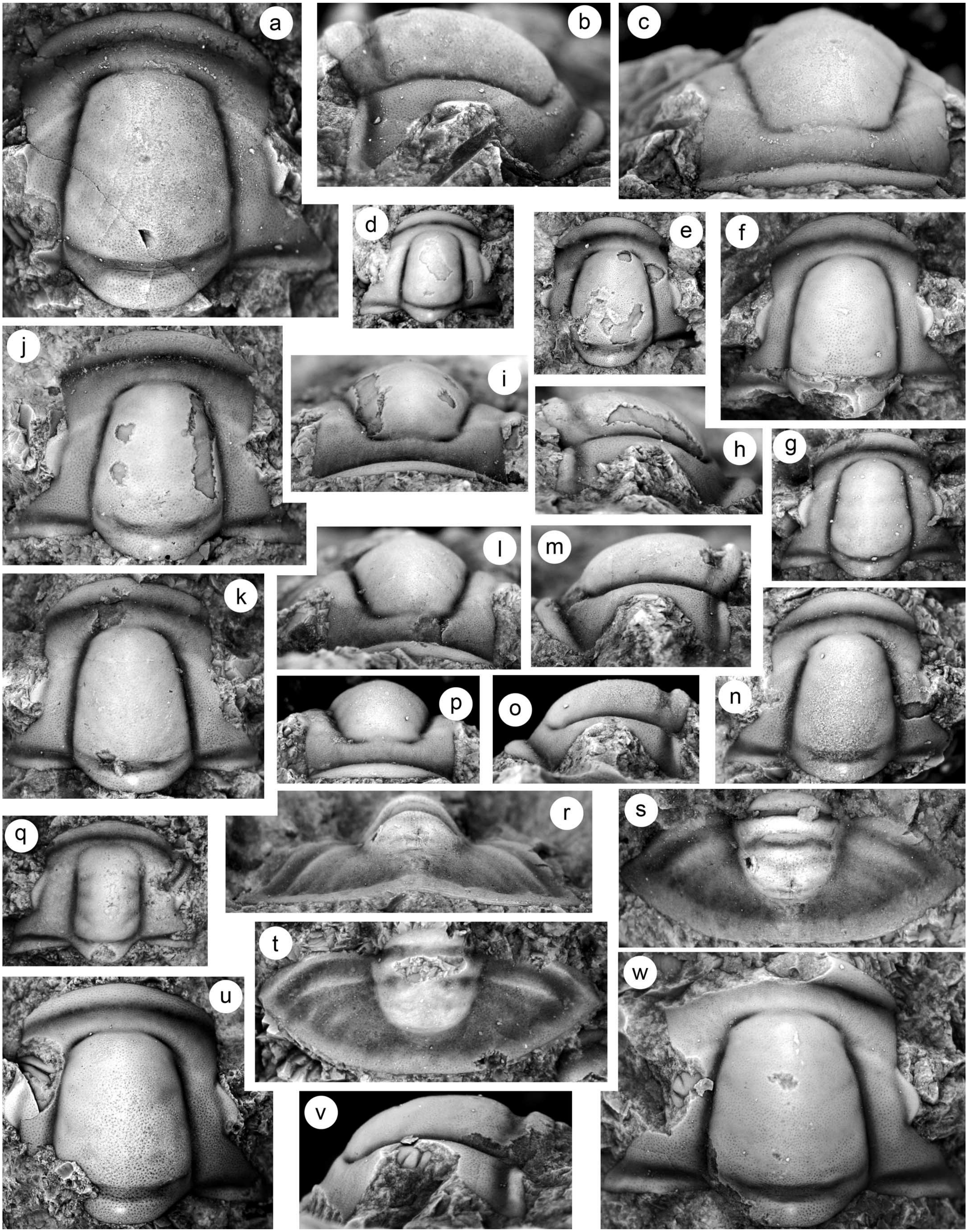

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Fig. 4. *Bartonaspis wilsoni* n. sp., Sneakover Member, Orr Formation, Orr Ridge, northern House Range, Utah, collection ORR 60.3 – ORR 60.4. **(*a–c*)** cranidium, OU 12161 (**holotype**), anterior, lateral, and anterior views, ×9. (*d*) cranidium, OU 12162, dorsal view, ×12. (*e*) cranidium, OU 12163, dorsal view, ×12. (*f*) cranidium, OU 12164, dorsal view, ×9. (*g*) cranidium, OU 12165, dorsal view, ×12. **(*h–j*)** cranidium, OU 12166, lateral, anterior, and dorsal views, ×9. **(*k–m*)** cranidium, OU 12167, dorsal, anterior, and lateral views, ×9. **(*n–p*)** cranidium, OU 12168, dorsal, lateral, and anterior views, ×9. **(*q*)** cranidium, OU 12169, dorsal view, ×25 (see Fig. 5*a* for SEM image). **(*r, s*)** pygidium, OU 12170, posterior and dorsal views, ×12. **(*t*)** pygidium, OU 12171, dorsal view, ×12. **(*u*)** cranidium, OU 12172, dorsal view, ×9. **(*v, w*)** cranidium, OU 12173, lateral and dorsal view, ×9.

Fig. 5. *Bartonaspis* n. gen, Sneakover Member, Orr Formation, Orr Ridge, northern House Range, Utah, collection ORR 60.3 – ORR 60.4. All scale bars = 100 µm. **(*a*)** *Bartonaspis wilsoni* n. sp., cranidium, OU 12169, dorsal view (see Fig. 4*q* for a light photograph). **(*b, c*)** *Bartonaspis* sp. indet. (*b*) cranidium, OU 12174, dorsal view. (*c*) cranidium, OU 12175, dorsal view. **(*d*)** *Bartonaspis palmeri* n. sp. cranidium, OU 12176, dorsal view (see Fig. 8*n* for a light photograph).

