

Systematics of *Dokimocephalus* and related trilobites from the Late Cambrian (Steptoean; Millardan and Furongian Series) of Laurentian North America

Stephen R. Westrop^{a*}, Raina A. Waskiewicz Poole^b and Jonathan M. Adrain^c

^aOklahoma Museum of Natural History and School of Geology and Geophysics, University of Oklahoma, Norman, Oklahoma 73072, USA; ^bSchool of Geology and Geophysics, University of Oklahoma, Norman, Oklahoma 73072, USA; ^cDepartment of Geoscience, University of Iowa, 121 Trowbridge Hall, Iowa City, Iowa 52242, USA

(Received 21 April 2009; accepted 19 April 2010)

Dokimocephalidae Kobayashi, 1935, is a large group of mostly Laurentian trilobites, the majority of which are confined to the Late Cambrian (Millardian and Furongian series) Steptoean Stage. We begin a long overdue revision of the family with a critical review of a 'core group' of closely related genera: *Dokimocephalus* (Walcott, 1924), *Iddingsia* (Walcott, 1924), *Plataspella* (Wilson, 1949) and *Burnetiella* (Lochman, 1958), all of which share apomorphic character states of the librigena, anterior border and palpebral lobe. The poorly known *Edithiella* (Kurtz, 1975) is also included as a potential member of this group, which is referred to informally as Dokimocephalidae *sensu stricto*. The study includes examination of relevant types as well as new material from the Honey Creek Formation of Oklahoma and from the Orr Formation and correlatives of the Great Basin. Parsimony analysis supports monophyly of all five genera. In addition, a new genus, *Stittella*, is established for two species that are characterized by very short anterior borders and, consequently, frontal areas; characters of the librigena and pygidium are also diagnostic. New species named formally are *Dokimocephalus stewarti*, *D. blacki*, *D. oliveri* and *Stittella beeae*.

Keywords: Cambrian; Trilobita; Dokimocephalidae; systematics

Introduction

Kobayashi (1935) first proposed the family Dokimocephalidae for a group of Late Cambrian trilobites centred on *Dokimocephalus* (Walcott, 1924), a genus with spectacular elaboration of the anterior cranidial border into spine-like to tongue-like projections. In a subsequent revision, Palmer (1965) reduced Dokimocephalidae to one of two subfamilies within Elviniidae Kobayashi, 1935. Palmer's views have prevailed for 40 years (e.g. Stitt 1971; Westrop 1986), although some workers (e.g. Shergold 1980) have raised doubts about the relationship between dokimocephaline and elviniine trilobites. However, Elviniidae is essentially a phenetic construct based on general similarities in such features as glabellar morphology, and there are no obvious apomorphies in Palmer's (1965, pp. 32, 33, 39) diagnoses.

As conceived by Palmer, Elviniidae is a large group of mostly North American trilobites (see Shergold 1980; Peng 1992 for examples of extra-North American occurrences) that are conspicuous components of virtually every Steptoean (Furongian) fauna described to date from Laurentia (e.g. Frederickson 1948, 1949; Wilson 1948, 1949, 1951; Bell *et al.* 1952; Palmer 1960, 1965, 1968; Stitt 1971, 1977; Westrop 1986). They have played a major role in develop-

*Corresponding author. Email: swestrop@ou.edu

ISSN 1477-2019 print / 1478-0941 online Copyright © 2010 The Natural History Museum DOI: 10.1080/14772019.2010.489364 http://www.informaworld.com ment of Late Cambrian biostratigraphy. A modern revision is a daunting task, but is long overdue. Here we take the first step, evaluating the core group of dokimocephalid trilobites represented by Dokimocephalus Walcott and related genera with new material from Oklahoma and the Great Basin, as well as restudy of primary types from museum collections. They will be referred to herein as Dokimocephalidae sensu stricto, and their relationship to many other genera assigned to Dokimocephalinae - e.g. Kindbladia (Frederickson, 1948) and Dellea (Wilson, 1949) and to Elviniidae, including the Drumaspidinae Longacre, 1970 (see Westrop 1986) will be explored in subsequent works. Dokimocephalidae s.s. is a distinct monophyletic group that diversified in the late Steptoean (Elvinia Zone and correlatives) only to be extinguished in the extinction event at the base of the overlying Sunwaptan Stage.

Stratigraphic setting

Dokimocephalus and related genera are widely distributed in Laurentian North America, and a full treatment of the stratigraphic setting of various occurrences is beyond the scope of this paper. A brief outline of the various stratigraphic units and localities that yielded material illustrated herein is presented below.

Oklahoma

Dokimocephalid trilobites are well represented in the Honey Creek Formation of southern Oklahoma (e.g. Resser 1942; Frederickson 1948, 1949; Stitt 1971, 1977), and this unit is the source of 16 of the 28 species treated herein. New material was obtained from collections made at the Kimbell Ranch and Dotson Ranch sections in the Slick Hills and the Arbuckle Mountains, respectively (see Westrop & Adrain 2007 for locality information). Archival specimens described by Resser (1942) and Frederickson (1948, 1949) are from the same general areas as our new material, as is a previous unstudied float block collected by J.H. Stitt from his (1971) Rover Ranch section (RR 140). Resser's (1942) collection site located four miles east of Alpers is probably the same as Frederickson's (1948, 1949) locality 12, and is situated approximately 1 km south-south-west from section DR. Frederickson's (1948, 1949) locality 11 probably coincides with Resser's collection site located four miles south-east of Hennepin, and is about 750 m west of section DR.

The Kimbell Ranch locality is particularly important, and we measured and sampled three sections along the flank of Ring Top Mountain (Fig. 1); Frederickson's (1948, 1949) locality 8 is likely to be the same as our section KR1. These sections were correlated physically by walking out a metre-scale bioclastic carbonate unit along strike. Stratigraphic ranges of six species of *Dokimocephalus*, three species of *Burnetiella*, two species of *Stittella* gen. nov., and one species of *Plataspella* are shown in Fig. 1. The biostratigraphy is discussed below.

Nevada-Utah

Various units in the Great Basin supplied material representing several species, including silicified sclerites of *Edithiella* Kurtz. Specimens of *Dokimocephalus* and *Edithiella* were recovered from the Corset Spring Shale and Sneakover members of the Orr Formation at Orr Ridge, Utah (Hintze & Palmer 1976; Westrop *et al.* 2007). A single sclerite of *Dokimocephalus* was recovered from the Corset Spring Shale Member at Patterson Pass, Nevada (Westrop & Adrain 2007), and two specimens are from the same unit in the Fish Springs Range, Utah (Hintze & Palmer 1976).

