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Late Cambrian ptychaspidid trilobites from western Utah: implications for trilobite systematics and biostratigraphy

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Abstract – The Notch Peak Formation (Late Cambrian, Sunwaptan) of western Utah yields diverse silicified trilobite faunas that provide new information on the anatomy of many taxa. The family Ptychaspididae Raymond, 1924, is represented by species of *Keithiella* Rasetti, 1944; *Idiomesus* Raymond, 1924; *Euptychaspis* Ulrich *in* Bridge, 1931; and *Macronoda* Lochman, 1964. At least four species are new, of which *E. lawsonensis* and *M. notchpeakensis* are named formally. Much previous work on Late Cambrian trilobites has emphasized biostratigraphic utility and the recognition of geographically widespread species. Data from new silicified collections indicate that this approach is difficult to justify because many putative 'index species' actually represent a plexus of closely related species whose biostratigraphic significance has yet to be determined. One such plexus is represented by *E. kirki* Kobayashi, 1935, whose previously reported occurrences in Texas, Oklahoma, Utah, Nevada and northern Canada record at least four distinct species. Similarly, *Macronoda* can now be shown to consist of at least five late Sunwaptan species in south-central and western North America.

Keywords: Cambrian, Great Basin, Trilobita.

1. Introduction

Secondarily silicified sclerites recovered by acid digestion of limestone offer unparalleled insight into morphology, variation and ontogenetic development of trilobites. Silicified material has advanced our understanding of Ordovician (e.g. Evitt, 1951; Whittington, 1956, 1959; Whittington & Evitt, 1954), Silurian (e.g. Chatterton & Perry, 1983; Adrain, 1997; Adrain & Edgecombe, 1997) and Devonian (e.g. Chatterton, 1971) faunas significantly, but information from the Cambrian has been more limited. The Great Basin of the western United States has been known for its silicified Early Ordovician trilobite faunas for half a century (Ross, 1951; Hintze, 1953) and a new program of field work is yielding diverse silicified faunas in the underlying Cambrian strata (Adrain & Westrop, 2004). Here, we document latest Cambrian (Sunwaptan) ptychaspidid trilobites using silicified sclerites from the Notch Peak Formation in western Utah.

The order of authorship is alphabetical and does not indicate seniority.

2. Localities and stratigraphy

The stratigraphy of the Notch Peak Formation (Walcott, 1908*a*,*b*) has been revised by Hintze, Taylor & Miller (1988) and more recently by Miller *et al.* (2001). The formation is composed of shallow-water carbonates and is divided into three members, in ascending order, the Hellnmaria, Red Tops and Lava Dam members (Hintze, Taylor & Miller, 1988). All of the trilobites described in this paper are from the Lava Dam Member, a unit of lime mudstones, bioclastic, intraclastic oolitic grainstones, intrarudites and microbial boundstones that is up to 89 metres in thickness (Hintze, Taylor & Miller, 1988; Miller *et al.* 2001). The Lava Dam Member ranges in age from late Sunwaptan (Millardan Series) to early Skullrockian (Ibexian Series), with the stage boundary lying near the middle of the member (Miller *et al.* 2001, fig. 1). The Cambrian–Ordovician boundary lies in the Barn Canyon Member of the overlying House Limestone (Miller *et al.* 2001, fig. 1).

Trilobites were collected from sections (Fig. 1) in the southern House Range (Lava Dam Five, LD5 herein) and the northern Wah Wah Mountains (Lawson Cove, LAW herein). Detailed lithological logs of stratigraphic sections and descriptions of the localities have been published recently by Miller *et al.* (2001, appendix) and need not be repeated here. Miller and colleagues have painted footages on the sections, and our collections are tied into their measurements, which we have converted into metres.

2.a. Section Lava Dam Five

Two collections were made *in situ* at LD5 25.3 m (34.1 kg) and LD5 30.5 m (73.3 kg) and a third from

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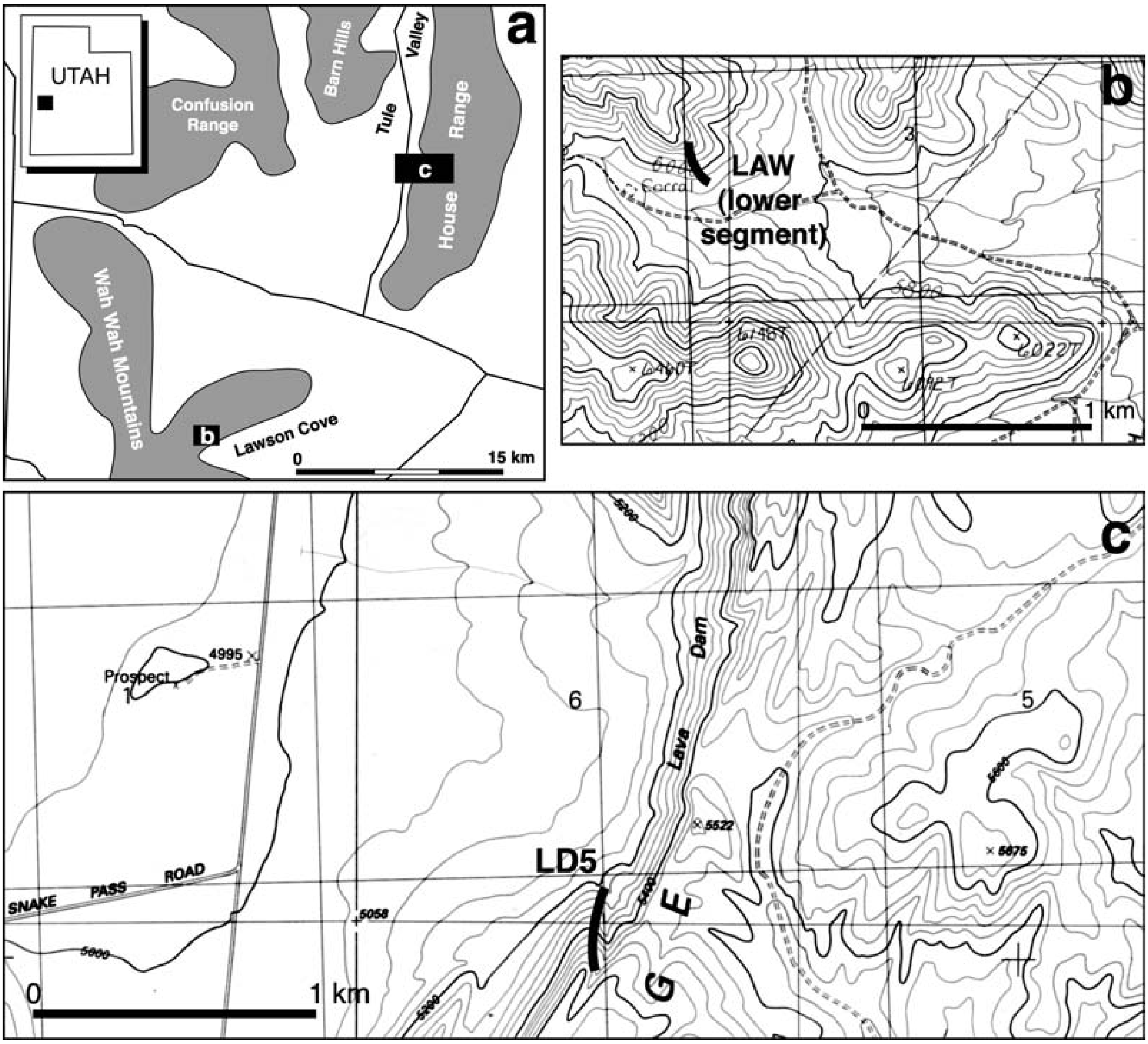

Figure 1. Maps showing the locations of the Lava Dam Five (c) and Lawson Cove (b) measured sections (see Miller *et al.* 2001, for detailed lithological logs of the sections). Base maps taken from United States Geological Survey Grassy Cove (b) and Red Tops (c) 7.5′ quadrangle maps (public domain).

talus at LD5 16.8T m (23.8 kg). Both LD5 16.8T m and LD5 25.30 m are from unit 32 of Miller *et al.* (2001, p. 61) at 55 and 83 feet, respectively, above the base of their measured section. LD5 30.5 m is from unit 35, a 15 cm thick unit between 100.5 and 101 feet above the base of the section. These numbers correspond to those painted on the section. Note that the remeasurements of Miller *et al.* (2001, pp. 58–9) deviate slightly (0.9 m) from these. The talus collection includes several blocks and may therefore represent more than one horizon. However, the blocks were found in close association with one another on a small patch of slope. Care was taken during acid digestion to keep the blocks separate in case they yielded distinct faunal assemblages. It was found that the blocks and both of the *in situ* horizons at LD5 contain similar associations of the same species in similar relative abundances. Hence, all of the talus collection is reported using a single designation.

2.b. Section Lawson Cove

A 70.3 kg collection was made from a single horizon in the Lava Dam Member (LAW 25.3 m). It was collected from a 30 cm thick ledge of bioclastic wackestone in unit 9 of Miller *et al.* (2001, p. 54), between 82 and 83 feet in the lower segment of the section.

2.c. Relative stratigraphic position of collections

The relative positions of the collecting horizons can be estimated by reference to the base of the Tank Canyon Bed of Miller *et al.* (2001), a regional marker bed composed of ooid and intraclast grainstone. Horizon LD5 30.5 m is 10.0 m beneath the Tank Canyon Bed, and LD5 25.3 m is 15.2 m below it. At Lawson Cove, horizon LAW 25.3 m is 23.3 m below the Tank Canyon Bed. The talus collection LD5 16.8T m is

23.7 m beneath the Tank Canyon Bed. Hence, LAW 25.3 m is the oldest *in situ* collection, and the talus collection from LD5 was probably derived from strata intermediate in position between it and LD5 25.3 m (assuming, as seems likely, that the talus travelled downslope more than 40 cm). The talus collection from LDN 16.8T m does not appear to have been derived from either LD5 25.3 m or LD5 30.5 m, as the amount of insoluble residue present and relative abundances of taxa do not match those at the higher *in situ* horizons. The silicification of the Lawson Cove horizon is quite different from that of all of the Lava Dam Five collections. The latter are quite coarsely silicified with abundant sclerites. The Lawson Cove sample is finely silicified, with a tendency for more fragmentary specimens, and sclerites are much less abundant per unit volume of rock. Although common species such as *Euptychaspis lawsonensis* sp. nov. and *Macronoda notchpeakensis* sp. nov. are shared among all collections from both sections, there are several species, including *Euptychaspis* sp. nov. A and other taxa awaiting description, which occur only at the Lawson Cove horizon.

3. Sampling, systematics and biostratigraphy

Much of the earlier work on Sunwaptan trilobites has focused on biostratigraphy, and an emphasis on establishing interregional correlations has led to the recognition of geographically widespread species that are commonly based only on cranidial morphology. However, new silicified material is revealing significant character variation in other sclerites (pygidia and librigenae). Moreover, as discussed below, restudy of type material shows that even cranidial morphology of such supposedly widespread, biostratigraphically important species as *Euptychaspis kirki* Kobayashi, 1935 also varies between occurrences. Many traditional trilobite species may prove to be groups of closely related species and it is essential that standards of documentation in the literature be improved greatly in order to evaluate this hypothesis. The data generated in this study (see also Adrain & Westrop, 2004) indicate that it is no longer possible to justify cursory illustration and taxonomic treatment because species have been ‘well described and illustrated’ (Loch, Stitt & Derby, 1993, p. 507; Stitt & Straatmann, 1997, p. 96) in other regions. Many putative occurrences of ‘index species’ cannot be evaluated critically from the supporting published information and this clearly undermines the biostratigraphic conclusions that are based on them. Although our comments are directed towards the literature on North American Late Cambrian trilobites, the problems of inadequate documentation pervade trilobite studies in general.

Euptychaspis provides an important illustration of the impact of inadequate taxonomic treatment on biostratigraphic interpretation. A number of workers (e.g. Loch, Stitt & Derby, 1993) have attempted to apply a standard zonation to the Sunwaptan succession of Laurentian North America. This zonation is based upon the trilobite faunas of Texas (Winston & Nicholls, 1967; Longacre, 1970) and Oklahoma (Stitt, 1971, 1977), and *E. kirki* Kobayashi, 1935 is among the species used to recognize the youngest *Prosaukia serotina* Subzone. However, as discussed below, the type material of this species, from Upper Cambrian strata of Nevada, is poorly preserved so that it is impossible to determine whether the limited number of cranidia illustrated from Texas (Winston & Nicholls, 1967, pl. 9, fig. 18) and Oklahoma (Stitt, 1971, pl. 6, fig. 21) represent the same species. We demonstrate that silicified sclerites from the Notch Peak Formation, identified by Taylor (*in* Miller *et al*. 1982) as *E. kirki*, represent a new species (Figs 4, 5, 6a–v, aa, bb, hh), and sclerites from the Rabbitkettle Formation of northern Canada, attributed to *E. kirki* by Westrop (1995, pl. 7, figs 17–21), likely belong to a second new species. Thus, a primary criterion used to correlate the *P. serotina* Zone across North America collapses completely under critical scrutiny. Rather than a single ‘index species’, there is a plexus of closely related species. Using the base of the Ibexian Series (bases of the *Cordylodus proavus* and *Eurekia apopsis* zones) as a reference point, each member of this group of species is of late Sunwaptan age. However, most are poorly documented, including their stratigraphic ranges, and it is not yet possible to use them for more than local biostratigraphic correlation. Adrain & Westrop (2004) documented similar problems in *E. typicalis* Ulrich *in* Bridge, 1931 and concluded that the published record also represents a group of closely related species.