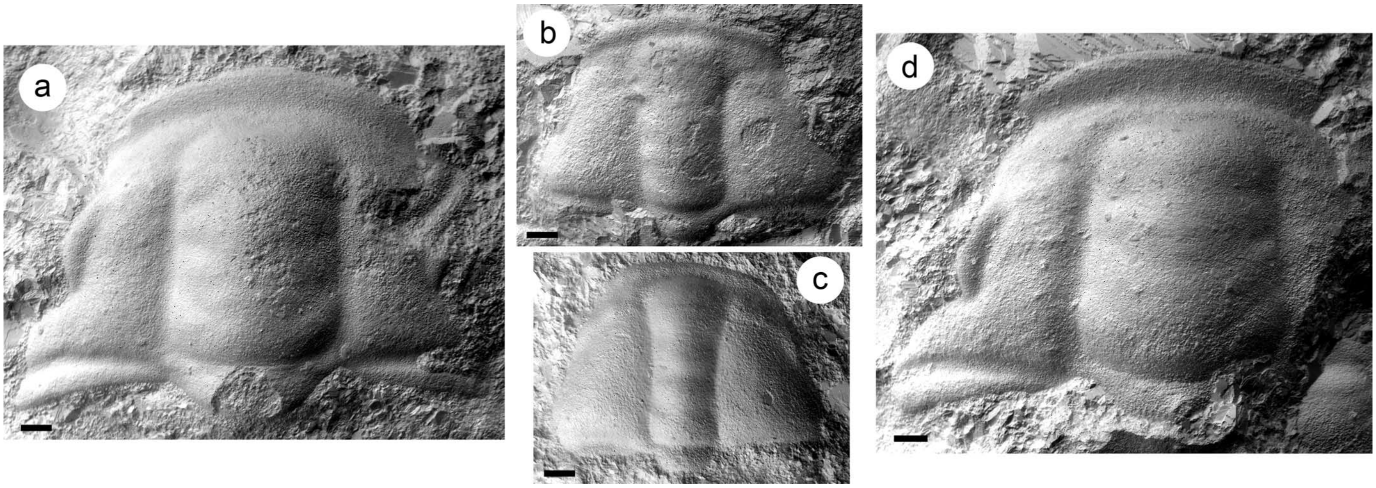
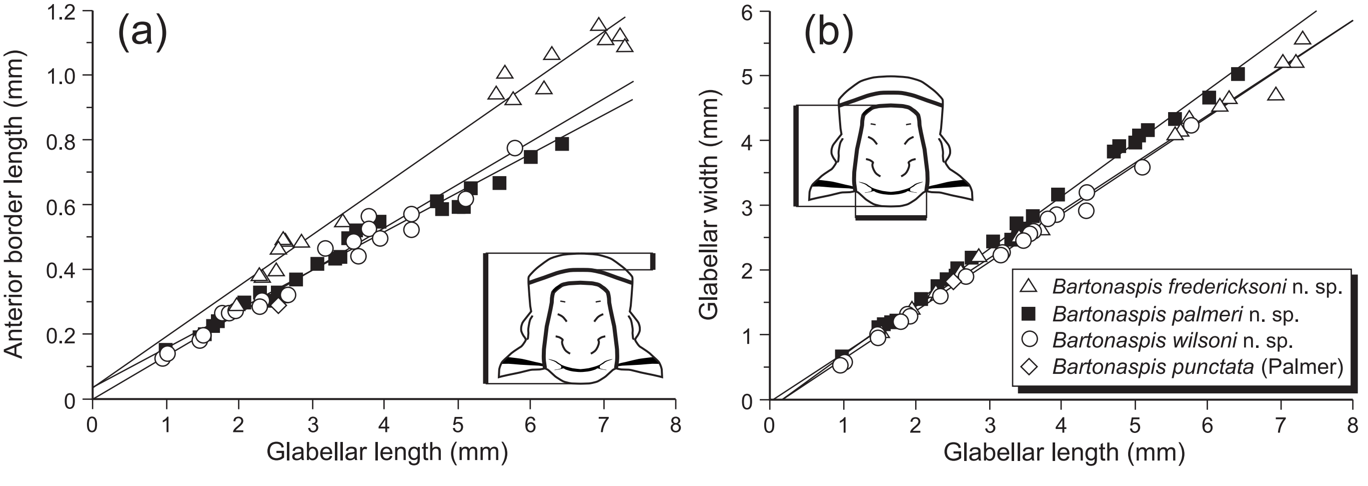


Fig. 6. Bivariate plots, with reduced major axis regressions computed using PAST v.1.44 (Hammer et al. 2006); see Table 1 for regression coefficients and for pairwise comparisons between species that yielded significant differences (comparisons made using the method described by Imbrie 1956 and Jones 1988). Note that all comparisons in Table 1 remain significant if a Bonferroni correction for multiple comparisons is applied. Number of cranidia measured: *B. wilsoni*, 23; *B. palmeri*, 26; *B. fredericksoni*, 20. (*a*). Anterior border length against cranidial length**.** (*b*) Glabellar width against glabellar length.



DIAGNOSIS: A species with short anterior border that occupies 11% (9%–12%) of cranidial length. Glabella relatively short and wide, with width at occipital furrow in larger individuals (cranidial length (sag.) > 3 mm) equal to 78% (75%–82%) of glabellar length (sag.). Pygidium with relatively long axis that accounts for 84% (83%–85%) of pygidial length. Posterior pygidial margin flexed up medially in posterior view.