Other regions

Type specimens from several additional regions are included in the study. Sclerites from Missouri that were illustrated by Walcott (1925), Resser (1942) and Kurtz (1975) were collected from the Davis Formation in the St. Francois Mountains area in the south-eastern part of the state. The Ore Hill Member of the Gatesburg Formation in south-central Pennsylvania was the source of several specimens figured previously by Resser (1942) and Wilson (1951). Finally, the holotype of *Burnetiella urania* (Walcott, 1890) from central Texas was probably collected from the Morgan Creek Member of the Wilberns Formation, and a single cranidium from the Open Door Limestone at the Warm Springs Creek section (Saltzman 1999) in western Wyoming provides the first record of *Dokimocephalus* in that state.

Biostratigraphy

All known occurrences of dokimocephalid (s.s.) species are from the Upper Steptoean Elvinia Zone and correlatives. With the elevation of the basal Sunwaptan Irvingella major Subzone (= upper Elvinia Zone of Palmer 1965) to a distinct zone (Chatterton & Ludvigsen 1998), the Elvinia Zone can be divided into two informal units: a lower division with Kindbladia (Frederickson, 1948), Plataspella (Wilson, 1949) and Bynumina (Resser, 1942) and an upper division that includes species of such genera as Camaraspis (Ulrich & Resser in Ulrich, 1924), Cliffia (Wilson, 1949) and Dellea (Wilson, 1949) (Westrop et al. 2007; see also Wilson 1949; Stitt 1977). Only two regions included in the study, Oklahoma and the Great Basin, have sufficient collections for a discussion of the biostratigraphy. In both regions, species of Dokimocephalidae s.s. occur throughout the Elvinia Zone, indicating that this clade was a genuine casualty of the extinction initiated at the base of the overlying Sunwaptan Stage (Irvingella major Zone).

At the Kimbell Ranch site in Oklahoma, Plataspella is confined to the lower part of the carbonate marker bed that was traced around Ring Top Mountain (Fig. 1). The most fossiliferous interval of the Honey Creek Formation occurs above this marker unit, so that almost all of the dokimocephalid (s.s.) species described from Oklahoma occur in the upper division of the Elvinia Zone. Turnover of species is rapid and most are restricted to single horizons; total ranges of the majority of species can be no more than a few metres, and the youngest of these occurs only 10 cm below the base of the Irvingella major Zone. Species of Dokimocephalus with anterior projections of the anterior border (D. stewarti sp. nov., D. blacki sp. nov., D. oliveri sp. nov.) are confined to the upper three metres of the Steptoean, as are species of Stittella gen. nov. Dokimocephalus intermedius (Resser, 1942) and D. lingula (Resser, 1942), which lack anterior projections of the border, occur lower in the formation, although both enter the succession above the highest occurrence of *Plataspella*. Species of *Burnetiella* occur throughout the upper division of the Elvinia Zone. Development of a revised biostratigraphic zonation of the Honey Creek Formation is deferred until the rest of the diverse trilobite fauna is revised. However, the stratigraphic range data presented here (Fig. 1) indicates that there is



Figure 1. Stratigraphic columns for three measured sections (KR1 – KR3) through the Steptoean portion of the Honey Creek Formation at Ring Top Mountain, Kimbell Ranch, northern Comanche County, Oklahoma; map shows locations of sections. Solid line connecting sections marks the top of a resistant, metre-scale bioclastic carbonate unit that was traced around the flanks of Ring Top Mountain to provide physical correlation of the section. Dots show stratigraphic occurrences of various dokimocephalid (*s.s.*) species. Note that the marker unit contains *Plataspella simplicitas* (Resser, 1942) in all three sections, providing biostratigraphic confirmation of the physical correlation. The dashed line at the top of section KR1 shows the base of the basal Sunwaptan *Irvingella major* Zone (22 m above the base of the section).

potential for dokimocephalid (*s.s.*) trilobites to contribute to a finely divided zonal scheme of at least regional utility.

In the Great Basin, cranidia from the Great Basin assigned questionably to the type species, D. pernasutus (Walcott, 1884) occur in the Corset Spring Shale. At Patterson Pass, Nevada, this species occurs four metres below the first appearance of Housia cf. H. ovata Palmer, 1965 and Pseudosaratogia cf. P. abnormalis Palmer, 1960, and 16 metres below Bynumina globosa (Walcott, 1884), a species that is associated with Kindbladia cf. K. affinis (Walcott, 1884) at Shingle Pass, about 22 km west of Patterson Pass (Westrop et al. 2007). This data indicates that D. pernasutus occurs towards the base of the Elvinia Zone, as suggested by Palmer (1965, p. 35), and is older than any species of Dokimocephalus in Oklahoma. A younger occurrence of the genus is recorded by incomplete sclerites of an unnamed species from the uppermost Steptoean in the Sneakover Member of the Orr Formation at Orr Ridge (Fig. 5B-D).

At Patterson Pass, the type species of *Iddingsia*, *I. similis* (Walcott, 1884), enters the succession 34 metres above *D. pernasutus* and eight metres above an assemblage that includes *Edithiella* sp. indet. 1, *Elvina* cf. *E. roemeri* (Shumard, 1861) and *Sigmacheilus flabellifer* (Hall & Whitfield, 1977); the latter occurs with *Kindbladia* at Shingle Pass. This interval of the Corset Spring Shale with *Iddingsia* is transitional with the overlying Whipple Cave Formation and is composed of bioturbated wackstone and packstone. It is broadly correlative with the transition between the Corset Spring Shale and the Sneakover Member at Orr Ridge, Utah. At Orr Ridge, this transitional interval yields sclerites of *Kindbladia* and *Cliffia*, so that it falls within the lower informal division of the *Elvinia* Zone.