A similar pattern is emerging from our work on *Macronoda* Lochman, 1964. The late Sunwaptan record of this genus can now be shown to comprise at least five distinct species: *M. prima* Lochman, 1964; *M. extrema* (Lochman, 1964); *M. punctata* Derby, *in* Loch, Stitt & Derby, 1993; *M. notchpeakensis* sp. nov.; and an unnamed species from the Wilberns Formation of Texas. As with the *E. kirki* group, these species are broadly coeval but most are not documented well enough for biostratigraphic purposes.

If *Euptychaspis* and *Macronoda* are any indication, the empirical basis for trilobite-based biostratigraphic correlation in the Sunwaptan is problematic at best. The utility of the Texas–Oklahoma zonation is undermined by the woefully inadequate documentation of most of the species (Frederickson, 1949; Bell & Ellinwood, 1962; Winston & Nicholls, 1967; Longacre, 1970; Stitt, 1971, 1977) on which it is based. Until these species are given a comprehensive revision that includes extensive illustration, the use of a standard Sunwaptan trilobite zonation is difficult to justify and will give a misleading impression of the current state of knowledge.

Finally, we note that many of the classic works dealing with older Cambrian faunas of Laurentia (e.g. Palmer, 1960, 1962, 1965; Robison, 1964) also provide photographic documentation of a limited number of

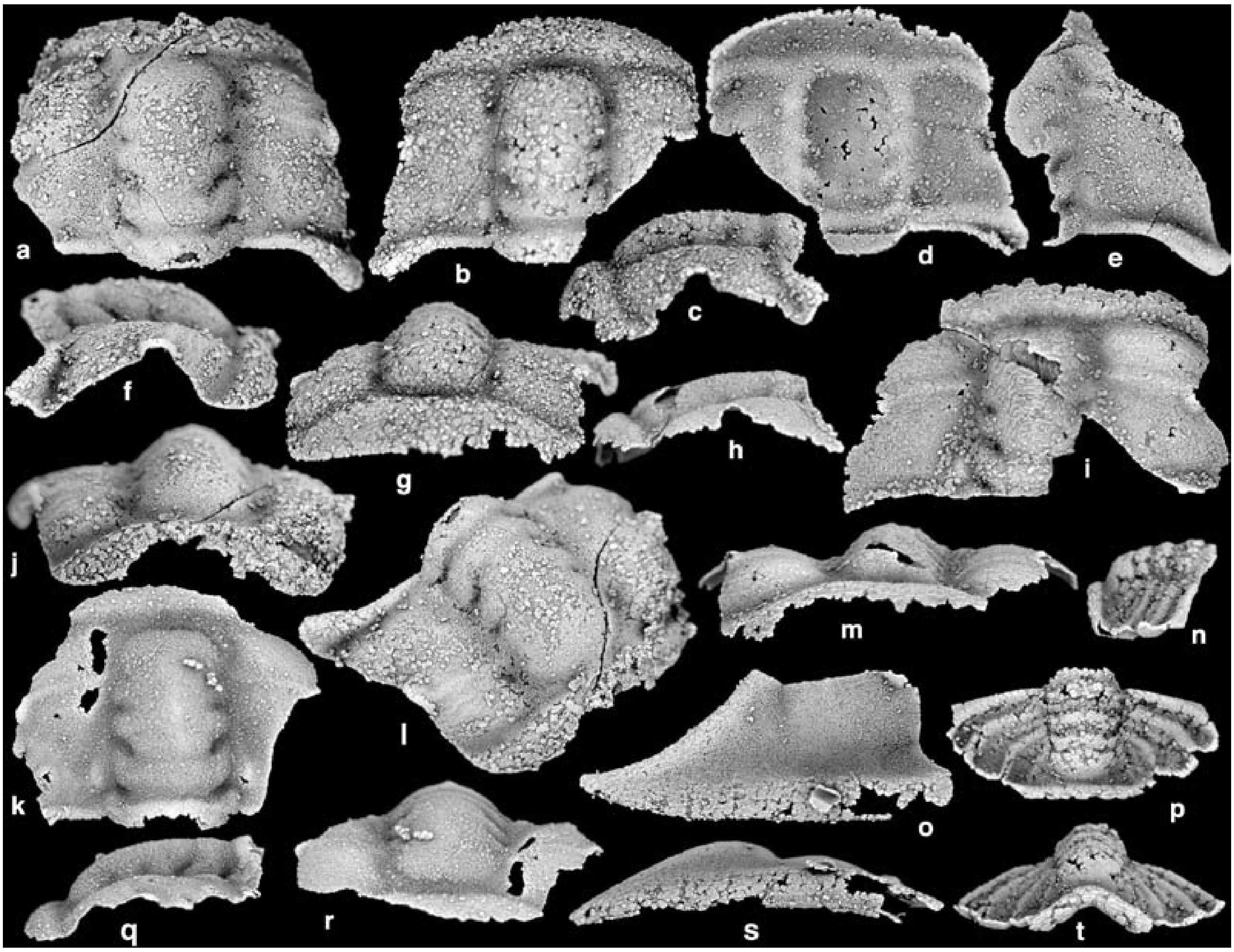

Figure 2. *Keithiella* sp. nov. A. (a, f, j, l) Cranidium, SUI 97618, dorsal, right lateral, anterior, and oblique views, ×7.5 (LD5 16.8T m); (b–d, g) cranidium, SUI 97619, dorsal, left lateral, ventral, and anterior views, ×7.5 (LD5 30.5 m); (e) cranidium, SUI 97620, dorsal view, ×6 (LD5 16.8T m); (h, i, m) cranidium, SUI 97621, left lateral, dorsal, and anterior views, ×5 (LD5 30.5 m); (k, q, r) cranidium, SUI 97622, dorsal, left lateral, and anterior views, ×6 (LAW 25.3 m); (n, p, t) pygidium, SUI 97623, right lateral, dorsal, and posterior views, ×7.5 (LD5 30.5 m); (o, s) right librigena, SUI 97624, external and ventrolateral views, ×7.5 (LD5 16.8T m).

specimens for each species, and it is likely that future studies will reveal problems similar to those that we describe herein. In our opinion, confidence in trilobite biostratigraphy cannot be restored without new standards of documentation.

4. Systematic palaeontology

Type and figured material is deposited in the Paleontology Repository, Department of Geoscience, University of Iowa (prefix SUI) and the National Museum of Natural History, Washington, D.C. (prefix USNM). In the descriptions, measurement data (proportions in%) are reported as mean values with the range in parentheses.

Family PTYCHASPIDIDAE Raymond, 1924
Subfamily PTYCHASPIDINAE Raymond, 1924
Genus *Keithiella* Rasetti, 1944

Type species. *Arionellus cylindricus* Billings, 1860, from the Lévis Formation, Quebec, Canada.

Keithiella sp. nov. A
Figure 2

Material and occurrence. SUI 97618–97624; occurs at all sampled horizons.

Description. Cranidium subrectangular in outline, length (sag.) about 80 % of maximum width, with gently curved anterior margin; strongly arched, with maximum height in anterior view 51 % of cranidial width. Axial and preglabellar furrows shallow, clearly defined grooves. Glabella parallel-sided and subrectangular in outline, width at S2 56 % (54–57) of length, with bluntly rounded anterior margin; strongly convex, height in anterior view accounting for about 60 % of cranidial height, and raised well above fixigenae. Longitudinal profile nearly flat between occipital ring and S2 furrow, becoming curved downward along frontal lobe. S0 moderately impressed, roughly transverse medially but curved forward and somewhat deeper near axial furrows; L0 accounts for 17 % (16–18) of glabellar length (sag.). S1 well-incised near axial furrow, directed backward at 40° (37–43) from transverse plane; connected across glabella by faint, nearly transverse groove. L1 equal in length (exsag.) to L0 (sag.). S2 short, oblique, directed backward at 38° (36–40); L2 equal in length to L0. S3 ranging from short (Fig. 2k) to a barely perceptible notch in smaller specimens (Fig. 2a, b, d). Anterior border furrow shallow groove, gently curved forward and confluent with preglabellar furrow. Anterior border transversely sub-semielliptical in outline, length (sag.) equal to about 18 % of cranidial length, shorter exsagittally; convex, with steeply sloping anterior margin. Palpebral lobe small, length (exsag.) about 20 % of glabellar length (sag.), midlength located opposite S2 glabellar furrow. Weak but clearly defined eye ridge curved gently forward from palpebral lobe, intersecting axial furrow opposite S3. Anterior branches of facial sutures nearly parallel before swinging inward along anterior cranidial margin; posterior branches weakly divergent and follow faintly sigmoid course. Fixigena broad, maximum width equal to 73 % of glabellar width (73–74), and moderately arched in lateral and anterior views. Small bacculae present opposite L1 glabellar lobe. Posterior border transverse near axial furrow, but deflected backward distally at angle of 37° (33–43); longer (exag.) distally; posterior border furrow well-incised groove. External surface of exoskeleton and sculpture not preserved.

Librigena with short, subtriangular genal spine. Librigenal field moderately arched and separated from convex lateral and posterior borders by broad, shallow border furrows. Lateral border extends posteriorly on dorsal aspect of genal spine. Visual surface tiny. External surface smooth, apart from terrace ridges on borders.

Pygidium sub-semielliptical in outline, maximum length about half maximum width, and strongly convex, with maximum height in posterior view about 40 % of maximum width. Conspicuous median arch evident in posterior view (Fig. 2t). Axis long, occupying about 85 % of pygidial length, very gently tapered and rounded posteriorly; convex, accounting for about 55 % of maximum pygidial height in posterior view, and with lateral profile that slopes gently backward before dipping steeply downward at posterior margin. Three subequal, roughly transverse axial rings and slightly longer terminal piece separated by shallow axial ring furrows. Pleural fields slope downward from axis, with dip increasing from about 30° at anterior end of pygidium to about 50° near posterior end of axis. Strongly incised pleural furrows separate convex anterior and posterior pleural bands that are subequal in length; interpleural furrows are narrow grooves. Posterior and lateral borders are narrow, convex rims, with closely spaced terrace lines on posterior aspect.

Discussion. A species of *Keithiella* occurring in the Notch Peak Formation is clearly new, but the fragmentary nature and sparseness of the available material precludes formal naming. Comparison can be made with the poorly known *Keithiella patula* Winston & Nicholls (1967, pl. 10, figs 4, 7) from the Wilberns Formation of Texas, which was erected on the basis of tiny stereopair photographs of two cranidia. Both species possess a relatively wide fixigena, a clearly defined eye ridge, small palpebral lobes, and anterior sections of the facial suture that are not strongly anteriorly divergent. The course of the posterior branches of the facial sutures is not clearly visible on Winston & Nicholls' figures, but it appears that, like the Notch Peak species, *K. patula* has weakly divergent posterior sutures. There are numerous differences. In *K. patula*, S1 is a complete and well-impressed transverse furrow. The two illustrated specimens of *K. patula* are internal moulds, which will serve to enhance this feature. However, even in ventral view (Fig. 2d), the S1 of *Keithiella* sp. nov. A has only very weak expression medially. The anterior glabellar lobe of *K. patula* is inflated and forwardly expanding. Smaller specimens of *Keithiella* sp. nov. A (Fig. 2a, b) have a moderately inflated anterior lobe, but in large specimens (Fig. 2i, k) the lobe is subdued and markedly narrower than the posterior glabella. The frontal area between the eye ridge and anterior border furrow of *Keithiella* sp. nov. A is much shorter (exsag.) than that of *K. patula*. Finally, the palpebral lobe of *K. patula* (Winston & Nicholls, 1967, pl. 10, fig. 7) is large, with a conspicuous palpebral furrow, whereas that of *Keithiella* sp. nov. A is tiny, corresponding to the very small eye (Fig. 2o), and is set off from the interocular fixigena by a break in slope, with no impressed furrow. A single cranidium from the Signal Mountain Limestone of Oklahoma, identified by Stitt (1971, p. 43, pl. 7, fig. 13) as *K.* cf. *K. patula*, is not conspecific with *Keithiella* sp. nov. A. It differs in having a relatively narrower glabella, inflated fixigenae and, consequently, elevated palpebral lobes.

Relatively wide fixigenae are also characteristic of *K. scrupulosa* Ellinwood (*in* Bell & Ellinwood, 1962, pl. 58, figs 19–21), which is known from three fragmentary cranidia from the Wilberns Formation, Texas. However, this species differs from *Keithiella* sp. nov. A in having somewhat larger palpebral lobes that are set further back on the cranidium (centred opposite L2 rather than S2). Also, the anterior border furrow is expressed on internal moulds of *K. scrupulosa* as a continuous, deep groove that is tangential to, but does not merge with, the preglabellar furrow. The external surface of the exoskeleton is not preserved in any of the cranidia illustrated from Texas but, on internal moulds, the glabella is 'finely but unevenly pustulose' (Bell & Ellinwood, 1962, p. 405). In contrast, the underside of the glabella of *Keithiella* sp. nov. A is smooth (Fig. 2d). The status of an exfoliated cranidium attributed to *K. scrupulosa* by Stitt (1977, pl. 3, fig. 7) is uncertain and it may prove to represent a separate species. As recognized by Stitt (1977, p. 43), the surface of the mould carries a much stronger tuberculate sculpture than the type material from Texas and extends over the glabella, fixigenae and border. It also appears to have larger palpebral lobes, more inflated fixigenae and weaker eye ridges.