DESCRIPTION: Cranidia of *Bartonaspis palmeri* are sufficiently similar to those of *B. wilsoni* that a description is unnecessary; cranidial comparisons between these species are presented earlier in the text. Associated early meraspid cranidia (Figs. 5*b*, 5*c*) may belong to either *B. palmeri* or *B. wilsoni*. Glabella narrow and terminates anteriorly at short, flat anterior border; cylindrical in larger cranidium (Fig. 5*b*) but anteriorly expanded in smaller cranidium (Fig. 5*c*). Occipital

Fig. 7. *Bartonaspis palmeri* n. sp., Sneakover Member, Orr Formation, Orr Ridge, northern House Range, Utah, collection ORR 60.3 – ORR 60.4. **(a–c)** cranidium, OU 12177 (**holotype**), dorsal, anterior, and lateral views, ×8. **(*d*)** cranidium, OU 12178, dorsal view, ×8. **(*e–g*)** cranidium, OU 12179, dorsal, lateral, and anterior views, ×12. **(*h–j*)** cranidium, OU 12180, lateral, dorsal, and anterior views, ×12. **(*k*)** cranidium, OU 12181, dorsal view, ×9. **(*l–n*)** cranidium, OU 12182, dorsal, lateral, and anterior views, ×12. **(*o*)** crandium, OU 12183, dorsal view, ×9. **(*p–r*)** cranidium, OU 12184, lateral, dorsal, and anterior views, ×9. **(*s*)** cranidium, OU 12185, dorsal view, ×12.