Phylogenetic analysis

Our analysis included Dokimocephalus and several genera that have been regarded as close relatives, including Iddingsia (Walcott, 1924), Plataspella (Wilson, 1949) (considered as a junior subjective synonym of Iddingsia by some workers, e.g. Westrop 1986; Hohensee & Stitt 1989) and Burnetiella (Lochman, 1958). These genera share potential apomorphies related to the morphology of the librigena, including the orientation of the genal spine. The poorly known Edithiella (Kurtz, 1975) was also included as a potential member of the ingroup because it shares features of the frontal area with Burnetiella. With the exception of Burnetiella leechi (Chatterton & Ludvigsen 1998, figs 22.1, 22.4–22.6, 22.8, 22.9) and *Plataspella* sp. indet. (=Iddingsia anatina Resser of Westrop 1986, pl. 29, figs 2-6), all species of the above genera were coded from images in this paper. Finally, we also added two species that share some characters with Dokimocephalus and relatives, but are probably not part of the ingroup. The type species of Pseudosaratogia (Wilson, 1951), P. magna (Wilson, 1951, pl. 94, figs 9-16), shares large eyes with such genera as Dokimocephalus, Burnetiella and Plataspella. Calocephalites vulgaris (Kurtz, 1975, pl. 3, figs 7-9), the type species of Calocephalites Kurtz, has tuberculate sculpture that is well expressed on internal moulds. This trait is shared with species of Burnetiella and Stittella gen. nov., although it does not occur in other members of the ingroup. We selected Dunderbergia? anyta (Hall & Whitfield, 1877; Palmer 1965, pl. 4, figs 8, 10, 14-16) as the outgroup. Dunderbergia has been regarded widely as a basal member of the Elviniidae (e.g. Palmer 1965, p. 33), and D.? anyta has a relatively broad pygidium and very long genal spines that most closely resemble those of species of Dokimocephalus. In addition to published photographs, we used sclerites from the Candland Shale Member of the Orr Formation at Orr Ridge (Westrop, unpublished) to code D.? anyta. This material was almost certainly collected from the same horizon (USGS loc 2998 – CO) that was sampled by Palmer (1965, pl. 4, figs 8, 10, 15, 16.).

Species excluded from the analysis

Iddingsia robusta (Walcott, 1884). This species is known from the incomplete holotype cranidium (Palmer 1965, pl. 2, fig. 10), a second incomplete cranidium (Palmer 1960, pl. 11, fig. 16) and a cranidial fragment (Palmer 1965, pl. 2, fig. 11). *Iddingsia nevadensis* (Resser 1942, pl. 16, figs 15–17), a possible synonym of *I. robusta* (see Palmer 1965), is represented by an incomplete cranidium and a librigena.

Burnetiella urania (Walcott, 1890). The type species of *Burnetiella* was described from only a single incomplete cranidium (Fig. 21E–G). The species name is restricted herein to this cranidium.

Burnetiella alta (Resser, 1942). This species is based on a single incomplete cranidium reillustrated herein (Fig. 28J, K). The cranidium attributed to this species by Deland & Shaw (1956, pl. 65, fig. 1), lacks most of the glabella and the posterior fixigena. Although unquestionably recording the occurrence of *Burnetiella* in Wyoming, the species-level identification of this and associated sclerites (1956, pl. 65, figs 2, 3) cannot be corroborated.

Burnetiella exilis (Resser, 1942). This species is known from several cranidia (e.g. Figs 22A–I, 23A–E, G–I). However, it did not differ in cranidial coding from other species of *Burnetiella* in the matrix and was excluded using the 'safe taxonomic reduction' method (Wilkinson 1995).

Burnetiella cava (Resser, 1942). Known from only two sclerites, the holotype is an incomplete cranidium (Resser 1942, pl. 20, figs 1–2). The paratype librigena (Resser 1942,

pl. 20, fig. 3) is misassigned and belongs to a species of *Pseudosaratogia* (Wilson 1951).

Burnetiella pennsylvanica (Resser, 1942). The holotype as photographed by Resser (1942, pl. 21, figs 29, 30) is a composite that was reconstructed with a cast from an external mould. Both part and cast from incomplete counterpart are refigured here (Fig. 24A–D). The paratype (Fig. 24E–G) is not conspecific with the holotype (see below).

Burnetiella? pumila (Lochman, 1964). This species is based on incomplete, flattened material (Lochman 1964, pl. 10, figs 24, 25).

Iddingsia occidentalis (Deland & Shaw, 1956, pl. 65, fig. 14). This species is known only from a single cranidium.

Iddingsia intermedia (Palmer, 1965). Both the librigena (Palmer 1965, pl. 2, fig. 6) and pygidium (Palmer 1965, pl. 2, fig. 8) are almost certainly misidentified. The librigena clearly belongs to a trilobite with smaller eyes than *Iddingsia*, and the pygidium, which has a relatively longer, narrower axis and a concave border, is unlike any pygidium that is associated with *Iddingsia* in our collections (e.g. Fig. 15E, F).

'Iddingsia' haspis (Hohensee & Stitt, 1989). This species is based on three very small cranidia; the holotype is incomplete and paratypes are from a different locality. The cranidia apparently have pitted sculpture, although this is not evident from the illustrations. The frontal area of holotype (Hohensee & Stitt 1989, fig. 4.10) is incomplete but the paratypes (Hohensee & Stitt 1989, fig. 4.10) have very short anterior borders that are unlike those of species of *Iddingsia* described herein.

Characters excluded from the analysis

Orientation of the palpebral ridges. Orientation of ridges from nearly transverse to strongly oblique is linked to the position of the palpebral lobe and eyes. The coding of palpebral ridges is simply a restatement of the coding of the latter.

Width and profile of librigenal lateral border. These traits co-vary with the cranidial border morphology, so that coding is redundant.

Divergence of posterior branches of the facial sutures. This varies as a function of eye size and position, so that coding is redundant.

Results

The analyses were performed with PAUP* 4.0b10 (Swofford 2000) and checked using TNT v.1.1 (Goloboff *et al.* 2008); character optimization was performed in PAUP* and WinClada v. 1.00.08 (Nixon 2002). The matrix (Table 1) was composed of 24 ingroup species and 26 characters (17 binary; nine unordered multistate; Appendix); autapomorphies of individual species were not included and zerolength branches were not collapsed in the analyses. Characters with states that were inapplicable for some species (characters 15-17 in Appendix, which describe the variation of the anterior projection of the anterior border, where present) were coded using absence coding and reductive coding (Strong & Lipscomb 1999) in alternate analyses; the positions of two species of Dokimocephalus were sensitive to this variation in coding (see below). Under reductive coding (inapplicable states coded as '?'), a branch-andbound search (implicit enumeration) yielded 45 equally parsimonious trees (length, 51; consistency index, 0.68; retention index, 0.83; rescaled consistency index, 0.56), with the strict consensus tree shown in Fig. 2A. When inapplicable states are coded as character states (0) rather than missing data, characters describing the variation in shape of anterior projection of the border (characters 15-17; inapplicable to D. intermedius and D. lingula) are decisive in determining the position of D. intermedius and D. lingula. The latter species shift to basal positions in Dokimocephalus (Fig. 2B), and species with anterior projections form a subclade. In contrast, reductive coding results in a decisive role for characters without inapplicable states, and the analysis yields trees in which species of Dokimocephalus with occipital spines (character 2) form a subclade. Finally, composite coding (Strong & Lipscomb 1999), with characters 15-17 recast as a single multistate character, produced ingroup relationships of Dokimocephalus that were comparable to the results of reductive coding (Fig. 2B). The optimized character distribution for one of the set of 45 trees generated using reductive coding is shown in Fig. 3.