The type species of *Keithiella*, *K. cylindrica* (Billings, 1860) (Ludvigsen, Westrop & Kindle, 1989, pl. 19, figs 10–16) from Quebec and Newfoundland, has narrower interocular fixigenae and more strongly divergent anterior and posterior branches of the facial sutures than *Keithiella* sp. nov. A. Consequently, cranidial width across the palpebral lobes is about 70 % of the posterior width (tr.) of the fixigenae in *K. cylindrica*, but is about 80 % in *Keithiella* sp. nov. A. In addition, glabellar furrows are expressed as more prominent ridges on the ventral surface of the exoskeleton (as indicated by the depth of the furrows on internal moulds) of *K. cylindrica*, and well-defined S3 and S4 are present; S1 is particularly well-expressed and curves sharply backward, almost isolating the lateral portions of L1. The librigena of the two species are quite distinct. For example, *K. cylindrica* (Ludvigsen, Westrop & Kindle, 1989, pl. 19, fig. 11) has a broad, convex lateral border whose maximum width is greater than that of the librigenal field, whereas the lateral border of *Keithiella* sp. nov. A (Fig. 2o, s) is relatively narrow.

Keithiella depressa Rasetti (1944; Ludvigsen & Westrop, 1983, pl. 16, fig. 12) was originally described from Quebec and has been reported subsequently from New York State (Ludvigsen & Westrop, 1983, pl. 16, figs 1–11) and Newfoundland (Ludvigsen & Westrop, *in* Ludvigsen, Westrop & Kindle, 1989, pl. 20, figs 1–4). All cranidia previously assigned to this species differ from those of *Keithiella* sp. nov. A in having larger palpebral lobes, more divergent branches of the posterior facial sutures and, consequently, relatively greater width (tr.) along the posterior cranidial margin. With one exception (Ludvigsen, Westrop & Kindle, 1989, pl. 20, figs 1–2), all previously illustrated cranidia of *K. depressa* have anterior border furrows that are expressed only in front of the fixigenae and, unlike those of *Keithiella* sp. nov. A, do not merge with the preglabellar furrow. Librigenae from New York (Rasetti, 1946, pl. 1, fig. 7; Ludvigsen & Westrop, 1983, pl. 16, fig. 7) are closely comparable to that of *Keithiella* sp. nov. A, differing only in the possession of much better impressed lateral and posterior border furrows. Information on pygidial morphology is limited but suggests that the current concept of *K. depressa* may prove to include more than one species. Pygidia from the Hoyt Formation of New York (Ludvigsen & Westrop, 1983, pl. 16, fig. 8; see also Rasetti, 1946, pl. 1, figs 8–9) uniformly possess four well-defined axial rings and a terminal piece, whereas the single pygidium illustrated from the Shallow Bay Formation of Newfoundland (Ludvigsen, Westrop & Kindle, 1989, pl. 20, fig. 3) has only three well-defined rings and a terminal piece. Cranidia from New York have tuberculate sculpture (Rasetti, 1946, pl. 1, figs 4–6; Ludvigsen & Westrop, 1983, pl. 16, figs 5–6, 9–11), although it is poorly expressed on some internal moulds (Westrop & Ludvigsen, 1983, pl. 16, figs 1–4). Well-preserved internal moulds of cranidia from Newfoundland (Ludvigsen, Westrop & Kindle, 1989, pl. 20, figs 1–2, 4) show no trace of tuberculate sculpture, and the surfaces are finely pitted. Ludvigsen & Westrop (1983) considered *K. maior* Rasetti (1945), from the Lévis Formation, Quebec, to be a synonym of *K. depressa*. However, *K. maior* clearly possesses tuberculate sculpture (Ludvigsen & Westrop, 1983, pl. 16, fig. 13) and it is possible that this species should be reinstated, and include material from New York.

Genus *Idiomesus* Raymond, 1924

Type species. *Idiomesus tantillus* Raymond, 1924 from the Gorge Formation, Vermont, USA.

Idiomesus cf. *I. intermedius* Rasetti, 1959
Figure 3

1959 *Idiomesus intermedius* Rasetti, p. 393, pl. 51, figs 25, 26.

Material and occurrence. Assigned specimens SUI 97625–97645; occurs at all sampled horizons.

Discussion. Opinion has varied on the status of *Idiomesus intermedius* (e.g. see Longacre, 1970; Stitt,

Figure 3. *Idiomesus* cf. *I. intermedius* Rasetti, 1959. Specimens are from LD5 16.8T m and are ×10 except where noted. (a, f, m, t, aa) Cranidium, SUI 97625, dorsal, left lateral, anterior, oblique, and ventral views; (b, g, n, u) cranidium, SUI 97626, dorsal, left lateral, anterior, and ventral views; (c, h, o) cranidium, SUI 97627, dorsal, left lateral, and anterior views; (d, i, k) cranidium, SUI 97628, dorsal, right lateral, and anterior views; (e, j, l) cranidium, SUI 97629, dorsal, right lateral, and anterior views; (p, r, x) cranidium, SUI 97630, dorsal, left lateral, and anterior views; (q, s, z) cranidium, SUI 97631, dorsal, left lateral, and anterior views; (v, w, bb) cranidium, SUI 97632, dorsal, left lateral, and anterior views; (y, ee, ii) cranidium, SUI 97633, left lateral, dorsal, and anterior views; (cc, dd, hh) cranidium, SUI 97634, dorsal, right lateral, and anterior views; (ff, gg, kk) cranidium, SUI 97635, dorsal, anterior, and right lateral views, (LD5 25.3 m); (jj, uu, yy) cranidium with attached librigena and thoracic segments, SUI 97636, dorsal, left lateral, and anterior views, ×15 (LD5 25.3 m); (ll, mm, rr) cranidium, SUI 97637, right lateral, dorsal, and anterior views (LD5 30.5 m); (nn, ss, ww) cranidium, SUI 97638, dorsal, left lateral, and anterior views (LD5 30.5 m); (oo, pp, tt) cranidium, SUI 97639, dorsal, anterior, and left lateral views (LAW 25.3 m); (qq, vv, zz) left librigena, SUI 97640, external, ventral, and anterior views (LD5 30.5 m); (xx, ccc, ggg) right librigena, SUI 97641, internal, external, and ventral views; (aaa, eee) left librigena, SUI 97642, internal and external views; (bbb) left librigena, SUI 97643, external view (LD5 30.5 m); (ddd) left librigena, SUI 97644, external view; (fff) right librigena, SUI 97645, external view, ×15.

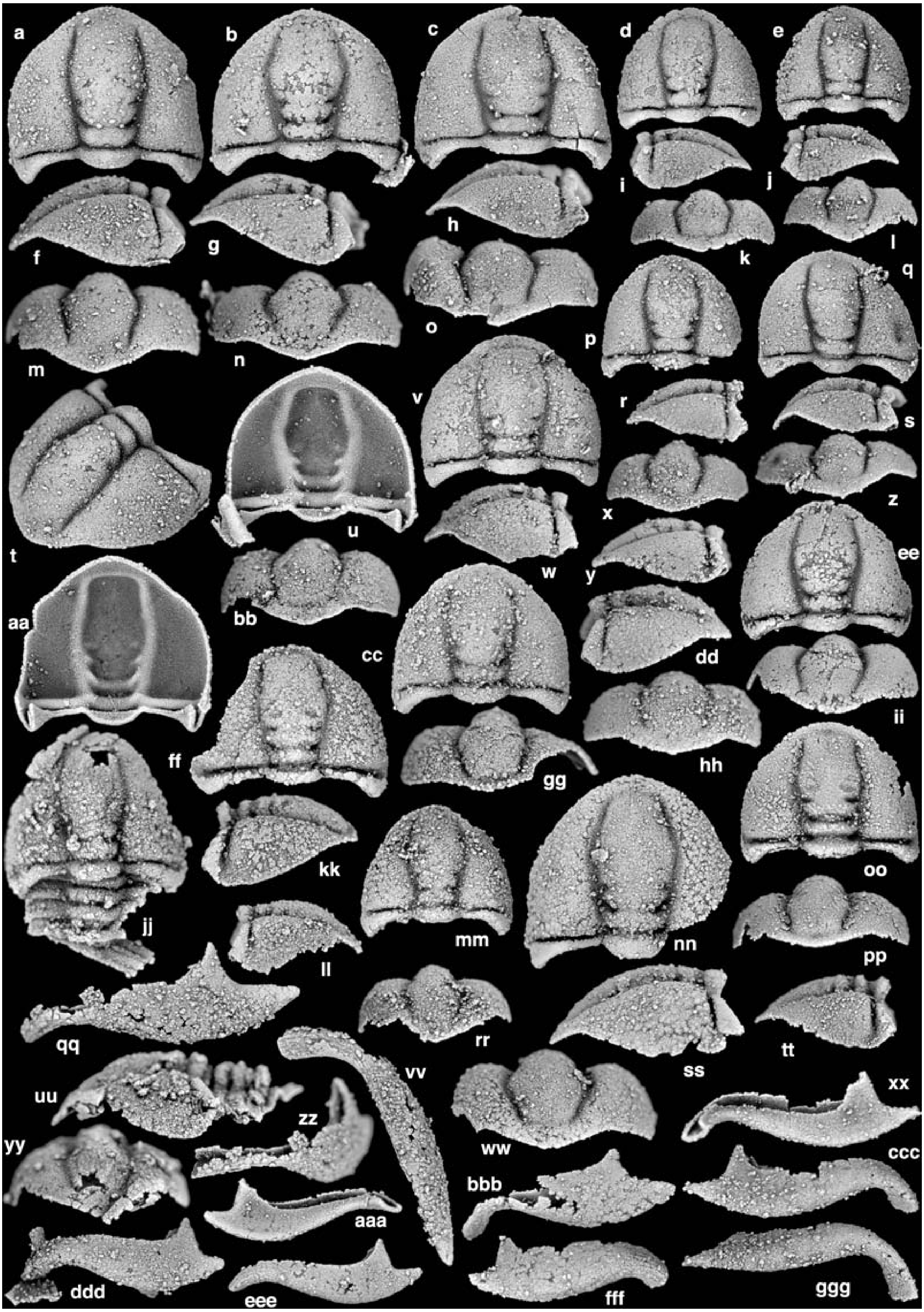

Figure 3. For caption see facing page.

1971), but recent work (e.g. Ludvigsen & Westrop, 1986; Loch, Stitt & Derby, 1993; Westrop, 1995) has followed Taylor (1976) in assigning to the species cranidia with narrow (tr.) posterior segments of the axial furrows and S3 that are faint or absent. Critical evaluation of these assignments is hindered by the limited information available for other sclerites. However, the few pygidia that have been illustrated to date raise the possibility that more than one species may be represented amongst material previously assigned to *I. intermedius*. Pygidia preserved as internal moulds from the *Eurekia apopsis* Zone at Wilcox Peak (Westrop, 1986*b*, pl. 11, fig. 16) and Mt Wilson (Loch, Stitt & Derby, 1993, fig. 6.14), Alberta, possess conspicuously tapered axes that are composed of at least five relatively short rings. Silicified pygidia from the Mackenzie Mountains (Ludvigsen, 1982, fig. 57I, M; Ludvigsen & Westrop, 1986, fig. 4C) have more parallel-sided axes that are divided in four longer rings. This problem cannot be resolved because pygidia have not been recovered from the type area of *I. intermedius* in Pennsylvania and Maryland (Rasetti, 1959). In the absence of associated pygidia, the cranidia and librigenae from the Notch Peak Formation are placed in open nomenclature, and previous reports of *I. intermedius* outside of the type area should also be treated in this way.

The lack of pygidia in the Notch Peak samples similar to those assigned by Ludvigsen (1982) and Westrop (1986*b*) is curious, as in some samples, cranidia and librigenae of the species are quite common. The previously assigned pygidia, furthermore, are well within the size range of the smaller cranidia illustrated in Figure 2 and should therefore be expected to be fairly abundant. The sample of *Idiomesus intermedius* illustrated by Adrain & Westrop (2004) also entirely lacked assignable pygidia. In isolation, these silicified samples would suggest that *Idiomesus* was strongly micropygous, with the tiny pygidia not preserved in the relatively coarse silicification characteristic of the samples. The assignment of pygidia in the Survey Peak Formation samples (Westrop, 1986*b*; Loch, Stitt & Derby, 1993), however, is strongly supported by their relative abundance, the fact that *Idiomesus* is a common component of a low-diversity fauna, and the absence of any other species with which the ptychaspidine pygidia might be associated. Further, Ludvigsen's (1982) pygidia from the Rabbitkettle Formation are a close match. It is conceivable that the absence of pygidia in both the Windfall (Adrain & Westrop, 2004) and Notch Peak samples is due to taphonomic factors, though small pygidia of other taxa are common in both formations.

Librigenae of *I.* cf. *I. intermedius* illustrated herein (Fig. 3qq, vv, xx, zz, aaa–ggg) have shorter genal spines and somewhat narrower (tr.) librigenal fields than those of specimens assigned to *I. levisensis* (Rasetti, 1944) from the Windfall Formation of eastern Nevada by Adrain & Westrop (2004, pl. 4, figs 18–20, 22, 23).