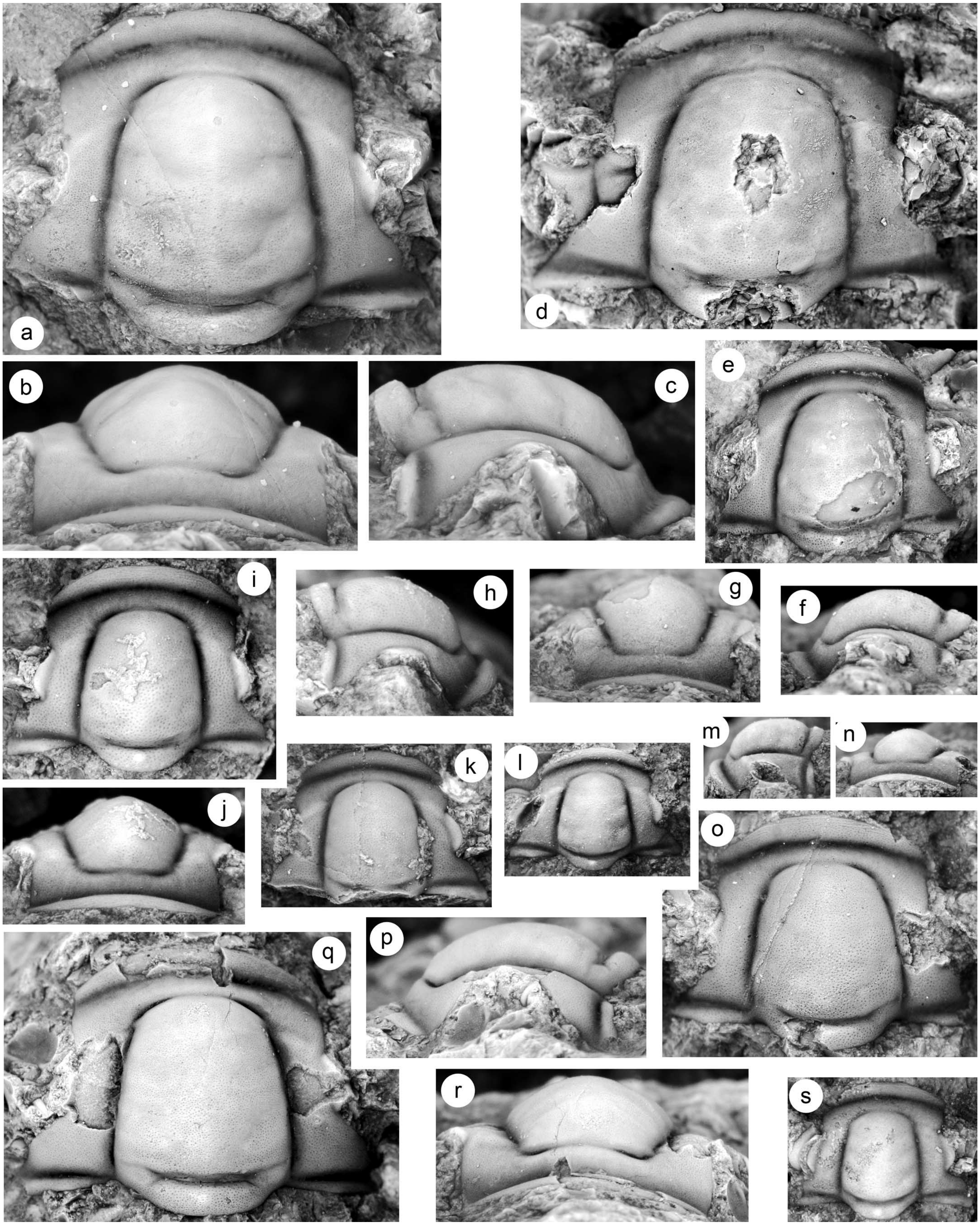


Fig. 8. *Bartonaspis* n. gen, all Sneakover Member, Orr Formation, Orr Ridge, northern House Range, Utah, collection ORR 60.3 – ORR 60.4, except *g–j* (Barton Canyon Limestone, Barton Canyon, Cherry Creek Range, Nevada. **(*a–j*, *n*, *p*, *q*)** *Bartonaspis palmeri* n. sp. (*a*) pygidium, OU 12186, dorsal view, ×12. (*b*, *c*) pygidium, OU 12187, posterior and dorsal views, ×12. (*d*, *e*) pygidium, posterior and dorsal views, OU 12188, ×12. (*f*) pygidium, OU 12189, dorsal view, ×12. (*g–i*) cranidium, OU 12190, dorsal, anterior and lateral views, ×9. (*j*) cranidium, OU 12191, dorsal view, ×10. (*n*) cranidium, OU 12176, dorsal view, ×25 (see Fig. 5*d* for SEM image). (*p*, *q*) hypostome, OU 12192, posterior and dorsal views, ×12. **(*k–m*, *o*, *r*, *s*)** *Bartonaspis* spp. (*k*, *l*) librigena, OU 12193, lateral and dorsal views, x12. (*m*) librigena, OU 12194, dorsal view, ×12. (*c*) librigena, OU 12195, dorsal view, ×10. (*r*, *s*) librigena, OU 12196, lateral and dorsal views, ×1.

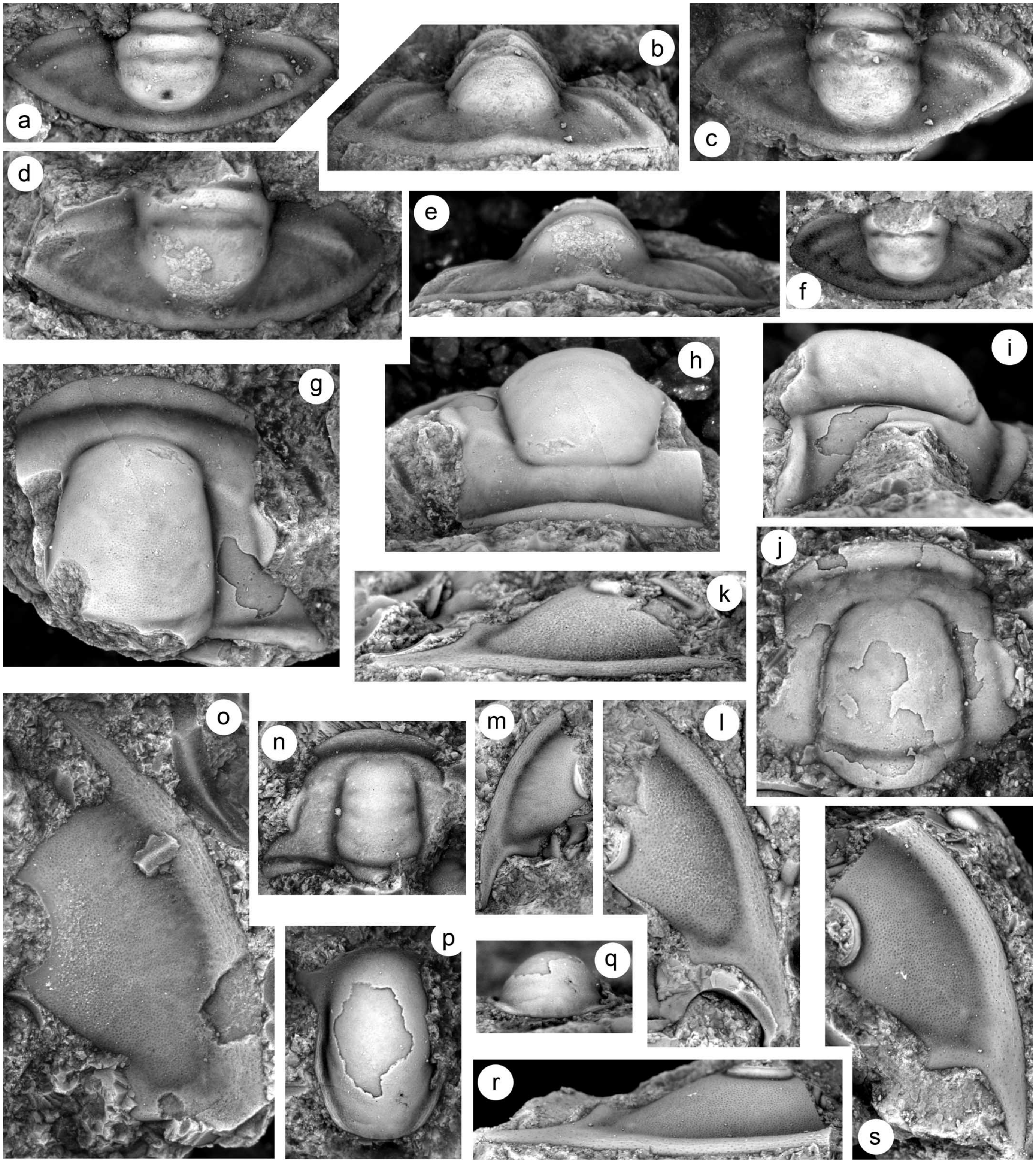


Fig. 9. *Bartonaspis* cf. *B. palmeri*, Sneakover Member, Orr Formation, Orr Ridge, northern House Range, Utah, collection ORR 60.3 – ORR 60.4. (*a*) cranidium, OU 12197, dorsal view, ×7.5. (***b–d***) cranidium, OU 12198, anterior, lateral, and dorsal views, ×7.5.