The results support monophyly of *Dokimocephalus Iddingsia*, *Plataspella*, *Burnetiella* and *Edithiella*. Dokimocephalidae *s.s.* includes *Dokimocephalus*, *Iddingsia*, *Plataspella*, *Burnetiella* and *Stittella* gen. nov., all of which share apomorphic features of the librigena. The long genal spine is initially curved outward and backward, with interruption of the curvature of the lateral librigenal margin [22 (1)]; the lateral border is inflated at the intersection with the genal spine [23 (1)]. Although lacking these character states, *Edithiella* is nested within Dokmocephalidae *s.s.*, with which it shares a posteriorly positioned palpebral lobe [7 (2)].

Several characters support monophyly of *Dokimo-cephalus*, including anterior facial sutures that are bowed gently outward between palpebral lobe and anterior border furrow, so that there is no net increase in the width of preocular field [19 (1)]. Most species have a very long, curved occipital spine [2 (1)], although *D. pernasutus* and *D. gregori* retain the plesiomorphic, aspinose condition. There is evidence that the exoskeleton curves beneath the anterior border to produce a 'pocket' or tube [18 (1)], implying that the dorsal sutures do not extend along the entire length of the border. A subset of five species has a long spinose to spatulate extension of the anterior border [14 (1)]. *Iddingsia* is a grouping of species that share strongly upsloping

	-	5	с	4	5	9		6	10		5	3	4	15	16	17	18	19	20	21	22	23	24	25	26
Dunderbergia ? anyta Calocephalties vulgaris Pseudosaratogia magna Dokimocephaltus premasutus Dokimocephaltus gregori Dokimocephaltus intermedius Dokimocephaltus extensus Dokimocephaltus extensus Dokimocephaltus stewarti Dokimocephaltus stewarti Dokimocephaltus blacki Dokimocephaltus blacki Dokimocephaltus blacki Dokimocephaltus blacki Dokimocephaltus blacki Dokimocephaltus blacki Dokimocephaltus oliveri Iddingsia aimilis Iddingsia aimilis Burnetiella cechi Stittella beeae Stittella beeae Stittella sp. nov. 1 Plataspella sp. nov. 1	0	0000000000000-0-0	0000	00000000000000000		0000		0	000000000000000000000000000000000000000			00000011000001					0 ~ ~ - ~ ~ ~ ~ ~ ~ ~ ~ ~ ~ ~	00000000000000000000000000000000000	00000000000000000000000000000000000000	0 ~ 0 - ~ - ~ ~ ~ ~ - ~ ~ ~ ~ ~ ~ ~ ~ ~	0 ~ 0 - ~ - ~ ~ ~ ~ - ~ ~ ~ ~ ~ ~ ~ ~ ~	000000000000000000000000000000000000000	000000000000000000000000000000000000000	0~0~~~~~~	0 ~ - ~ ~ ~ ~ ~ ~ ~ 0 0 ~ ~ ~ 0 0 ~ 0 ~
<i>Edithiella</i> sp. 1 <i>Edithiella</i> sp. 2	0 0	0 0	0 0	0 0	0 0		0.0		0 0	 		4 4	 0 0	! !		 	ن» 0	0 0	20	0 ~·	0 6	0 ~	c· c·	c· c·	c· c·

 Table 1. Data matrix for analysis. ? = missing data; - - = inapplicable state. Inapplicable states were coded as '?' and '0' in separate analyses



Figure 2. Consensus trees from parsimony analyses that differed in coding strategies for inapplicable states. Bremer support of nodes > 1 is indicated by numbers in italics. A, Strict consensus tree using reductive coding (inapplicable states codes as '?'); **B**, strict consensus trees using absence coding (inapplicable states codes as '0'). Note that *Dokimocephalus intermedius* and *D. lingula* shift to a basal position in *Dokimocephalus*.



Figure 3. Optimized character distribution for one of the 45 trees generated discovered by parsimony analysis using reductive coding for inapplicable states. Only those states that are unambiguous (i.e. occur at the same node under both ACCTRAN and DELTRAN optimization) are shown. Filled circles indicate character states confined to a single node; open circles indicate those that occur at more than one node.

palpebral area of the fixigena [4 (1)]. Burnetiella is based on pygidial apomorphies, including a relatively narrow axis [25 (1)] composed of five, rather than four, segments, and a concave border [26 (1)]. Plataspella emerges as a monophyletic grouping of species with low bacculae on the fixigenae [5 (1)] and, along with Edithiella, it lacks of glabellar furrows on both the dorsal surface and the internal mould [1 (2)]. Two new species (Figs 27, 28A-E, 29) are assigned Stittella, which is characterized by a very short frontal area [10 (1)]. Sclerites other than the cranidium are known only for S. beeae sp. nov., and were not coded in the analysis. However, these sclerites offer additional apomorphic character states that have been included in the diagnosis of the genus. For example, the librigena has a novel, steeply upsloping genal spine (Fig. 28A-C) and the pygidium (Fig. 28D, E) is relatively narrow and lacks a border and border furrow. Finally, Edithiella now comprises three species, all of which share an anterior border that slopes steeply and evenly forward without change in slope between it and the preglabellar field [13 (4)]. Two of the three species possess a very long occipital ring [3(1)].

Systematic palaeontology

Figured specimens are housed at the Oklahoma Museum of Natural History, University of Oklahoma (OU), the National Museum of Natural History, Washington, DC (USNM), the Paleontology Repository, Department of Geoscience, University of Iowa, Iowa City (SUI) and the Peabody Museum, Yale University (YPM). New collections are designated by the following prefixes, with numbers indicating metres above base of the section: KR1, KR2, KR3, Kimbell Ranch section, Oklahoma; DR, Dotson Ranch section, Oklahoma; ORR, Orr Ridge, Utah; FSR2, Fish Springs Range, Utah; PP, Patterson Pass, Nevada; WSC, Warm Springs Creek, Wyoming.

Proportions expressed in percentages in descriptions and diagnoses are means, with numbers in parentheses indicating the range of values. All measurements were made on digital images to the nearest tenth of a millimetre using the Measure Tool of Adobe PhotoshopTM.

Sclerites associations were established on the basis of such criteria as similarities in surface sculpture, recurrent co-occurrence in multiple collections, and data on associations from the literature.

In all figures, sclerites are oriented in dorsal view to maximize cranidial or pygidial length.