Subfamily EUPTYCHASPIDINAE Hupé, 1953

Genus *Euptychaspis* Ulrich *in* Bridge, 1931

Type species. *Euptychaspis typicalis* Ulrich *in* Bridge, 1931, from the Eminence Dolomite, Missouri, USA.

Discussion. Over the last 35 years, most workers (e.g. Longacre, 1970; Stitt, 1971, 1977; Ludvigsen, 1982; Westrop, 1986*b*, 1995; Loch, Stitt & Derby, 1993) have recognized three distinct species of *Euptychaspis*: *E. typicalis* Ulrich *in* Bridge, 1931; *E. kirki* Kobayashi, 1935; and *E. jugalis* Winston & Nicholls, 1967. However, as discussed by Adrain & Westrop (2004), this approach is poorly founded because the types of *E. typicalis* and *E. kirki* have not been restudied since the 1930s, little information is available on sclerites other than cranidia, and individual studies have tended to illustrate very few specimens. Indeed, conventional species concepts of *Euptychaspis* are largely the product of work in Texas (Winston & Nicholls, 1967; Longacre, 1970) and Oklahoma (Stitt, 1971, 1977), and yet figured material from these areas is restricted to three cranidia assigned to *E. typicalis*, two cranidia attributed to *E. kirki* and three cranidia of *E. jugalis*.

Adrain & Westrop (2004) suggested that '*E. typicalis*' may include several distinct species, and described a new species from the Windfall Formation in Nevada. Here, we reillustrate the type material of *E. typicalis* and *E. kirki*, and document two new species from Utah. One of these is based on numerous

Figure 4. *Euptychaspis lawsonensis* sp. nov. Magnifications are ×7.5 except where noted. (a, e, j) Cranidium, SUI 97646, dorsal, anterior, and right lateral views, ×6 (LD5 16.8T m); (b, f, k) cranidium, SUI 97647, dorsal, left lateral, and anterior views, ×6 (LD5 25.3 m); (c, g, h, l) cranidium, SUI 97648, dorsal, anterior, right lateral, and ventral views (LD5 16.8T m); (d, i, m) cranidium, SUI 97649, dorsal, right lateral, and anterior views (LD5 30.5 m); (n, s, v) cranidium, SUI 07650, dorsal, left lateral, and anterior views (LD5 16.8T m); (o, p, t) cranidium, SUI 97651, dorsal, right lateral, and anterior views (LD5 16.8T m); (q, r, u) cranidium, SUI 97652, anterior, dorsal, and right lateral views (LD5 float); (w, z, cc) cranidium, SUI 97653, anterior, left lateral, and dorsal views (LD5 30.5 m); (x, dd, hh) cranidium, SUI 97654, anterior, dorsal, and right lateral views (LD5 16.8T m); (y, aa, bb) cranidium, SUI 97655, anterior, dorsal, and right lateral views (LD5 25.3 m); (ee, ii, nn) cranidium, SUI 97656, dorsal, right lateral, and anterior views (LD5 16.8T m); (ff, jj, oo) cranidium, SUI 97657, right lateral, dorsal, and anterior views (LD5 30.5 m); (gg, kk, pp) cranidium, SUI 97658, right lateral, dorsal, and anterior views (LD5 30.5 m); (ll, mm, qq) cranidium, SUI 97659, right lateral, dorsal, and anterior views, ×10 (LD5 16.8T m).

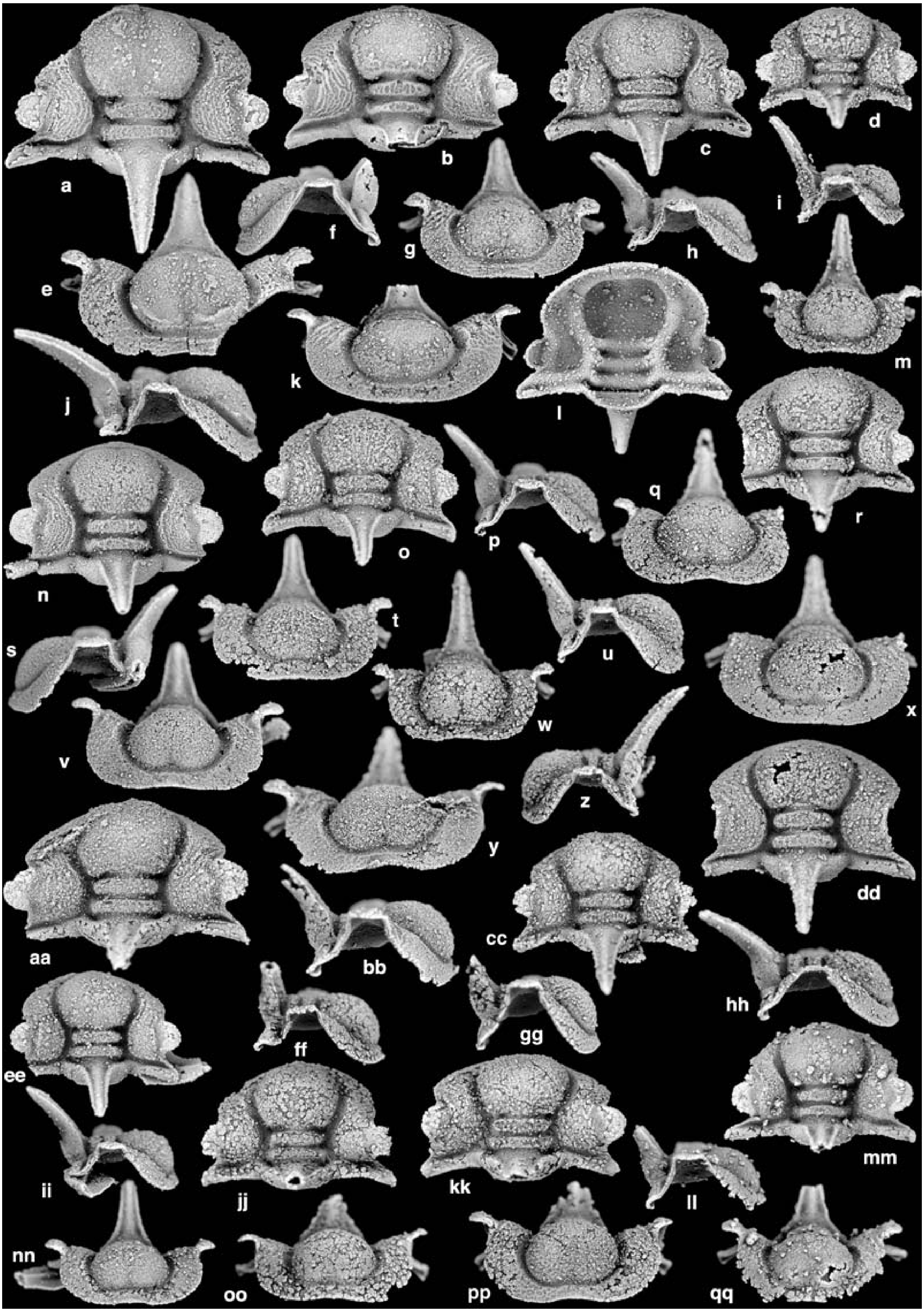

Figure 4. For caption see facing page.

silicified cranidia, librigenae and pygidia, which allows intraspecific variability in these sclerites to be assessed for the first time.

Finally, the nature of the pygidial border of *Euptychaspis* needs to be clarified. Following Taylor (*in* Taylor & Halley, 1974) and Ludvigsen (1982), the border has been regarded as the down-sloping area posterior of the ridge that extends across the pygidium. As discussed below under *E*. sp., most of this region is actually part of the pleural field, and the border consists of a narrow rim.

Euptychaspis lawsonensis sp. nov.
Figures 4, 5, 6a–v, aa, bb, hh

Holotype. A cranidium (SUI 97685) from the Notch Peak Formation, Lawson Cove (LAW 25.3 m), western Utah (Fig. 6a, e, i, o).

Assigned specimens. SUI 97646–97692; occurs at all sampled horizons.

Diagnosis. A species of *Euptychaspis* with bulb-shaped glabella, transglabellar S2 and conspicuously expanded frontal lobe. Anteriorly, axial furrows converge forward and steeply downward around frontal lobe. Frontal area short, occupying less than half of cranidial height (excluding occipital spine) in anterior view. Librigena with long, strongly tapered genal spine; prominent sculpture restricted to carina running along spine. Pygidium with long axis occupying about 80 % of pygidial length and composed of four rings and terminal piece.

Etymology. For Lawson Cove, northern Wah Wah Mountains, western Utah.

Description. Cranidial measurements were made on 21 figured specimens. Cranidium subrectangular in outline, length (excluding occipital spine) equal to 68 % (62–76) of maximum width across palpebral lobes, with gently rounded anterior margin; strongly arched, with height (sag.; excluding occipital spine) in anterior view equal to 47 % (41–53) of maximum frontal area width (tr.). Glabella bulb-shaped in outline and gently waisted at S1, with maximum L2 width (tr.) equal to 92 % (86–98) of L1, and maximum frontal lobe width 144 % (134–160) of L1 width; strongly convex, occupying 79 % (73–83) of cranidial height (sag.; excluding occipital spine). In front of L0, longitudinal profile nearly flat before curving downward along frontal lobe. S0, S1, and S2 deeply incised, transverse grooves. Axial furrows, also well-incised grooves, converging gradually forward to mid-point of L2, then diverging forward and sharply downward to join gently curved preglabellar furrow. Posteriorly, axial and posterior border furrows are confluent. Most specimens have faint median furrow at anterior end of glabella. L0 with long spine expressed as low, slender, median inflation rimmed by low ridges that merge anteriorly with posterior borders; spine curved upward and backward, average orientation over the length from base to tip is 49° (31–60) from horizontal. Glabellar lobes sculptured and sharply demarcated from unsculptured furrows. L1 and L2 transverse bands, accounting for 12 % (9–14) and 15 % (12–17) of pre-occipital glabellar length, respectively. Frontal lobe strongly expanded, with maximum width (tr.) 147 % (134–160) maximum width of L1, and occupies 64 % (61–68) of pre-occipital glabellar length; subcircular in outline with rounded anterior margin and nearly transverse posterior margin. Frontal area steeply downsloping, partially to completely overhung by glabella. Anterior border expressed only as very narrow, unsculptured rim along cranidial margin (Fig. 6j). Palpebral lobes upwardly curved, semicircular shelves elevated slightly above maximum level of glabella, length equal to 33 % of pre-occipital glabellar length. Anterior branches of facial sutures weakly divergent in front of palpebral lobes before swinging inward and downward along anterior cranidial margin; posterior branches divergent between palpebral lobes and posterior border furrows oriented at 45° (32–57) to transverse plane, becoming nearly parallel at posterior margin. Fixigena gently

Figure 5. *Euptychaspis lawsonensis* sp. nov. Magnifications are ×7.5 except where noted. (a) Right librigena, SUI 97660, external view (LD5 30.5 m); (b) left librigena, SUI 97661, external view, ×6 (LD5 25.3 m); (c) right librigena, SUI 97662, external view (LAW 25.3 m); (d) left librigena, SUI 97663, external view (LD5 float); (e, f) right librigena, SUI 97664, external and internal views (LD5 16.8T m); (g) right librigena, SUI 97665, external view (LD5 30.5 m); (h, l) left librigena, SUI 97666, external and ventrolateral views (LD5 30.5 m); (i) right librigena, SUI 97667, external view, ×6 (LD5 30.5 m); (j, m) left librigena, SUI 97668, external and ventrolateral views (LD5 25.3 m); (k) right librigena, SUI 97669, external view (LD5 16.8T m); (n, w) left librigena, SUI 97670, external and dorsal views (LD5 30.5 m); (o) left librigena, SUI 97671, external view, ×10 (LAW 25.3 m); (p, q) right librigena, SUI 97672, ventrolateral and external views, ×6 (LD5 25.3 m); (r–t, x) left librigena, SUI 97673, external, internal, ventrolateral, and dorsal views, ×6 (LD5 16.8T m); (u, v, dd) pygidium, SUI 97674, posterior, dorsal, and left lateral views (LD5 16.8T m); (y, z, ee) pygidium, SUI 97675, dorsal, left lateral, and posterior views, ×10 (LD5 30.5 m); (aa–cc, gg) pygidium, SUI 97676, left lateral, dorsal, posterior, and ventral views (LD5 16.8T m); (ff, jj, rr) pygidium, SUI 97677, dorsal, right lateral, and posterior views (LD5 25.3 m); (hh, ii, qq) pygidium, SUI 97678, dorsal, posterior, and left lateral views (LAW 25.3 m); (kk, ll, ww) pygidium, SUI 97679, right lateral, dorsal, and posterior views (LD5 16.8T m); (mm–oo) pygidium, SUI 97680, left lateral, dorsal, and posterior views, ×10 (LD5 16.8T m); (pp, ss, yy) pygidium, SUI 97681, dorsal, left lateral, and posterior views (LD5 25.3 m); (tt, zz, aaa) pygidium, SUI 97682, dorsal, posterior, and left lateral views (LAW 25.3 m); (uu, vv, bbb) pygidium, SUI 97683, left lateral, dorsal, and posterior views, ×10 (LD5 30.5 m); (xx, ccc, ddd) pygidium, SUI 97684, dorsal, left lateral, and posterior views, ×10 (LD5 float).