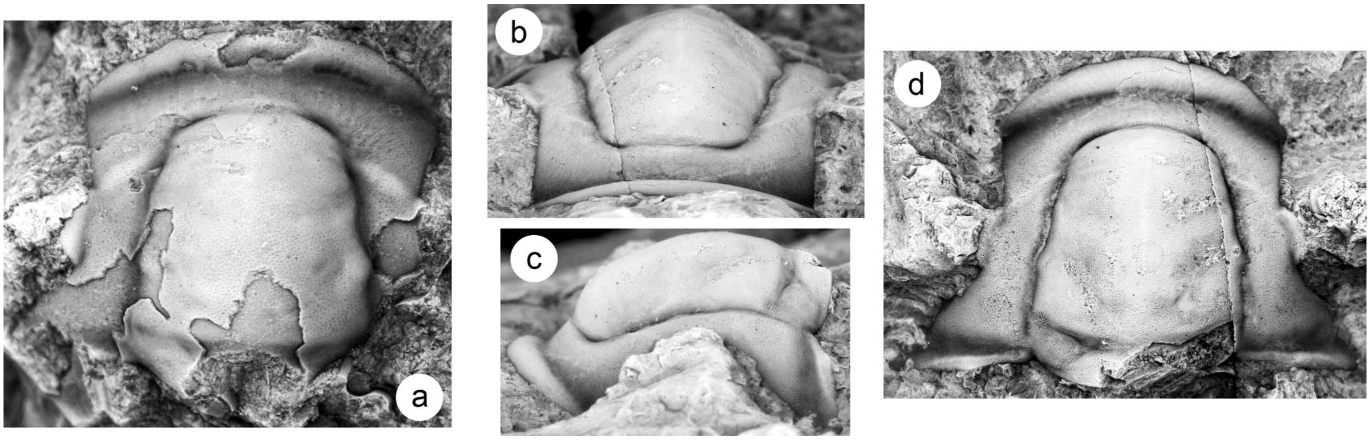


Fig. 10. *Bartonaspis fredericksoni* n. sp, Honey Creek Formation, all from Dotson Ranch, Arbuckle Mountains, Oklahoma, collection DR-12.2 – DR-12.45, except 15, 16, 18 (Kimbell Ranch, Wichita Mountains, float block about 22 m above base of section). (***a–c***) cranidium, OU 12199, dorsal, lateral, and anterior views, ×7. (***d–f***) cranidium, OU 12200, dorsal, lateral, and anterior views, ×7. (***g***) cranidium, OU 12201, dorsal view, ×12. (***h–j***) cranidium, OU 12202, dorsal, lateral, and anterior views, ×7. (***k***) cranidium, OU 12203, dorsal view, ×7. (***l–n***) cranidium, OU 12204, lateral, anterior, and dorsal views, ×10. (***o*, *p*, *r***) cranidium, OU 12205 cranidium, anterior, lateral and dorsal views, ×10. (***q***) cranidium, OU 12206, dorsal view, ×10. (***s*, *t***) librigena, OU 12207, lateral and dorsal views, ×6.

furrow well-incised and transverse; transverse S1, S2, and S3 furrows well expressed on smaller cranidium. Palpebral lobe located opposite S3; palpebral ridges curve forward from palpebral lobe to intersect axial furrow opposite midpoint of frontal glabellar lobe. External surface of cranidium is smooth.

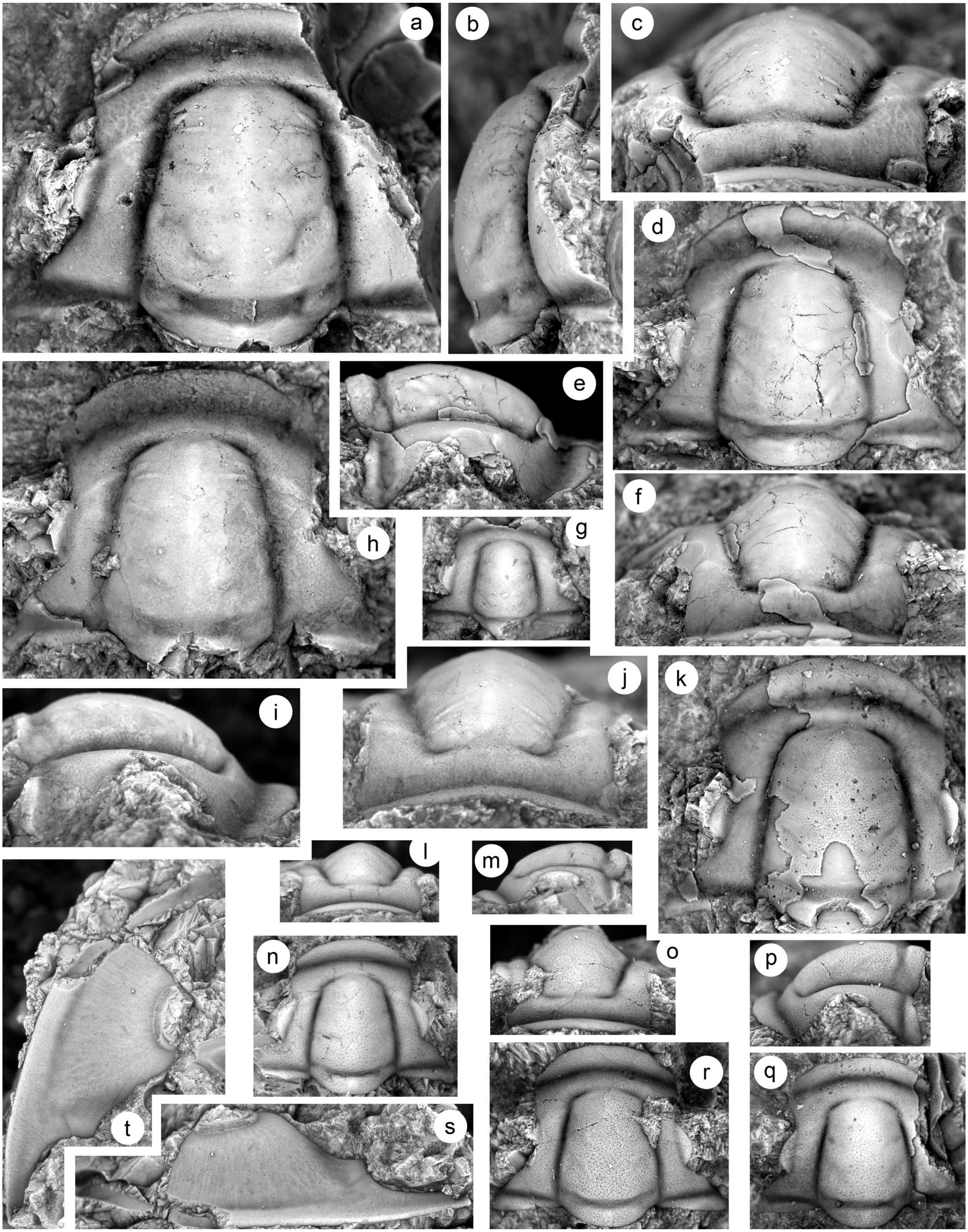
Associated librigenae (Figs. 8*k*–8*m*, 8*o*, 8*r*, 8*s*) at Orr Ridge belong to *B. palmeri* or *B. wilsoni*. Long, weakly convex genal spine present; in smaller specimens (Fig. 8*m*) faint furrow extends along length of spine and convex ridge running along inner edge merges anteriorly with posterior border furrow. Broad (tr., exsag.) librigenal field accounts for about 85% (83%–87%) of librigenal height in lateral view; rim-like eye socle present. Lateral and posterior border furrows are shallow but well defined and merge at posterior corner of librigenal field. Lateral border is convex rim. External surface, except for eye socle, with punctate sculpture; faint caecal markings on librigenal field; fine terrace ridges on outer edge of lateral border.