Family Dokimocephalidae Kobayashi, 1935, sensu stricto

Remarks. As noted above, this study deals with the 'core group' of dokimocephalid trilobites (Dokimocephalidae *sensu stricto*) that comprises *Dokimocephalus* and the related genera *Iddingsia*, *Plataspella*, *Burnetiella*, *Edithiella* and *Stittella* gen. nov. A formal diagnosis of the family is deferred until the relationship between the core group and such other genera as *Sulcocephalus* Wilson, 1948, *Kindbladia* Frederickson, 1948 and *Dellea* Wilson, 1949 has been investigated. However, there is character support for monophyly of Dokimocephalidae *sensu stricto*, including librigena with a long genal spine that is initially curved outward and backward, with interruption of the curvature of the lateral librigenal margin. The lateral border is inflated at the intersection with the genal spine.

Genus Dokimocephalus Walcott, 1924

Type species. *Ptychoparia pernasutus* Walcott, 1884, from the Dunderberg Formation, Eureka District, Nevada, by original designation.

Diagnosis. Anterior branches of facial sutures bowed very gently outward between palpebral lobe and anterior border furrow, so that there is no net increase in width (tr.) of preocular field. Anteriorly, exoskeleton folded under to produce tubular or flap-like region at front of border; dorsal facial sutures do not extend along the full length of anterior border. Occipital ring with very long occipital spine that is curved downward distally (absent in some species).

Remarks. Dokimocephalus is most closely similar to Burnetiella Lochman, 1958; indeed, Resser (1942) assigned several species now included in Dokimocephalus to the latter (under the preoccupied name Burnetia Walcott, 1924). These two genera share very long cranidial borders and, with a few exceptions (e.g. Fig. 4F-H), very short preglabellar fields. Species of Dokimocephalus possess one unequivocal synapomorphy in the orientation of the anterior branches of the facial sutures, which are bowed very gently outward between the palpebral lobe and the anterior border furrow (e.g. Figs 4A-C, 6A-C, 8A-C, 9A-C, 14A-C). In contrast, species of Burnetiella (and other genera of the Dokimocephalidae s.s.) retain the plesiomorphic state, divergent sutures between palpebral lobe and anterior border furrow, so that preocular area of fixigena expands forward (e.g. Figs 23E, G, 25F-H). Broken margins of the anterior border of several species of Dokimocephalus indicate that the exoskeleton is curved under to produce a flap-like or tubular 'pocket' (e.g. Figs 4K, 7M, 8A, C, L, 9G). The full extent of this structure is unknown, but it is possible that the entire projection is floored by exoskeleton. Where the anterior border is tongueshaped, rather than spatulate or spinose, it is possible that a distinct inflexion in the lateral cranidial margin (e.g. Fig. 9A. E. G) marks the farthest anterior extent of the sutures. Silicified sclerites will be needed to describe the ventral morphology of the border. The construction of the anterior border of Dokimocephalus is unusual but there are parallels among some lichids, such as Probolichas Phleger, 1936

(see Evitt 1951, pl. 88, fig. 9a–d). Complete exoskeletons of *Burnetiella* demonstrate the presence of a broad (tr.) rostral plate that extends to the anterior cranidial margin (e.g. see Chatterton & Ludvigsen 1998, fig. 22.1), suggesting that the pocket may prove to be another synapomorphy of *Dokimocephalus*. Finally, species of *Dokimocephalus* are characterized by very long, curved occipital spines (e.g. Figs 5F–H, 6A–C, G–I, 11D–E), although the type species, *D. pernasutus* (Walcott; Fig. 4G–N), retains the plesiomorphic aspinose condition.

Iddingsia is differentiated from *Dokimocephalus* by a single apomorphy, steeply upsloping fixigenae in larger holaspids (e.g. Figs 15B, N, 16B, F). The fixigenae of *Dokimocephalus* are flat to weakly inflated (e.g. Figs 4A–C, 8A–C). At least some species of *Plataspella* share a long, curved occipital spine with *Dokimocephalus* (e.g. Westrop 1986, pl. 29, figs 3–4). However, the former is bacculate and the lateral glabellar furrows are effaced.

When he established the genus, Walcott (1924, 1925) assigned only two species, D. pernasutus (Walcott, 1884) and D. gregori Walcott, 1925, but Resser (1942) added four more from the Honey Creek Formation. Following the work of Frederickson (1948) and Palmer (1965), Dokimocephalus was reduced to three species, D. pernasutus, D. intermedius (Resser, 1942) and D. curtus (Resser, 1942). Restudy of type material and new collections from Oklahoma, Utah and Wyoming demonstrates that there are at least seven distinct species, and possibly as many as 12. Six of these species occur in the Honey Creek Formation of Oklahoma, and their distribution appears to have biostratigraphic significance. Although Resser remains among the most notorious 'splitters' in the history of trilobite research (Hughes & Labandeira 1995), most of his Oklahoman species of Dokimocephalus are recognized as valid herein.

Dokimocephalus pernasutus (Walcott, 1884) (Figs 4A–C, 5A, ?4D, 4E, I–N)

- 1884 *Ptychoparia? pernasutus* Walcott: 49, pl. 10, fig. 8, 8a-b.
- 1924 Dokimocephalus pernasutus (Walcott); Walcott: 55, pl. 11, fig. 1.
- 1925 Dokimocephalus pernasutus (Walcott); Walcott: 84, pl. 16, figs 29–31.
- 1960 Dokimocephalus pernasutus (Walcott); Palmer: 95, pl. 11, figs 18–20.
- *non* 1965 *Dokimocephalus pernasutus* (Walcott); Palmer: 35, pl. 3, fig. 18 [= *Dokimocephalus* sp. indet.]

Types. Holotype, USNM 24608a, an incomplete internal mould of a cranidium (Fig. 4F–H); paratype, librigena, USNM 24608b (Fig. 5A).

Diagnosis. Occipital spine absent. Preglabellar field long, equal to 19% (16–24) of preoccipital glabellar length; anterior border extends into long, narrow, anteriorly-tapered projection that is flexed downward anteriorly. Coarsely

granulose sculpture on glabella and on fixigenae between posterior border furrow and anterior end of glabella is poorly expressed on internal moulds.

Material. In addition to the types, three cranidia are assigned questionably to this species.

Occurrence. The types are from Dunderberg Shale, Eureka District, Nevada (Walcott 1925). Other cranidia attributed questionably to the species herein are from the lower part of the Corset Spring Shale at Patterson Pass, Nevada (PP 276), and the Fish Springs Range, Utah (FRS2 100.3).