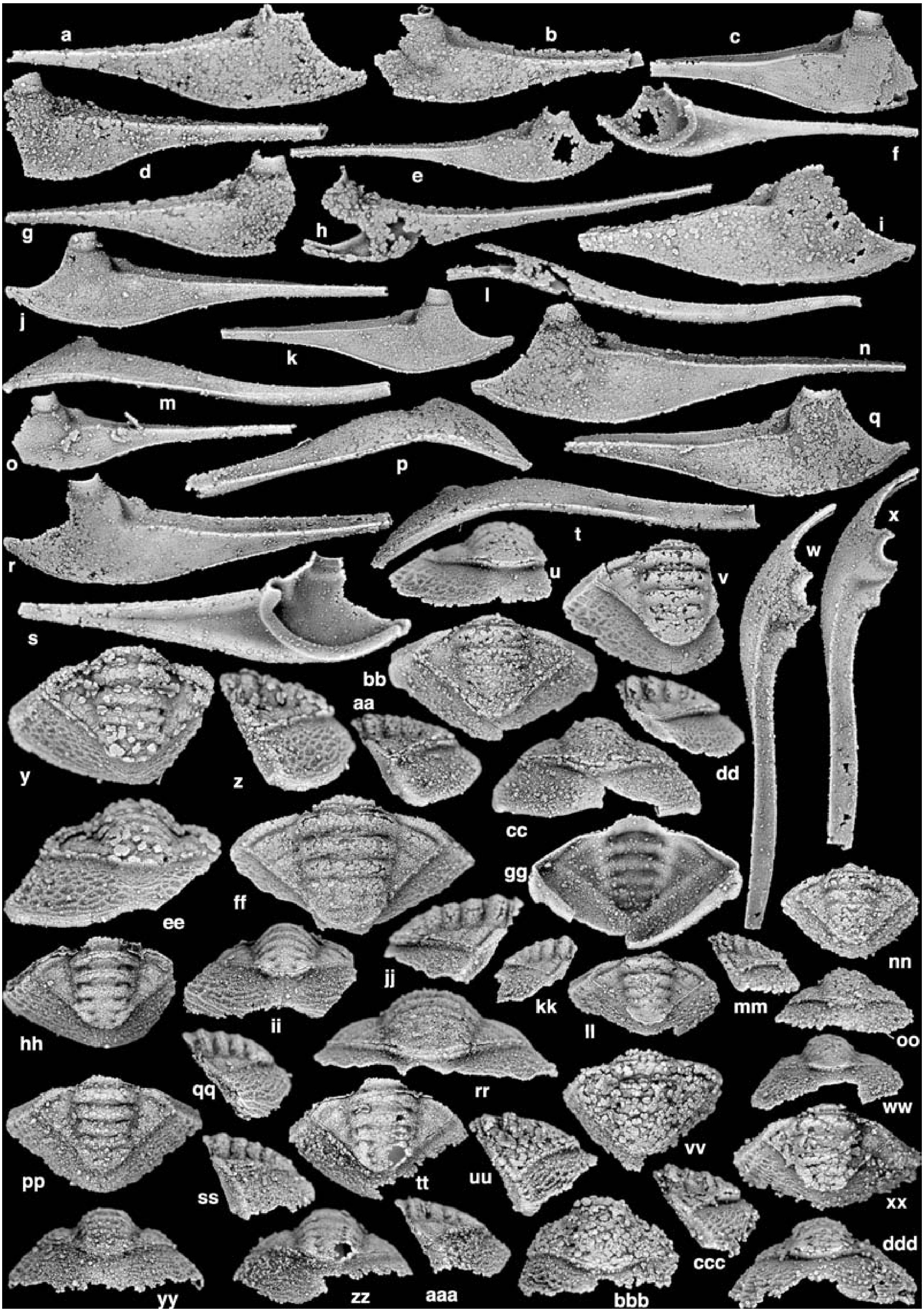

Figure 5. For caption see facing page.

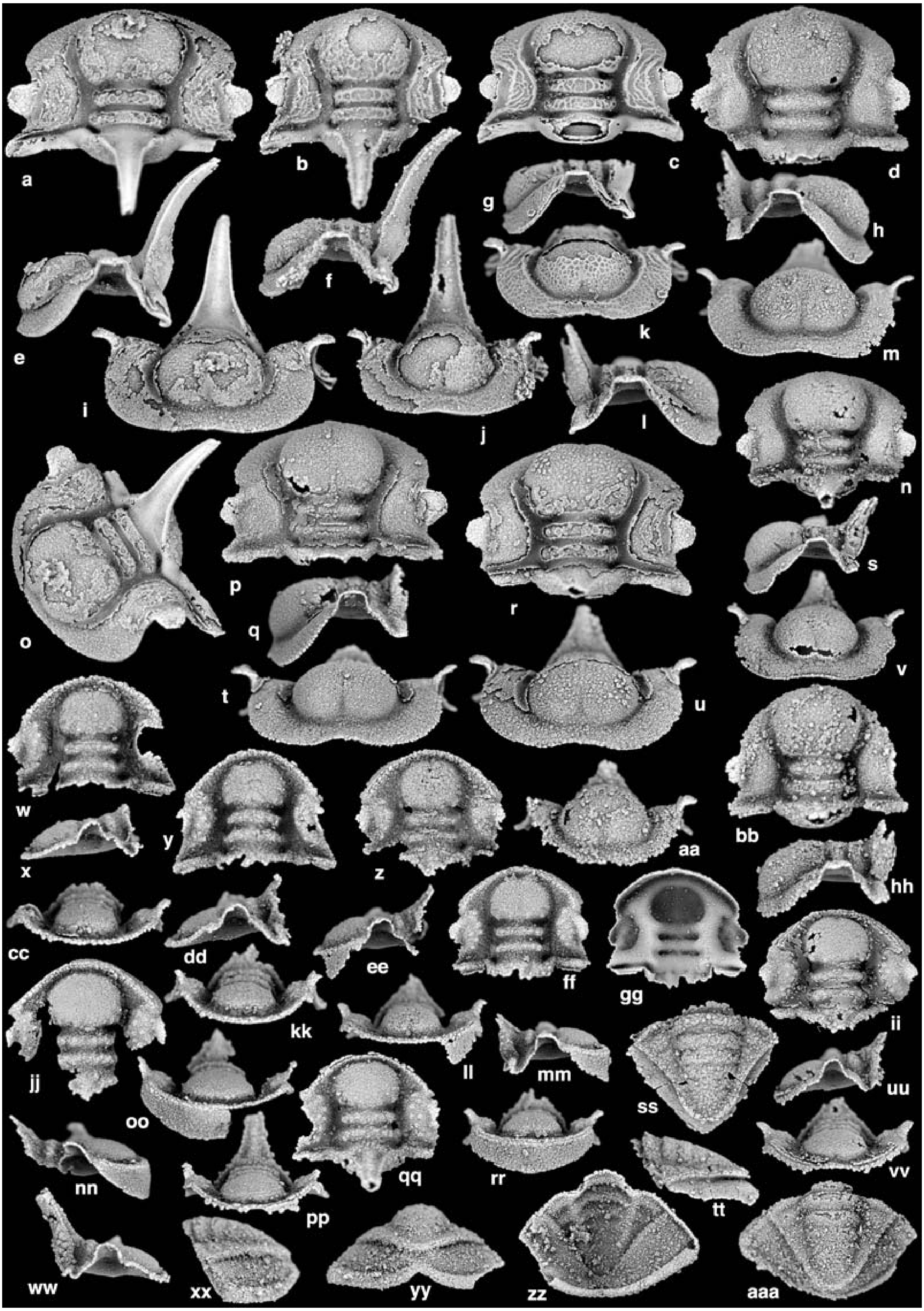

Figure 6. For caption see facing page.

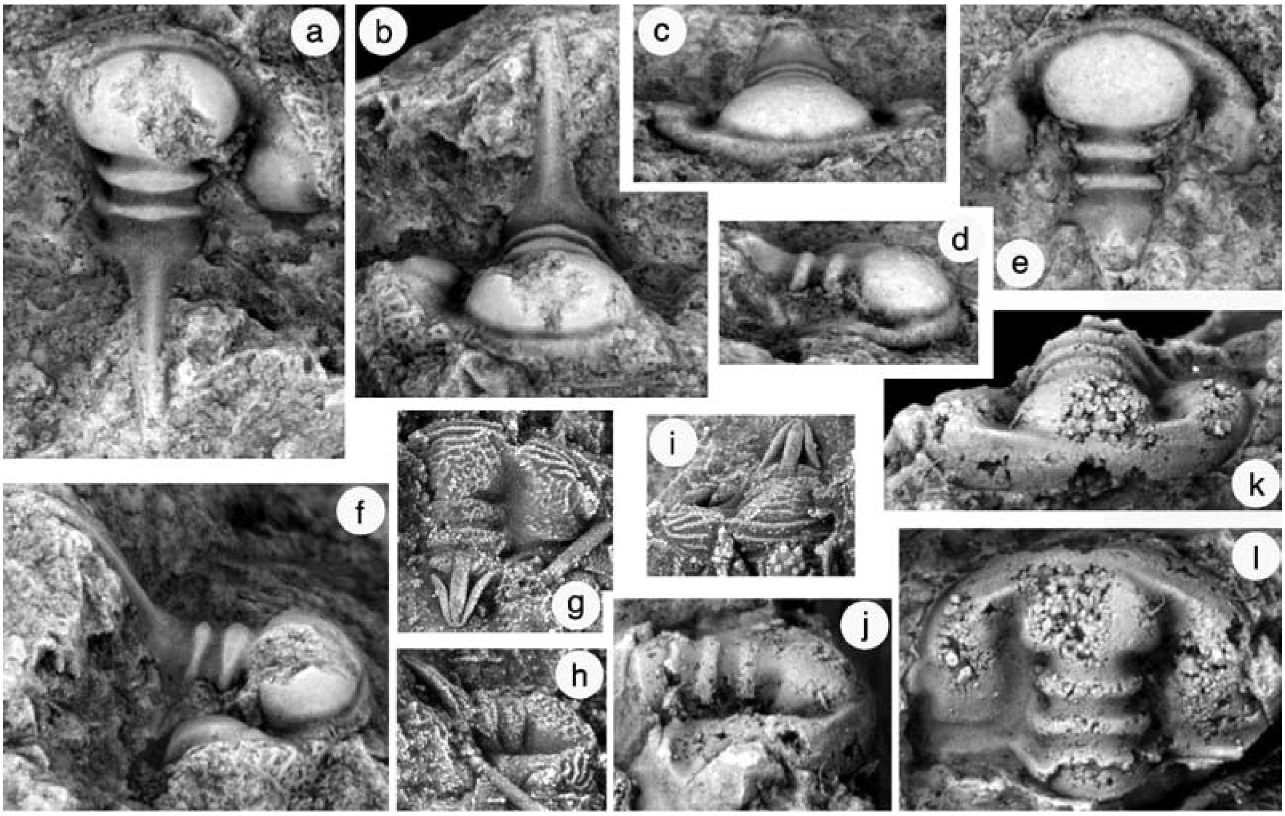

Figure 7. (a–f) *Euptychaspis kirki* Kobayashi, 1935, Upper Cambrian strata, Eureka District, Nevada, all ×15. (a, b, f) Cranidium, internal mould, paratype, USNM 93053a, dorsal, anterior and right dorsolateral views; (c–e) cranidium, internal mould, lectotype (selected here), USNM 93053b, anterior, right dorsolateral and dorsal views. (g–l) *Euptychaspis typicalis* Ulrich *in* Bridge, 1931, Eminence Dolomite, south-central Missouri, all ×15. (g–i) cranidium, cast from external mould, paratype, USNM 83493b, dorsal, right dorsolateral and anterior views; (j–l) cranidium, external mould, lectotype (selected here), USNM 83493a, right dorsolateral, anterior and dorsal views.

inflated, occupying 18 % (15–21) of cranidial width across midlength of palpebral lobes, and separated from palpebral lobes by broad, shallow, weakly curved palpebral furrow. Posterior border narrow, convex band, maintaining even length (exsag.) along entire posterior cranidial margin; posterior border furrow narrow, well-incised groove, slightly narrowing (exsag.) distally. Fixigenae, pre-occipital glabellar lobes and frontal area carry sculpture of anastomosing striate ridges (Figs 6a, b, 7a, b, c, k) that are not expressed on ventral surfaces (Fig. 6i). On frontal glabellar lobe and frontal area, ridges finely woven to produce reticulate sculpture. Borders, occipital ring and spine, palpebral lobes and cranidial furrows smooth.