Hypostome (tentatively assigned) subrectangular in outline, maximum width about 67% of length. Median body subelliptical in outline; median furrow and macculae absent so that anterior and posterior lobes not expressed. Rim-like lateral borders separated from median body by narrow, well-incised border furrows that become shallower posteriorly; posterior border furrow absent. Anterior wings triangular in outline, maximum length (exsag.) equal to about 25% of hypostomal length.

Pygidium subelliptical in outline, with maximum width opposite anterior end of terminal piece; length 43% (38%–48%) of maximum width; convex, with height in posterior view about one third of pygidial width. Posterior margin flexed upward medially in posterior view. Articulating facet at anterior corner with width (tr.) about half width of pleural field. Axis tapers gently backward, length 99% (92%–104%) of width at first axial ring; relatively long and occupies 84% (83%–85%) of pygidial length; width at first axial ring 37% (34%–39%) of maximum pygidial width. Axis composed of three segments, although second ring poorly differentiated from terminal piece; articulating half-ring semielliptical in outline and slightly shorter than first axial ring; one well-defined, transverse ring furrow and second barely perceptible furrow present (Fig. 8*a*); axis strongly convex and accounts for about 67% of pygidia height in posterior view. Pleural field flexed gently downward and separated from weakly convex border by shallow border furrow. One well-defined pleural furrow present at anterior; remaining pleural and interpleural furrows poorly defined. Border accounts for 11% of pygidial length. External surface of axis with sculpture of punctae; remainder of surface is smooth, as are internal molds.

DISCUSSION: Differences between *Bartonaspis palmeri* n. sp., and *B. wilsoni* n. sp. were discussed earlier in the text. Cranidia differ from those of *B. fredericksoni* in having a significantly wider glabella (Fig. 6*a*) and a shorter anterior border (Fig. 6*b*). Pygidia attributed to *B. palmeri* are similar in general outline and proportions to the single specimen available for *B. fredericksoni* (Figs. 11*m*, 11*n*), with the latter differing only in being less rounded posteriorly and in having somewhat more firmly impressed pleural furrows.

Cranidia of *B. palmeri* show minor variation in width between the palpebral lobes and in the curvature of the anterior margin (e.g., compare Figs. 7*e* and 7*i*); punctae of the external surface may be finer and less clearly defined on some, usually larger, individuals (e.g., Fig. 7*a*) and are not exspressed at all on the smallest cranidia (e.g., Figs. 8*n*, 5*d*, 7*l*). Cranidia of *B. wilsoni* display a comparable range of variation (e.g., compare Figs. 4*e*, 4*f*, 4*j*, 4*k*, 4*q*). Variation in pygidial outline is also evident in *B. palmeri*, and some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specimens (Fig. 8*a*) are somewhat shorter and wider than others.

Large cranidia (Figs. 7*a*, 7*d*) display an incomplete row of pits in the anterior border furrow. They are well-defined in front of the fixigenae, but are restricted to a narrow (tr.) medial band in front of the glabella.

Bartonaspis cf. *B. palmeri*
Figs. 9*a*–9*d*

DISCUSSION: A few large cranidia from Orr Ridge resemble similarly sized specimens of *B. palmeri* (Figs. 7*a*–7*d*) in the presence of an abrupt expansion of the glabella opposite the S1 furrow. Weak expansion of the glabella may occur in some smaller specimens assigned to *B. palmeri* (e.g., Fig. 7*e*), but none show the conspicuous expansion of the larger individuals. The interpretation of these differences is unclear given the small sample size, and the large cranidia are placed in open nomenclature.