Description. Frontal area incompletely preserved on all available cranidia. Glabella moderately inflated and convex; tapered forward and rounded anteriorly, width at SO equal to 68% (68-69) length; occupies approximately 55% of the cranidial length (sag.). Axial and preglabellar furrows wide, shallow grooves. SO well incised, transverse medially but bifurcates distally to outline small lateral lobes of occipital ring; holotype (Fig. 4H) with median tubercle in furrow. LO occupies 18% (18-20) of glabellar length; weak median node on internal mould (Fig. 4H, J). Three pairs of lateral glabellar furrows present. S1 lateral furrows shallow but firmly impressed and oblique. S2 lateral furrows are shallow and faint; oblique, parallel to S1 furrows. S3 furrows faint. Frontal area long, accounting for at least 45% of cranidial length. Anterior border furrow broad (sag., exsag.), forwardly curved groove on internal mould; shallow medially but deepens somewhat laterally. Preglabellar field relatively long, downsloping, and equal to slightly more than 19% (16-24) of preoccipital glabellar length. Anterior border extended into long, narrow, anteriorly tapered projection that is curved downward distally; occupies at least 35% of the cranidial length (sag). Crosssection of incomplete specimen (Fig. 4K) indicates that anterior projection is floored by exoskeleton along most of its length. Palpebral area of fixigena gently inflated and wide, equal to 40% of glabella width at SO. Palpebral lobe is narrow arcuate band, equal to 33% of glabella length, and centred opposite anterior end of L1; depressed below level of maximum inflation of palpebral area. Palpebral furrow is clearly defined groove; deeper and somewhat wider (tr.) on internal mould. Palpebral ridge ill-defined, extends obliquely forward to intersect axial furrow opposite S3. Anterior branches of facial suture bowed gently outward between palpebral lobe and anterior border furrow, then swing inward along posterior border; full anterior extent of sutures unknown but they do not reach anterior margin of anterior projection of border. Posterior sutures diverge backward in faintly sigmoid curve. Posterior border is narrow, convex band that widens somewhat (exsag.) distally; posterior border furrow is well defined groove that curves very gently backward. External surface of glabella and fixigenae between posterior border furrow and anterior



tip of glabella with coarsely granulose sculpture; posterior border, palpebral lobe, and frontal area smooth. Weak to barely perceptible granulose sculpture on internal mould confined to glabella and fixigenae.

Poorly preserved librigena lacks most of librigenal field. Posterior and lateral border furrows are narrow and shallow; posterior furrow does not connect with lateral furrow but continues a short distance along inner edge of genal spine; lateral furrow stops short of the genal spine. Lateral border is inflated at intersection with genal spine. Genal spine incomplete but apparently long and oblique; directed outward so that it does not continue the curvature of the lateral librigenal margin. Internal mould of librigena smooth.

Remarks. The holotype of *Dokimocephalus pernasutus* (Walcott, 1884; Fig. 4F-H), from the Dunderberg Formation in the Eureka Mining District, Nevada, is incomplete and lacks the fixigenae, palpebral lobes and anterior tip of the anterior border. A few incomplete cranidia in our collections from correlative strata in eastern Nevada and western Utah (Fig. 4D, E, I-N) are assigned questionably to this species, and were used both to augment the description and to complete coding for phylogenetic analysis. These sclerites have somewhat shorter preglabellar fields than the larger holotype but are very similar in other respects. We are uncertain about the identity of the cranidium from Yucca Flat, Nevada that was included in D. pernasutus by Palmer (1965, pl. 3, fig. 18). It has a much narrower, spinose projection than both the holotype and the most complete specimen from Utah (Fig. 4D, E). In addition, Palmer's cranidium has the coarsely granulose to finely tuberculate sculpture clearly expressed on the internal mould of the glabella, whereas the sculpture is weak to absent on exfoliated surfaces of all other specimens from Nevada and Utah. We prefer to treat Palmer's specimen as an indeterminate (probably new) species of Dokimocephalus.

Palmer (1960, 1965) regarded *D. gregori* (Walcott, 1925; Fig. 4A–C), known from a single cranidium from the Davis Formation of eastern Missouri, as a synonym of *D. pernasutus*. While these species are certainly similar, the respective holotypes (Fig. 4A–C, F–H) differ in the expression of the sculpture on the internal mould. Also, the holotype of *D. pernasutus* has a relatively longer preglabellar field than *D. gregori*, although smaller cranidia from Nevada and Utah (Fig. 4D, E, I–N) are much closer to the latter in this respect. The significance of these differences is impossible to gauge at present state of knowledge, and *D. gregori* is best retained as a separate species until information on its variability is available. Palmer (1965, p. 35) felt that his specimen from Yucca Flat (see above) and the holotype of *D. gregori* "do not differ significantly in any observable feature". However, there are obvious differences in the relative width of the anterior projection of the anterior border (compare Fig. 4A–C with Palmer, 1965, pl. 3, fig. 18), and we doubt that these sclerites are conspecific.

All species from the Honey Creek Formation (Figs 6–12) differ from D. pernasutus in the presence of an occipital spine, and also have shorter preglabellar fields. In other respects, D. pernasutus is most similar to D. blacki sp. nov. (Fig. 11, 12) and D. oliveri sp. nov. (Fig. 14A-C, I-N) in possessing a long (sag.), narrow (tr.) anterior projection from the border. In detail, the projection of D. oliveri (Fig. 14A, L, K) expands anteriorly, has a rounded termination, and a concave upper surface, whereas the projection of D. pernasutus is flat and tapers anteriorly. Dokimocephalus blacki has a projection that is parallel-sided (Fig. 12G) to weakly expanded anteriorly (Figs 11F-H, 12E) with a bluntly rounded termination. Dokimocephalus intermedius (Resser, 1942; Figs 6, 7), D. lingula (Resser, 1942; Fig. 9) and D. extensus (Resser, 1942; Fig. 8A-L) clearly differ from D. pernasutus in possessing anterior borders that maintain a more even width (tr.) and, consequently, are much wider anteriorly.

Dokimocephalus gregori Walcott, 1925 (Fig. 4A-C)

- 1925 *Dokimocephalus gregori* Walcott: 84, pl. 16, figs 32, 33.
- 1944 *Dokimocephalus gregori* Walcott; Shimer & Shrock: pl. 264, figs 38, 39.
- **Type.** The holotype (USNM 70254) is a cranidium (Fig. 4A–C) from the Elvins Group, Missouri.