Measurements were made on three figured librigenae. Librigena convex, height in lateral view 20 % (18–22) of length (including spine) with long, slender genal spine. Librigenal field narrow, conical, with visual surface mounted on wire-like eye socle (Fig. 5o). Broad, shallow posterior border furrow defines weakly convex posterior border. Very narrow, rim-like lateral border extends along outer edge of genal spine; similar rim runs along inner edge of spine. Prominent carina, similar to, but more convex than, lateral

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Figure 6. (a–v, aa, bb, hh) *Euptychaspis lawsonensis* sp. nov. All from LAW 25.3 m and ×7.5 except where noted. (a, e, i, o) Cranidium (holotype), SUI 97685, dorsal, left lateral, anterior, and oblique views; (b, f, j) cranidium, SUI 97686, dorsal, left lateral, and anterior views; (c, g, k) cranidium, SUI 97687, dorsal, left lateral, and anterior views; (d, h, m) cranidium, SUI 97688, dorsal, right lateral, and anterior views; (l, r, u) cranidium, SUI 97689, right lateral, dorsal, and anterior views; (n, s, v) cranidium, SUI 97690, dorsal, left lateral, and anterior views; (p, q, t) cranidium, SUI 97691, dorsal, left lateral, and anterior views; (aa, bb, hh) cranidium, SUI 97692, anterior, dorsal, and left lateral views, ×12. (w–z, cc–gg, ii–rr, uu–ww) *Euptychaspis* sp. nov. A. All from LAW 25.3 m and ×10 except where noted. (w, x, cc) cranidium, SUI 97693, dorsal, left lateral, and anterior views; (y, dd, kk) cranidium, SUI 97694, dorsal, left lateral, and anterior views; (z, ee, ll) cranidium, SUI 97695, dorsal, left lateral, and anterior views, ×7.5; (ff, gg, mm, rr) cranidium, SUI 97696, dorsal, ventral, right lateral, and anterior views, ×7.5; (ii, uu, vv) cranidium, SUI 97697, dorsal, left lateral, and anterior views, ×7.5; (jj, nn, oo) cranidium, SUI 97698, dorsal, right lateral, and anterior views; (pp, qq, ww) cranidium, SUI 97699, anterior, dorsal, and right lateral views. (ss, tt, xx–aaa) *Euptychaspis* sp. Both from LD5 25.3 m and ×7.5. (ss, tt) Pygidium, SUI 97700, dorsal and left lateral views; (xx–aaa) pygidium, SUI 97701, left lateral, posterior, ventral, and dorsal views.

border, extends from posterior edge of librigenal field to tip of spine. Narrow, tubular doublure beneath borders and raised above adjacent doublure of genal spine. External surface with faint anastomosing ridges; doublure apparently smooth.

Pygidial measurements were made on three figured specimens. Pygidium convex, height 50 % (48–52) of maximum width, and subelliptical in outline, with length 57 % (56–60) of maximum width. Prominent articulating facet at anterolateral corner. Axis very gently tapered and rounded posteriorly, occupying 81 % (79–84) of pygidial length (sag.) and 32 % (30–35) of maximum pygidial width. Lateral profile of axis curves gently downward towards rear; maximum height in lateral view occupies 32 % of maximum pygidial height. Four subequal, transverse axial rings plus a tiny fifth, clearly demarcated by vestiges of a fifth ring furrow in some specimens (Fig. 5hh, tt), nearly merged terminal piece in others; anterior rings separated by ring furrows that shallow along crest of axis but deepen laterally towards pleural field (Fig. 5hh). Axial furrows shallow. Pleural field divided into furrowed and unfurrowed portions by narrow, rim-like ridge that also bounds posterior end of axis. Furrowed portion triangular in outline and narrow, anteriorly equal to 19 % (16–20) of maximum pygidial width; truncated by ridge opposite fourth axial ring furrow. Pleural and interpleural furrows indistinct to obsolete, with up to two pleural furrows evident on some specimens (Fig. 5ff). Behind ridge, unfurrowed pleural field is broad and steeply downsloping; dorsal surface carries reticulate sculpture that is not expressed on ventral surface. Border is narrow swollen rim with subparallel sculptural ridges and underlain by tubular doublure (Fig. 5gg). External surface of axis and furrowed part of pleural field poorly preserved but apparently smooth (e.g. Fig. 5v).

Discussion. With a bulb-shaped glabella, expanded frontal lobe and transglabellar S1 and S2, the silicified cranidia (Figs 4, 6a–v, aa, bb, hh) resemble those attributed to *Euptychaspis kirki* by other workers (Winston & Nicholls, 1967, pl. 9, fig. 18; Stitt, 1971, pl. 6, fig. 21; Westrop, 1995, pl. 7, figs 17–19). However, the type material of this species comprises two incomplete, mostly to completely exfoliated cranidia, only one of which preserves the occipital spine (Fig. 7a–f). Although there are general similarities with our silicified material, there are also differences. In particular, the glabella is less convex in the types, so that the frontal lobe occupies about half of cranidial height (excluding occipital spine) in anterior view (Fig. 7b). Around the frontal glabellar lobe, the axial and preglabellar furrows lie in a roughly horizontal plane (Fig. 7b–d, f), as in *E. typicalis* (Fig. 7j, k). In our cranidia, the axial furrows dip forward and downward (e.g. Fig. 4f–k), and the glabella accounts for considerably less than half of cranidial height in anterior view. There is little variation in these traits in our large sample (Figs 4, 6a–v, aa, bb, hh), so that it is difficult to dismiss the differences in the types as intraspecific variation. In view of these problems, and the general poor preservation, *E. kirki* is best restricted to the types until more material can be obtained from the type area in the Eureka District of Nevada. The specimens described herein are assigned to a new species, *E. lawsonensis*.

Identification of other material attributed previously to *E. kirki* is complicated by the paucity of pygidial and librigenal data. Pygidia of *E. lawsonensis* have axes that are composed of five rings, with the fifth small and variably differentiated from the terminal piece (Fig. 5u–z, aa–ddd). The only figured pygidium assigned to *E. kirki*, from the Rabbitkettle Formation of the Mackenzie Mountains (Westrop, 1995, pl. 7, fig. 21), has seven distinct rings. Cranidia from the Rabbitkettle Formation (Westrop, 1995, pl. 7, figs 17, 18) appear to be distinct from those of *E. lawsonensis* in their longer (sag.; exsag.) S1 and S2, with S2 deeply impressed medially versus shallower medially in *E. lawsonensis*, and in the presence of much stronger raised sculpture on the sloped frontal areas. A librigena (Westrop, 1995, pl. 7, fig. 20) has more convex lateral margins and much stronger sculpture on the field than those of *E. lawsonensis* (Fig. 5a–t, w, x), including punctate sculpture that is apparently absent in *E. lawsonensis*.

The material from the Rabbitkettle is certainly not conspecific with *E. lawsonensis*. Moreover, because differences are expressed most clearly in other sclerite types, isolated cranidia previously attributed to *E. kirki* (Winston & Nicholls, 1967; Stitt, 1971; Loch, Stitt & Derby, 1993) cannot be identified to the species level with any confidence. These problems in identification are of biostratigraphic significance because the first appearance of '*Euptychaspis kirki*' has been used as a proxy for the base of the *Saukiella serotina* Subzone in Texas (Longacre, 1970, p. 12) and Oklahoma (Stitt, 1977, p. 18).

The bulb-shaped glabella with expanded frontal lobe clearly differentiates *E. lawsonensis* from *E. typicalis* Ulrich (Fig. 7g–l) and *E. dougali* Adrain & Westrop (2004, pl. 6, figs 1–44), both of which are characterized by parallel-sided glabellae in which the frontal lobes are not expanded appreciably beyond the widths of L1 and L2. In addition, *E. typicalis* and *E. dougali* have shorter palpebral lobes, tubular occipital spines, and relatively shorter anterior glabellar lobes than *E. lawsonensis*. In lateral and anterior views, the axial and preglabellar furrows of both *E. typicalis* (Fig. 7 j, l) and *E. dougali* (Adrain & Westrop, 2004, pl. 6, figs 5–10) lie in roughly horizontal planes, whereas those of *E. lawsonensis* dip steeply forward and downward along the frontal lobe (Fig. 4e–j). Other differences in *E. dougali* include S2 that are not connected across the glabella (Adrain & Westrop, 2004, pl. 6, figs 1–3, 22), relatively longer frontal area (e.g. Adrain & Westrop, 2004, pl. 6, fig. 12), librigena with shallow but clearly defined lateral border furrow and sculpture of coarse striate ridges (e.g. Adrain & Westrop, 2004, pl. 6, figs 19, 24, 40), and a pygidium with a shorter axis that contains only three clearly defined axial rings plus terminal piece.

Euptychaspis jugalis Winston & Nicholls (1967, pl. 9, fig. 13; Stitt, 1971, pl. 6, fig. 20) is distinct from *E. lawsonensis* on the basis of a much longer frontal area, narrower fixigenae, weakly expanded anterior glabellar lobe and sharply triangular occipital ring.

Euptychaspis sp. nov. A
Figure 6w–z, cc–gg, ii–rr, uu–ww

Material and occurrence. SUI 97693–97699; occurs only at LAW 25.3 m.

Description. Measurements were made on six figured specimens. Cranidium (excluding occipital spine) subpentagonal in outline with strongly curved anterior margin; cranidial length (sag.; excluding spine) equal to 78 % (73–81) of cranidial width across midlength of palpebral lobes. Cranidium strongly convex, with maximum height in lateral view equal to 47 % (46–48) of cranidial length (sag.; excluding spine). Glabella nearly parallel-sided but gently waisted at L2; width of L2 89 % (84–98) of width at L1; moderately convex, with height accounting for 40 % of cranidial height in lateral view. L0 with slender, tubular occipital spine directed steeply upward and bounded laterally by slender, rim-like ridges that merge with posterior borders. S0, S1 and S2 deeply incised, transverse grooves. L1 and L2 transverse bands and equal in length (sag.); L1 accounts for 16 % (12–19) of preoccipital glabellar length. Frontal lobe subcircular in outline, with well-rounded anterior margin and nearly transverse posterior margin, and occupies 56 % (53–58) of pre-occipital glabellar length; weakly expanded, so that maximum width is 106 % of L1 width. Axial and preglabellar furrows broad, deeply incised grooves. Palpebral lobes steeply upsloping shelves centred opposite L2 and elevated slightly above crest of glabella; length equal to 33 % (31–35) of pre-occipital glabellar length. Palpebral furrows shallow grooves defined in part by sharp change in slope between palpebral lobe and fixigena. Anterior branches of facial sutures nearly parallel in front of palpebral lobes but curve inward and downward along anterior cranidial margin; posterior branches nearly straight and divergent, oriented at 64° (61–66) from transverse plane. Fixigena inflated, depressed slightly below crest of glabella, and narrow, equal to 14 % (13–16) of cranidial width between palpebral lobes. Posterior border short (exsag.), convex band that maintains even length along posterior cranidial margin. Posterior border furrow well-incised, narrows somewhat towards posterior corner of cranidium and merges adaxially with axial furrow. External surface poorly preserved. Most specimens show scattered coarse tubercles on fixigenae, also expressed as depressions on ventral surface (Fig. 6gg).

Discussion. A second species from the Lawson Cove section is clearly new but it will not be named because of the fragmentary nature of the material and the absence of information on sclerites other than cranidia. The nearly vertical frontal area and weakly expanded frontal glabellar lobe of *Euptychaspis* sp. nov. A are shared with *E. typicalis* Ulrich (Fig. 7g–l). In detail, the frontal area of *E. typicalis* descends from the anterior tip of the glabella (e.g. Fig. 7l), whereas the steeply sloping portion of the frontal area of *E.* sp. nov. A is consistently separated from the glabella by a short preglabellar field (e.g. Fig. 6w, y, z, ff, jj). The fixigena of *E.* sp. nov. A is narrower than that of *E. typicalis*. The lectotype of *E. typicalis* (Fig. 7l) is an internal mould and comparison with the ventral surface of *E.* sp. nov. A (Fig. 6gg) demonstrates clearly the difference in fixigenal width. In addition, the ventral surface also shows that the tuberculate sculpture of the fixigena would be expressed on internal moulds of *E.* sp. nov. A. Such sculpture is not present on *E. typicalis* and is not known on any other described species of the genus.

The cranidium of *E. dougali* Adrain & Westrop (2004, pl. 6, figs 1–18, 20–22) also has a parallel-sided glabella. Several character states differentiate it from *E.* sp. nov. A, including a less steeply sloping frontal area that carries sculpture of very coarse striate ridges, shallower axial and preglabellar furrows, much wider, less inflated fixigenae, and S2 lateral glabellar furrows that are not connected across the glabella.

Both *E. kirki* Kobayashi (Fig. 7a–f) and *E. lawsonensis* sp. nov. (Fig. 4) can be separated easily from *E.* sp. nov. A on the basis of their bulb-shaped glabellae with expanded frontal lobes. *Euptychaspis jugalis* Winston & Nicholls (1967, pl. 9, fig. 13) is the only described species with narrower fixigenae and, consequently, a narrower cranidium than *E.* sp. nov. A. Other differences in *E. jugalis* include a more gently inclined frontal area and a relatively longer anterior glabellar lobe.

Euptychaspis sp.
Figure 6ss, tt, xx–zz, aaa

Material and occurrence. SUI 97700 and 97701; restricted in occurrence to LD5 25.3 m.