Bartonaspis fredericksoni n. sp.
Figs. 10*a*–10*t*; 11*a*–11*n*

Dellea? *punctata* Palmer; Stitt, 1971, p. 48, pl. 1, fig 6.

DERIVATION OF NAME: For E.A. Frederickson

HOLOTYPE: A cranidium (OU 12208) from the Honey Creek Formation, Ring Top Mountain, Kimbell Ranch, Slick Hills, Oklahoma, (Figs. 11*a*–11c).

DIAGNOSIS: A species of *Bartonaspis* with relatively long anterior border that occupies 13% (12%–14%) of cranidial length. Glabella relatively long and narrow, with width at occipital furrow in larger individuals (cranidial length (sag.) > 3 mm) equal to 73% (66%–77%) of glabellar length (sag.). Pygidium with relatively short axis that accounts for 81% of pygidial length. Posterior pygidial margin nearly flat in posterior view.

DESCRIPTION: Cranidium exclusive of posterior projection subrectangular in outline, with width between palpebral furrows 81% (77%–86%) of cranidial length. Glabella tapers forward and bluntly rounded anteriorly; width at occipital furrow in larger individuals (cranidial length (sag.) > 3 mm) equal to 73% (66%–77%) of glabellar length (sag.); occupies 81% (77%–86%) of cranidial length; convex and raised well above fixigenae; longitudinal profile arched gently upward in front of occipital ring, but curves downward anteriorly. Preglabellar furrow lightly impressed medially but deepens laterally into slit-like fossulae at anterior corners of glabella; axial furrows shallow but well-defined grooves. Occipital ring with median node and variably expressed inflated lateral lobe; occupies 16% (13%–18%) of glabellar length. Occipital furrow nearly transverse and well incised medially but bifurcates at lateral lobe into short (tr.) posterior branch and longer, finely etched anterior branch that curves forward. Lateral glabellar furrows variably expressed. S1 well-defined, sigmoid and bifurcate with very short anterior branch on some individuals (Figs. 11*a*, 11*f*) but faint on others (Fig. 9*k*); internal molds show similar variation (Figs. 9*a*, 11*j*). S2 generally shallower than S1, also sigmoid; S3 indistinct and nearly transverse. On some internal molds, S3 and S4 expressed as short (tr.) transverse to forwardly oblique ridges (Figs. 10*a*–10*c*, 10*h*–10*j*). Frontal area subequally divided into steeply downsloping, weakly inflated preglabellar field and convex anterior border by forwardly curved anterior border furrow; relatively long anterior border accounts for 13% (12%–14%) of cranidial length. Posterior border furrow broad (exsag.) and firmly impressed; widens distally. Posterior border convex and widens laterally to reach maximum length (exsag.) at posterior corners of cranidium. Palpebral area of fixigenae weakly inflated and equal to 27% (22%–34%) of glabellar width at occipital furrow. Palpebral lobe is flap centered opposite L2 glabellar lobe and with length equal to 29% (24%–35%) of glabellar length; slopes gently upward from shallow and nearly straight palpebral furrow. Palpebral ridge weakly convex and extends obliquely forward to intersect axial furrow in front of S3 lateral furrow. Anterior branches of facial sutures diverge slightly between palpebral lobe and anterior border furrow, then curve sharply inward along anterior cranidial margin; posterior branches diverge backward, following a weakly sigmoid path. Sculpture of closely spaced punctae over entire cranidial surface except furrows.