Diagnosis. Anterior border extends into a moderately narrow, anteriorly tapering projection. Preglabellar field relatively long, equal to 14% of preoccipital glabellar length. External mould with well-defined coarsely granulose sculpture on glabella and on fixigenae between

Figure 4. A–C, *Dokimocephalus gregori* Walcott, 1925, Davis Formation near Potosi Missouri; holotype cranidium, exfoliated (USNM 70254); \times 2.1: A, dorsal view; B, lateral view; C, anterior view. D–N, *Dokimocephalus pernasutus* (Walcott, 1884): D, E, incomplete testate cranidium (OU 12408), Corset Spring Shale Member, Orr Formation, Fish Springs Range, Utah, collection FSR2 100.3, \times 3 (assigned questionably): D, dorsal view; E, anterior-oblique view. F–H, holotype cranidium, exfoliated (USNM 24608a), Dunderberg Formation, Eureka District, Nevada, \times 2.1: F, lateral view; G, anterior view; H, dorsal view. I–K, exfoliated cranidium (OU 12409), Corset Spring Shale, Patterson Pass, Nevada, collection PP 276, \times 4 (assigned questionably): I, lateral view; J, dorsal view; K, anterior view (arrows show exoskeleton wrapping around beneath border, indicating that the anterior extension of the border is tubular in construction). L–N, partly exfoliated cranidum (OU 12410), Corset Spring Shale Member, Orr Formation, Fish Springs Range, Utah, collection FSR2 100.3, \times 3 (assigned questionably): L, lateral view; M, anterior view; N, dorsal view.



posterior border furrow and anterior end of glabella; posterior border, palpebral lobe and frontal area are smooth.

Occurrence. Elvins Group, south-east Missouri.

Remarks. The type and only known specimen of *Dokimocephalus gregori* is very similar to *D. pernasutus* and differs only in the expression of the sculpture on the internal mould and in having a somewhat shorter preglabellar field. It is possible that these species will prove to be synonyms (as suggested by Palmer 1960), but a decision must await the discovery of additional material from the Davis Formation, so that the variation of *D. gregori* can be evaluated.

Dokimocephalus intermedius (Resser, 1942) (Figs 6, 7)

1942 Burnetia intermedia Resser: 80, pl. 17, figs 10, 11.

- 1948 Dokimocephalus intermedia (Resser, 1942); Frederickson: 801, pl. 123, figs 1–3 [specimens identified in the figure caption (p. 800) as Dokimocephalus lingula (Resser)].
- non 1949 Dokimocephalus intermedius (Resser, 1942); Wilson: 37, pl. 9, figs 1, 2, 4, 5 [fig. 1 = D. lingula (Resser); figs 2, 4, 5 = D. sp. indet.)
- non 1951 Dokimocephalus intermedius (Resser, 1942); Wilson: 640, pl. 90, fig. 25 [? = D. lingula (Resser)].
- ?1965 Dokimocephalus intermedius (Resser, 1942); Grant: 111, pl. 9, figs 29, 32.
- non 1971 Dokimocephalus intermedius (Resser, 1942); Stitt: 18, pl. 1, fig. 7 [? = D. lingula (Resser)].

Type. Holotype (USNM 108805), an incomplete internal mould of a cranidium (Fig. 6D–F).

Diagnosis. Long, wide, gently tapered, tongue-shaped anterior border that occupies 33% (31–34) of cranidial length in larger holaspids; border length of larger holaspids is 48% (46–51) of maximum border width. Preglabellar field long in larger holaspids (e.g. Fig. 6A–C, G–I), equal to 14% (13–16) of preoccipital glabellar length but somewhat shorter in smallest cranidia (e.g. Fig. 7H–J), equal to 12% of preoccipital glabellar length. Occipital ring with stout spine that curves upward and backward.

Material. In addition to Resser's holotype, figured material includes nine cranidia and an incomplete librigena. A few additional incomplete cranidia were also available for study.

Occurrence. Honey Creek Formation, Arbuckle and Wichita Mountains, Oklahoma (collections DR 9.1–9.27; KR2 49.2, KR2 49.4). The holotype is from the Resser's (1942) locality 12p, four miles south of Hennepin, Murray County.

Description. Cranidium (excluding occipital spine) subrectangular, width across palpebral lobes 77% (82-83) of cranidial length. Glabella tapers slightly forward from L2 lateral lobe, with width at SO equal to 71% (61-78, with higher values in smaller cranidia; e.g. Fig. 7K, L) of length; rounded anteriorly; moderately convex; occupies 52% of cranidial width (tr.) across palpebral lobes and 60% (59-62) of cranidial length. Axial furrows firmly impressed, shallow grooves that deepen toward LO; preglabellar furrow slightly shallower than axial furrow. SO wide (sag.), shallow and nearly transverse medially; curves forward, narrows (exsag.) and deepens near axial furrow. LO (excluding occipital spine) occupies 24% (20-30) of glabellar length and is inflated near axial furrow to form lateral lobes. Long, stout occipital spine curves upward and backward, becoming directly slightly downward at tip; most completely preserved spine equal to 96% of length of remainder of glabella. S1 furrows oblique and moderately impressed; oblique S2 furrows shorter and shallower than S1, expressed on external surface largely as area lacking sculpture; S3 furrows short, faint and nearly transverse on internal mould but expressed on external surface only as area lacking sculpture. Frontal area occupies 40% (38-41) of cranidial length (excluding occipital spine) in larger cranidia (e.g. Fig. 6A-C). Preglabellar field long in larger holaspids (e.g. Fig. 6A-C, H, I), equal to 14% (13-16) of preoccipital glabellar length but somewhat shorter in smallest cranidia (e.g. Fig. 7H–J), equal to 12% of preoccipital glabellar length. Anterior border furrow well defined, shallow groove on both external surface and internal mould; curved forward. Anterior border long, occupies 81% (78-85) of frontal area length in larger holaspids, and tapered forward and rounded anteriorly; tongue-shaped with length 48%

Figure 5. A, *Dokimocephalus pernasutus* (Walcott, 1884), Dunderberg Formation, Eureka District, Nevada; paratype librigena, mostly exfoliated (USNM 24608b), dorsal view, × 2.1; **B–D**, *Dokimocephalus* sp. indet. 1, Sneakover Member, Orr Formation, Orr Ridge, northern House Range, Millard County, Utah, collection ORR 59.4: **B**, **C**, testate cranidium (OU 12411), × 6; **B**, anterior-oblique view; **C**, dorsal view; **D**, testate librigena (OU 12467), dorsal view, × 6. **E**, *Dokimocephalus* sp. indet. 2, Open Door Limestone, Warm Springs Creek, Wind River Range, Fremont County, Wyoming collection WSC 56.25–56.42; testate cranidium, dorsal view (OU 12412), × 4. **F–H**, *Dokimocephalus curtus* (Resser, 1942), Honey Creek Formation, Blue Creek Canyon, northern Comanche County, Oklahoma; holotype cranidium, mostly exfoliated (USNM 108811), × 4: **F**, dorsal view; **G**, anterior view; **H**, lateral view. **I–K**, *Dokimocephalus oliveri* sp. nov., Honey Creek Formation, Ring Top Mountain, Kimbell Ranch, northern Comanche County, collection KR1 21.9; testate hypostome (OU 12413), × 6: **I**, posterior view; **J**, lateral view; **K**, ventral view. **L–O**, *Iddingsia utahensis* Resser, 1942, Orr Formation, Fandango Canyon, Dugway Range, Tooele County, Utah; holotype cranidium, partly exfoliated (USNM 108797), × 4: **L**, dorsal view; **M**, anterior view; **N**, anterior-oblique view; **O**, lateral view.