Discussion. A few pygidia from section LD5 differ from associated pygidia of *E. lawsonensis* sp. nov. in having a longer axis (occupying more than 90 % of pygidial length) and pleural field and less well-impressed ring furrows. The border is inflated and rim-like and isolated by a distinct border furrow whereas in pygidia of *E. lawsonensis* it is only weakly differentiated. The border is similar to those of such ptychaspidines as *Ptychaspis* (Westrop, 1986*b*, pl. 7, figs 6, 11, 14, pl. 9, figs 1–3) and *Keithiella* (Fig. 2n, p, t). Much of the region behind the ridge that bounds

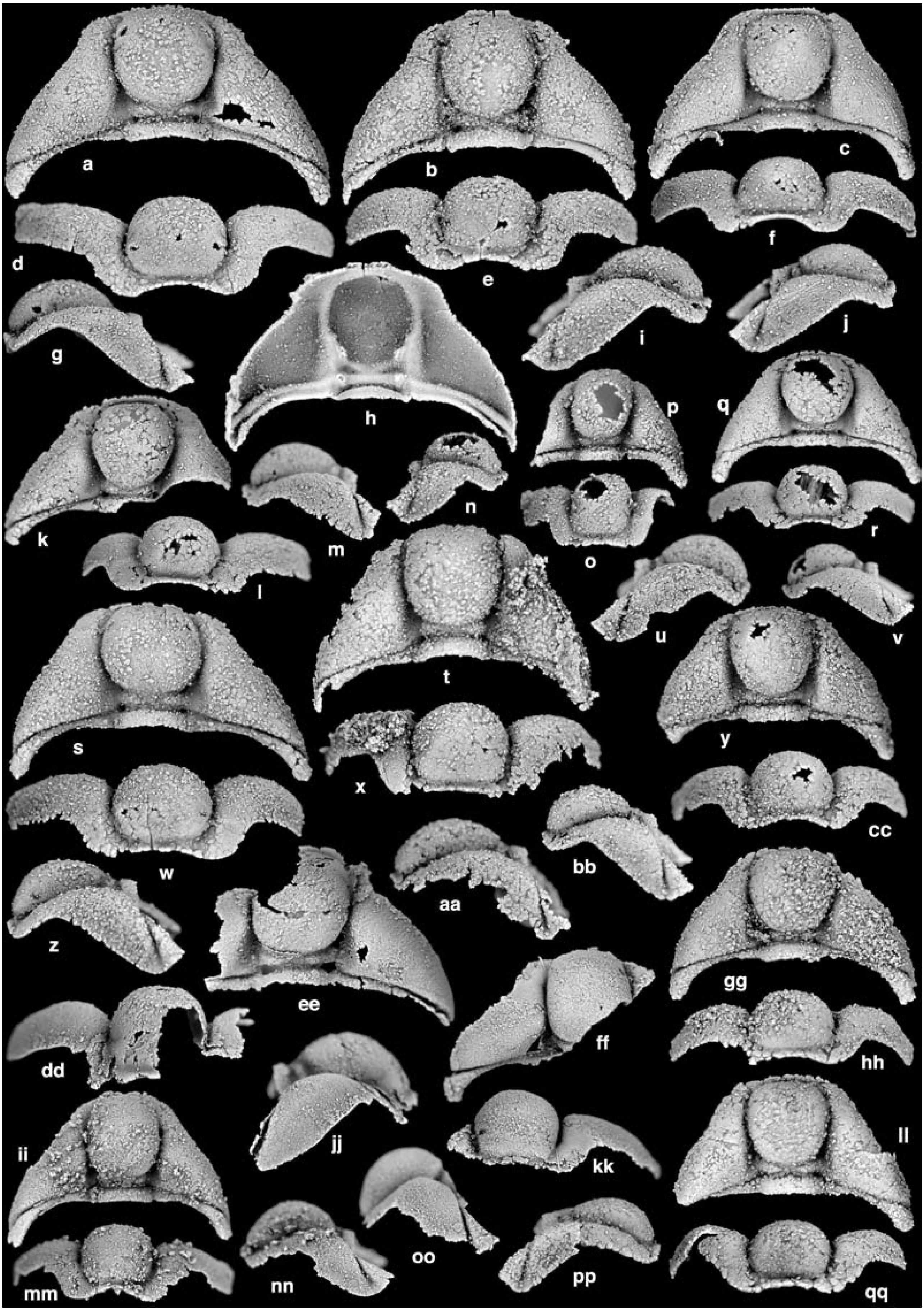

Figure 8. See caption in facing page.

the pleural field and axis in pygidia of this and other species of *Euptychaspis* (Fig. 5ee–ddd; Taylor & Halley, 1974, pl. 2, fig. 11; Ludvigsen, 1982, fig. 58S–U; Adrain & Westrop, 2004, pl. 6, figs 38, 39, 44) is an effaced portion of the pleural field.

Subfamily MACRONODINAE Westrop, 1986*a*

Genus *Macronoda* Lochman, 1964

Type species. *Macronoda prima* Lochman, 1964 from the Deadwood Formation, Montana, USA.

Discussion. Although first described 40 years ago (Lochman, 1964), *Macronoda* was known from only a few illustrated sclerites, many of which are poorly preserved (Winston & Nicholls, 1967; Westrop, 1986*b*; Loch, Stitt & Derby, 1993). Abundant silicified material from the Notch Peak Formation allows the anatomy of this genus to be evaluated fully for the first time. Pygidia originally described by Lochman (1964, pl. 14, figs 15, 18, 19, 21, 22) were incompletely preserved and her illustrations did not display the nature of the border. More recently, a single pygidium illustrated by Loch, Stitt & Derby (1993, fig. 6.24) revealed the presence of pits in the border furrow. Ventral surfaces of *M. notchpeakensis* (Fig. 9dd, nn, pp) show that these pits are deep pockets that do not perforate the dorsal cuticle. Smaller complementary pits are developed on the underside of the exoskeleton and are expressed as inflated tubercles along the outer edge of the border furrow. This is very similar to the arrangement of pits in the closely related macronodine *Sunwaptia* (Adrain & Westrop, 2004), except that the inflated tubercles of the latter extend inward from the border and overlie the pits in the border furrow.

The librigenae of *Macronoda* are documented here for the first time (Fig. 9a–r) and are yoked anteriorly with a conspicuous anterior arch. They differ from those of *Sunwaptia* (Adrain & Westrop, 2004, pl. 5, figs 13, 16, 19, 20) in lacking borders and border furrows (although there is a carina running along the lateral margin) and having a longer, slender spine.

Macronoda notchpeakensis sp. nov.

Figures 8, 9

Holotype. A pygidium (SUI 97731) from the Notch Peak Formation, Lava Dam 5 section (collection LD5 30.5 m), western Utah (Fig. 9hh, ii, mm, nn).

Material and occurrence. SUI 97702–97734; occurs at all sampled horizons.

Diagnosis. A species of *Macronoda* with four pairs of large, suboval pits in the pygidial border furrow; anteriormost pair of pits about half size of other three pairs. Pleural field broad, with maximum width (tr.) at anterior equal to 33 % (27–47) maximum pygidial width. Cranidium with wide posterior fixigenae, so that cranidial width at inflexion of facial sutures is 60 % (55–65) of maximum width across posterior fixigenae. L1 consists of two suboval, inflated lateral lobes isolated by narrow, medial depressed region. Frontal area short.

Etymology. For the Notch Peak Formation.

Description. Cranidial measurements were made on 11 figured specimens. Cranidium convex, with maximum height in anterior view 30 % (24–43) of width; boomerang-shaped in outline, with posterior corners of fixigenae swept strongly backward. Cranidial length 47 % (41–53) of maximum cranidial width across posterior fixigenae, and cranidial width at inflexion of sutures is 60 % (55–65) of maximum width across posterior fixigenae. Well-preserved specimens (e.g. Fig. 8d–f, r, mm) have arched anterior cranidial margin. Glabella occupies almost entire cranidial length, partly to completely overhanging very narrow, ledge-like anterior border; strongly convex (sag.), with height in anterior view 89 % (85–91) of maximum cranidial height (sag), and bulb-shaped in outline, with minimum width at L1 69 % (57–80) maximum width across frontal lobe; occupies 57 % (53–62) of cranidial width between inflexion point of sutures. Axial and preglabellar furrows deeply incised grooves. L0 transverse to slightly arcuate band and occupies 14 % (12–15) of cranidial length (sag.). L1 slightly narrower (85 %; 80–92) than L0 and consists of two suboval, inflated lateral lobes isolated by narrow, medial depressed region; isolation of lateral lobes expressed clearly on ventral surface (Fig. 8h). Frontal lobe subcircular in outline, maximum width equal to 99 % (85–111) of sag. length and strongly convex, raised well above level of L1. Eyes and palpebral lobes absent (palpebral lobe-like features on some specimens (e.g. Fig. 8a, right side) are artifacts of preservation). Facial sutures with distinct inward inflexion in front of midlength of frontal glabellar lobe. Anterior of inflexion, sutures converge gently forward

Figure 8. *Macronoda notchpeakensis* sp. nov. From LD5 30.5 m and ×7.5 except where noted. (a, d, g) Cranidium, SUI 97702, dorsal, anterior, and left lateral views, ×6; (b, e, h, i) cranidium, SUI 97703, dorsal, anterior, ventral, and right lateral views, ×6; (c, f, j) cranidium, SUI 97704, dorsal, anterior, and right lateral views; (k–m) cranidium, SUI 97705, dorsal, anterior, and left lateral views; (n–p) cranidium, SUI 97706, right lateral, anterior, and dorsal views, ×12 (LAW 25.3 m); (q, r, v) cranidium, SUI 97707, dorsal, anterior, and left lateral views; (s, w, z) cranidium, SUI 97708, dorsal, anterior, and left lateral views; (t, x, aa) cranidium, SUI 97709, dorsal, anterior, and left lateral views; (u, y, cc) cranidium, SUI 97710, right lateral, dorsal, and anterior views; (bb, gg, hh) cranidium, SUI 97711, left lateral, dorsal, and anterior views; (dd, ee, jj) cranidium, SUI 97712, anterior, dorsal, and right lateral views (LAW 25.3 m); (ff, kk, oo) cranidium, SUI 97713, dorsal, anterior, and left lateral views (LAW 25.3 m); (ii, mm, nn) cranidium, SUI 97714, dorsal, anterior, and left lateral views (LAW 25.3 m); (ll, pp, qq) cranidium, SUI 97715, dorsal, right lateral, and anterior views.

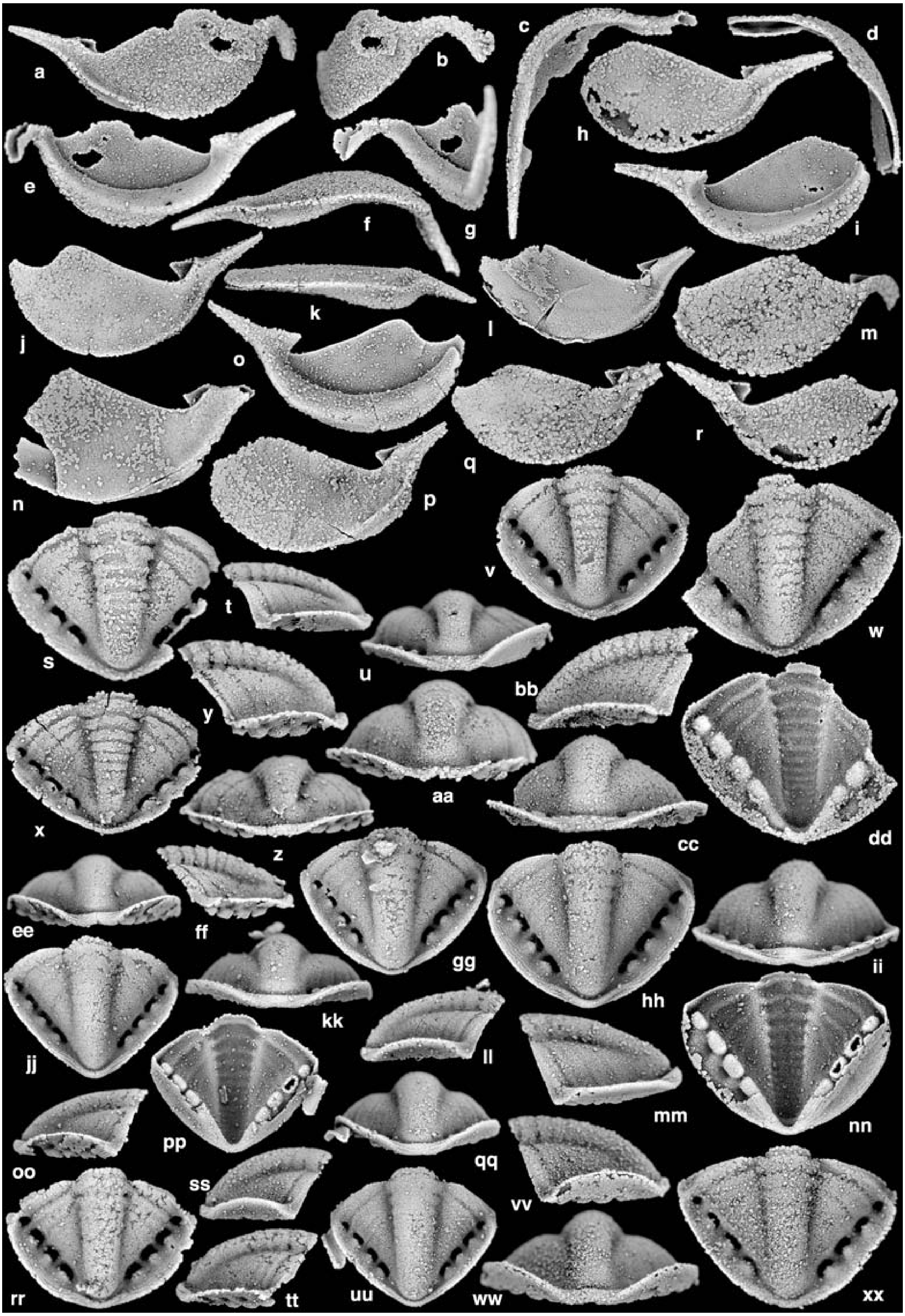

Figure 9. For caption see facing page.

and downward before swinging abruptly inward along anterior cranidial margin. Posterior branches diverge backward along gently curved path, becoming subparallel posteriorly. Fixigenae subtriangular in outline, gently arched near axial furrows but flexed sharply downward distally; very broad posteriorly, width opposite occipital ring 340 % of width at inflexion of facial sutures. Posterior border furrow narrow, deeply incised groove; posterior border narrows slightly away from occipital ring before expanding into broad, subtriangular distal region; minimum length (exsag.) 33 % (23–55) of maximum distal length. Sculpture not preserved on most specimens, but some (Fig. 8c, q) have fine terrace ridges on fixigenae.