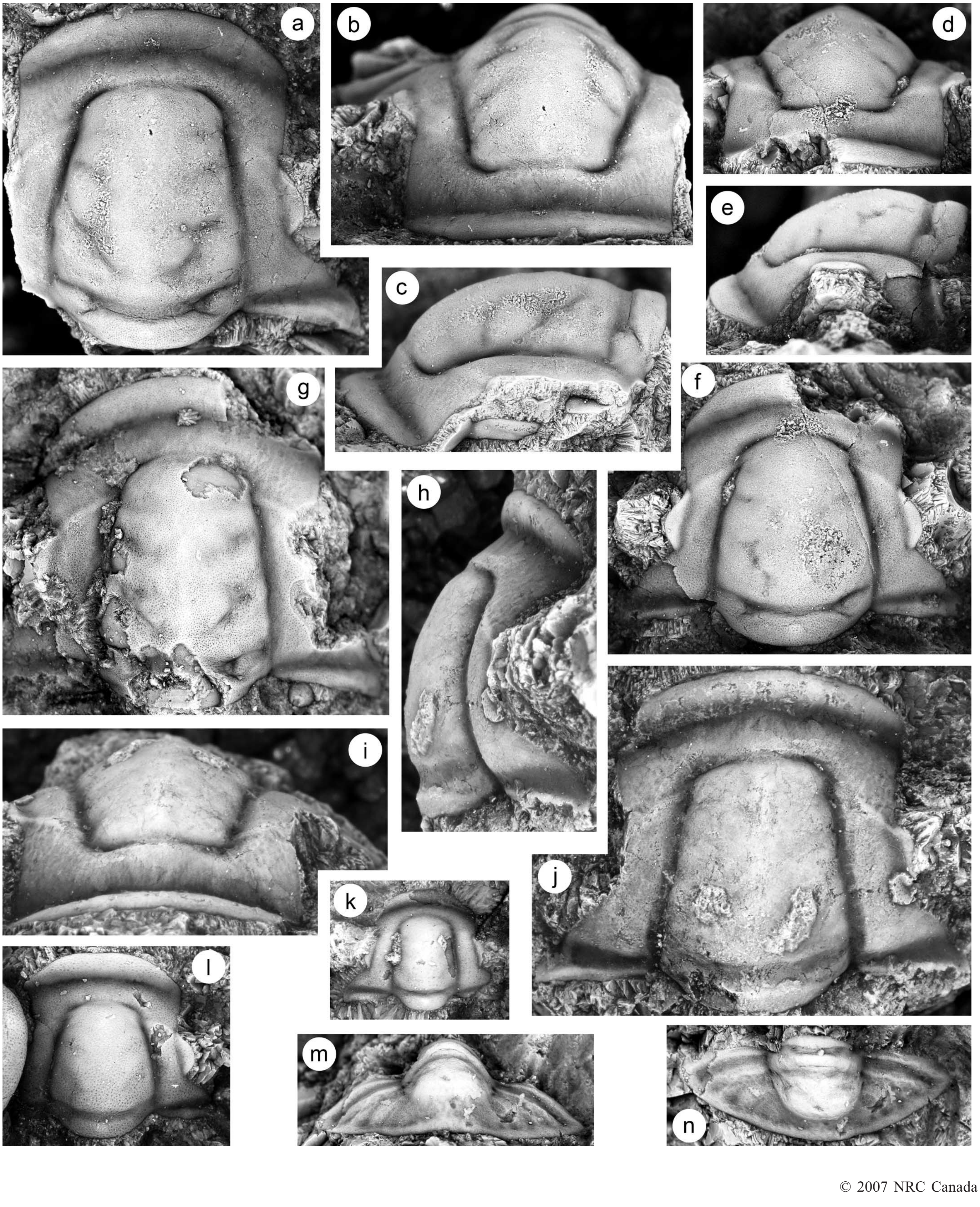
Librigena with long, flattened genal spine. Librigenal field broad (tr., exsag.) and elevated well above weakly convex lateral border; narrow eye socle present. Lateral border furrow shallow groove that becomes faint posteriorly, merges with shallow posterior border furrow. Posterior border weakly convex. Doublure narrow; anteriorly, row of tubercles developed along inner edge. External surface with sculpture of punctae, augmented by genal caecae on librigenal field and fine terrace ridges along outer edge of lateral border.

Pygidium subelliptical in outline, with maximum width opposite anteriormost axial ring furrow; length 39% of maximum width; convex, with height in posterior view about one third of pygidial width. Articulating facet at anterior corner with width (tr.) about half width of pleural field. Axis tapers gently backward, length 88% of width at first axial ring; relatively long and occupies 81% of pygidial length; width at first axial ring 36% of maximum pygidial width. Axis composed of three segments, although second axial ring indistinct; articulating half-ring semielliptical in outline and slightly shorter than first axial ring; one well-defined, transverse ring furrow and second, barely perceptible furrow present; axis strongly convex and accounts for about 70% of pygidial height in posterior view. Pleural field flexed gently downward and separated from weakly convex border by shallow border furrow. One well-defined pleural furrow present at anterior; remaining pleural and interpleural furrows poorly defined. Border accounts for 9% of pygidial length. External surface with sculpture of faint punctae.

DISCUSSION: Cranidia of *Bartonaspis fredericksoni* from Oklahoma consistently display significantly longer anterior borders than specimens of both *B. wilsoni* and *B. palmeri* from the Great Basin (Fig. 6*b*). The single cranidium available from Alberta (Westrop 1986, pl. 28, fig. 12) has a short anterior border comparable to those from the Great Basin, suggesting a biogeographic pattern to species differentiation.

Although all specimens from Oklahoma are united by a relatively long anterior border, there is some variation in glabellar outline and in the expression of glabellar furrows

Fig. 11. *Bartonaspis fredericksoni* n. sp, Honey Creek Formation, all from the Kimbell Ranch section, except 8–10 (Royer Ranch section, Arbuckle Mountains, collection RR142 (Stitt, 1971)); 1–6, 12, float block about 22 m above base of section; 7–8, collection KR1-22.3 – KR1-22.45; 11, 13, 14, collection KR1-24. **(*a–c*)** cranidium, OU 12208 (**holotype**), dorsal, anterior, and lateral views, ×8. **(*d–f*)** cranidium, OU 12209, anterior, lateral, and dorsal views, ×8. (*g*) cranidium, OU 12210, dorsal view, ×8. **(*h–j*)** cranidium, lateral, anterior, and dorsal views, ×8. **(*k*)** cranidium, OU 12211, dorsal view, ×12. *(l)* cranidium, OU 12212, dorsal view, ×12. **(*m–n*)** pygidium, OU 12213 posterior and dorsal views, ×12.



and the lateral lobes of the occipital ring. If end-member variants (e.g., Figs. 11*g*, 11*j*) are compared in isolation, a case could be made for the presence of more than one species. However, other cranidia fill in the "gap" in glabellar outline (e.g., Figs. 10*h*, 11*a*, 11*f*), and expression of glabellar furrows varies in otherwise closely comparable cranidia (e.g., Figs. 10*a*, 10*h*). Accordingly, only a single species is recognized at present.

Although the librigena has a row of small tubercles on the inner edge of anterior portion of the doublure (Figs. 10*s*, 10*t*), a complementary row of pits in the anterior border furrow is not evident on the cranidia. However, a pit row is present on at least some specimens of *B. palmeri* (Figs. 8*a*, 8*d*)

The pygidium of *B. fredericksoni* is most like that of *B. palmeri* (Figs. 5*m*–5*r*), differing only in having a slightly shorter axis and in lacking the arching of the posterior margin in posterior view.

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