Three figured librigenae provided measurements. Librigenae yoked anteriorly (Fig. 9b–d) with conspicuous anterior arch. Librigenal field broad, with maximum width 58 % (56–60) of length, and slopes steeply downward from suture. Stout genal spine equal to 34 % (30–37) of length of remainder of librigena. Narrow, carinate ridge extends forward from genal spine along lateral margin of librigena (Fig. 9a). Doublure expands slightly forward from genal spine, then narrows with maximum width equal to 22 % (18–26) of librigenal width (tr). External surface incompletely preserved but probably smooth; doublure with fine terrace ridges.

Ten figured pygidia provided measurements. Pygidium subtriangular (Fig. 9jj, uu) to suboval (Fig. 9hh, rr) in outline, with sag. length 80 % (74–85) of maximum width; moderately convex, with maximum height in posterior view 44 % (39–52) of width. Axis narrow, with width at anteriormost axial ring 33 % (27–43) of maximum pygidial width, very gently tapered, and long, occupying 94 % (93–96) of pygidial length; moderately convex, raised well above pleural fields. Longitudinal profile upwardly convex, with curvature increasing posteriorly. Articulating half-ring short, gently arcuate band. Axis multi-segmented, with transverse axial ring furrows faint (Fig. 9v, w) to obsolete (Fig. 9jj) on dorsal surface but more clearly expressed on ventral surface of exoskeleton. At least 12 rings present, with anteriormost pair somewhat wider than rest on at least some specimens (Fig. 9v, x). Pleural fields triangular in outline, maximum width (tr.) at anterior equal to 33 % (27–47) maximum pygidial width, with curved profile in posterior view. Two pairs of weak, gently curved pleural furrows present anteriorly on most specimens, and are clearly expressed on ventral surfaces (Fig. 9dd, nn, pp). Pleural furrows obsolete over remainder of pleural field. Interpleural furrows barely perceptible anteriorly and absent over most of pleural field. Lateral border furrows converge backwards at angles of 49° (43–53) from transverse plane and moderately well incised. Four pairs of large, deep, suboval pits in border furrows form pockets that do not perforate dorsal exoskeleton; smaller complementary pits developed on underside of exoskeleton expressed as inflated tubercles along outer edge of border furrow. Anteriorly, lateral border slopes upward from border furrow, becoming nearly vertical posteriorly. Border narrows sharply near posterior termination of axis and pleural fields, so that sagittal width is only 35 % (26–46) width at second border pit. Doublure slopes downward and inward, terminating beneath inner end of border furrow. Dorsal surface of exoskeleton poorly preserved but appears to have been smooth apart from terrace ridges on border; doublure also carries terrace ridges.

Discussion. The type species of *Macronoda*, *M. prima* Lochman, 1964 has an L1 in the form of an evenly inflated, transverse, band (e.g. Fig. 10e, g, h) and the posterior fixigenae are relatively narrow (tr). In contrast, *M. notchpeakensis* has very wide posterior fixigenae (e.g. Fig. 8a, s) and L1 consists of a pair of gently inflated, suboval lateral lobes that are isolated by medial depressed region (e.g. Fig. 8a, c, s, t, ll). Pygidial comparisons between these species are limited because the lateral border is not preserved in any of the specimens illustrated by Lochman (1964, pl. 14, figs 15, 18, 19, 21, 22). Loch, Stitt & Derby (1993, p. 512) noted that one of them (Lochman, 1964, pl. 64, figs 15, 19) appeared to show pits in along the margin of the pleural field. Restudy of this specimen (Fig. 10i–k) shows that, like *M. notchpeakensis*, four

Figure 9. *Macronoda notchpeakensis* sp. nov. (a–c, e–g) Right librigena and yoke, SUI 97716, external, anterior, ventral, internal, ventrolateral, and posterior views, ×5 (LD5 30.5 m); (d, m) right librigena and yoke, SUI 97717, dorsal and external views, ×7.5 (LD5 30.5 m); (h, i) left librigena, SUI 97718, external and internal views, ×7.5 (LD5 30.5 m); (j, k, o) left librigena, SUI 97719, external, ventrolateral, and internal views, ×5 (LD5 16.8T m); (l) left librigena, SUI 97720, external view, ×6 (LAW 25.3 m); (n) left librigena, SUI 97721, external view, ×6 (LD5 25.3 m); (p) left librigena, SUI 97722, external view, ×6 (LD5 25.3 m); (q) left librigena, SUI 97723, external view, ×7.5 (LD5 30.5 m); (r) right librigena, SUI 97724, external view, ×7.5 (LD5 30.5 m); (s, y, aa) pygidium, SUI 97725, dorsal, left lateral, and posterior views, ×7.5 (LD5 25.3 m); (t–v) pygidium, SUI 97726, left lateral, posterior, and dorsal views, ×6 (LD5 16.8T m); (w, bb–dd) pygidium, SUI 97727, dorsal, right lateral, posterior, and ventral views, ×6 (LD5 30.5 m); (x, z, ff) pygidium, SUI 97728, dorsal, posterior, and left lateral views, ×7.5 (LD5 25.3 m); (ee, jj, oo) pygidium, SUI 97729, posterior, dorsal, and right lateral views, ×7.5 (LD5 16.8T m); (gg, kk, ll) pygidium, SUI 97730, dorsal, posterior, and right lateral views, ×7.5 (LD5 16.8T m); (hh, ii, mm, nn) pygidium (holotype), SUI 97731, dorsal, posterior, left lateral, and ventral views, ×7.5 (LD5 16.8T m); (pp, qq, ss, uu) pygidium, SUI 97732, ventral, posterior, right lateral, and dorsal views, ×7.5 (LD5 16.8T m); (rr, tt) pygidium, SUI 97733, dorsal and right lateral views, ×10 (LD5 30.5 m); (vv–xx) pygidium, SUI 97734, left lateral, posterior, and dorsal views, ×6 (LD5 30.5 m).

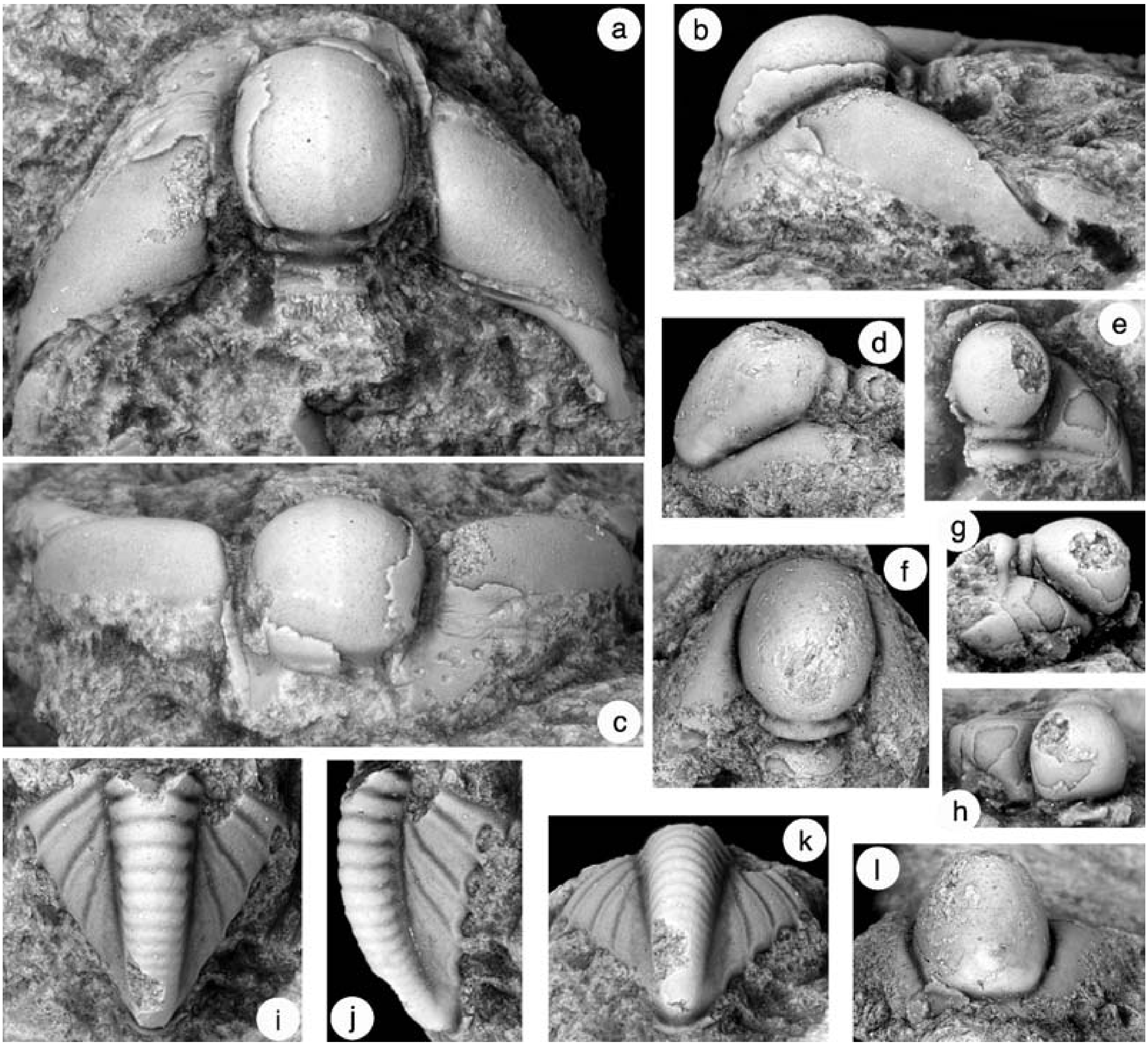

Figure 10. (a–c) *Macronoda* sp. nov., Wilberns Formation, central Texas, cranidium, internal mould, USNM 185840, dorsal, left lateral and anterior views, ×8. (d, f, l) *Macronoda extrema* (Lochman, 1964), subsurface Deadwood Formation, Montana, cranidium, internal mould, holotype, USNM 140699, left lateral, dorsal and anterior views, ×8. (e, g–k) *Macronoda prima* Lochman, 1964, Grove Creek Member, Snowy Range Formation, Montana. (e, g, h) cranidium, testate, holotype, USNM 140701, dorsal, right lateral and anterior views, ×12; (i, j, k) pygidium, internal mould, paratype, USNM 140702a, dorsal, right lateral and posterior views, ×12.

pairs of large pits are present. The anteriormost pit of *M. notchpeakensis* is about half the size of the other pits (Fig. 9s, v, w, x, gg, hh, jj, rr, uu, xx), whereas all pits of *M. prima* are similar in size (Fig. 10j). In addition, the pleural field of all pygidia of *M. prima* is much narrower (tr.) than in *M. notchpeakensis*.

Restudy of the holotype (Fig. 10d, f, l) of type species of *Promesus* Lochman (1964), *P. extremus* Lochman, confirms that the genus is a synonym of *Macronoda*, as suggested by Westrop (1986*b*). However, Westrop also considered *M. extrema* to be a synonym of *M. prima* but this now seems unlikely. The glabella of *M. extrema* is considerably more inflated than that of *M. prima* (Fig. 10e, g, h) and this level of glabellar variability is not evident in our large sample of cranidia of *M. notchpeakensis* (Fig. 8). Consequently, we regard *M. extrema* as a distinct species although more material will be required to characterize it fully.

Macronoda has also been reported from the Wilberns Formation of central Texas (Winston & Nicholls, 1967; Longacre, 1970). Restudy of the cranidium illustrated by Winston & Nicholls (Fig. 10a–c) shows that it shares relatively wide posterior fixigenae and isolated L1 lateral glabellar lobes (seen well in Fig. 10b) with *M. notchpeakensis*. However, as shown clearly in lateral and anterior views (Fig. 10b, c), the Wilberns cranidium has a much longer frontal area than *M. notchpeakensis* and is regarded herein as an undescribed species.

Isolated L1 lobes are also present in a cranidium from the Mistaya Formation, Wilcox Peak, Alberta, identified as *M*. cf. *prima* Lochman by Westrop (1986*b*, pl. 11, fig. 8), but the posterior fixigenae are much narrower than in *M. notchpeakensis*. The border is not preserved on the associated pygidium (Westrop, 1986*b*, pl. 11, figs 6–7) so that a detailed comparison cannot be made with *M. notchpeakensis*. The latter does, however, appear to have somewhat wider pleural fields. *Macronoda punctata* Derby (*in* Loch, Stitt & Derby, 1993, fig. 6.24–26) was described from correlative strata at Mt Wilson, Alberta. The single pygidium is unique in possessing numerous small pits in the border furrow, but the associated cranidia are too incomplete for a meaningful evaluation. There are not enough data to determine whether the specimens illustrated by Westrop belong to this species.

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