Figure 6. Dokimocephalus intermedius (Resser, 1942), Honey Creek Formation, Oklahoma. A–C, exfoliated cranidium (OU 12414), Dotson Ranch, Murray County, collection DR 9.1–9.27, \times 4: A, lateral view; B, dorsal view; C, anterior view. D–F, holotype cranidium, mostly exfoliated (USNM 108805), 4 miles southeast of Hennepin, Murray County, \times 4: D, anterior view; E, lateral view; F, dorsal view. G–I, mostly exfoliated cranidium (OU 4286), Frederickson (1948) locality 8, Blue Creek Canyon, northern Comanche County, \times 4: G, dorsal view; H, anterior view; I, lateral view.

559

(46-51) of maximum border width in larger holaspids; steeply sloping near border furrow but quickly flattens to become very gently upsloping at anterior cranidial margin; border curved under to form flap-like 'pocket' of uncertain length that is floored by exoskeleton. Palpebral area of fixigena slopes gently upward from axial furrow, width equal to 36% (33-39) of glabellar width at SO. Palpebral lobe long (exsag.), flat arcuate band, equal to 35% (32-40) glabellar length, centred opposite anterior third of L1 glabellar lobe. Palpebral furrows are well defined, strongly curved grooves. Palpebral ridge extends obliquely forward from palpebral lobe to intersect axial furrow opposite S3 furrow. Anterior branches of sutures very weakly divergent between palpebral lobe and anterior border furrow, then converge gradually forward, with distinct inflexion opposite point about 20% of distance from border furrow to anterior tip of border; full anterior extent of sutures unknown but they do not reach anterior margin of border. Posterior branches of sutures diverge backward. Posterior border furrow shallow and narrow; expressed clearly on external surface and internal mould. Posterior border is short, convex band. Glabella with coarsely granulose to finely tuberculate sculpture; coarse granules on fixigenae, becoming finer on preglabellar and preocular fields; anterior border and palpebral lobe with finely granulose sculpture. Surface of internal mould smooth.

Discussion. Frederickson (1948) considered D. lingula (Resser, 1942; Fig. 9) and D. extensus (Resser, 1942; Fig. 8A-L) to be synonyms of Dokimocephalus intermedius, and his interpretation has been followed by subsequent workers (e.g. Wilson 1949, 1951; Grant 1965; Stitt 1971). However, study of type material and new specimens collected from the Honey Creek Fomation shows that all three should be treated as distinct species. Dokimocephalus lingula (Fig. 9) is most similar to D. intermedius but differs consistently in having a relatively longer and more anteriorly tapered anterior border and a shorter preglabellar field (compare Figs 6A-I, 7A-C with Fig. 9A-F). In larger cranidia of D. lingula, border length is 68% (66-71) of maximum border width, whereas border length is 48% (46-51) of maximum border width in similarly sized cranidia of D. intermedius. Dokimocephalus extensus also has a shorter preglabellar field than D. intermedius, and has a longer, conspicuously tapered anterior border whose minimum width (tr.) is less than the width of the glabella at LO. In contrast, the minimum width of the anterior border of D. intermedius clearly exceeds the width of the glabella (compare Figs 6A-C and 8A-C, K, L).

Other species of *Dokimocephalus* from the Honey Creek Formation, including *D. stewarti* sp. nov. (Fig. 10), *D. blacki* sp. nov (Fig. 11, 12) and *D. oliveri* sp. nov (Fig. 14), possess strongly tapered anterior projections of the anterior border that contrast with the broad, tongue-shaped border of *D. intermedius*, and also have short preglabellar fields. *Dokimocephalus pernasutus* (Walcott; Fig. 4D–N) and the closely similar *D. gregori* Walcott (Fig. 4A–C) also have narrow anterior projections of the anterior border, and both species lack the occipital spines developed in *D. intermedius* and other species from Oklahoma.

Small cranidia from the Honey Creek Formation at the Kimbell Ranch section (Fig. 7G–L) provide new information about the holaspid ontogeny of the frontal area in *D. intermedius*. In the smallest individuals (Fig. 7H–J), both the preglabellar field and anterior border are much shorter than in large holaspids (e.g. Fig. 6A–C). Forward expansion of the anterior border is particularly great during ontogeny, with relative length changing from about 45% of preoccipital glabellar length to about 70%. Increase in length of the preglabellar field is less dramatic, but changes from 12 to 16% of preoccipital glabellar length between smallest and largest cranidia.

Dokimocephalus extensus (Resser, 1942) (Fig. 8A–L)

1942 Burnetia extensa; Resser: 81, pl. 17, figs 15-22.

Types. The holotype is an incomplete cranidium (USNM 108807a) from the Honey Creek Formation, at Resser's (1942) locality 89v, West Timbered Hills, Arbuckle Mountains, Oklahoma (Fig. 8A–C). Paratype cranidia from the same locality include USNM 10807b-d (Figs 8D–J).

Diagnosis. Spatulate extension of anterior border that tapers gently forward. Border long, slightly longer than preoccipital glabellar length (103%; 101-104) and with width at mid-length of anterior projection 82% (74–88) of glabellar width at SO. Preglabellar field very short, equal to 8% (7–10) of preoccipital glabellar length. Occipital spine present.

Material. In addition to the types, a single cranidium (Fig. 8K, L) was available for study.

Occurrence. Honey Creek Formation, Arbuckle Mountains, Oklahoma.

Description. Cranidium (excluding occipital spine) subrectangular in outline, width across palpebral lobes approximately 68% of cranidial length. Glabella convex, standing well above level of fixigenae, and occupies slightly more than half of cranidial length; gently tapered and rounded anteriorly, width at SO equal to 71% (68–73) of glabellar length. Axial and preglabellar furrows are shallow grooves. SO shallow and nearly transverse medially but curves forward and deepens near axial furrow. LO accounts for 23% (22–25) of glabellar length; weakly inflated near axial furrows to form lateral lobes. Stout occipital spine present but only base preserved in available material. S1 lateral furrows firmly impressed and oblique; S2 lateral furrows shorter and weakly incised; S3 may be expressed as a small area without sculpture. Frontal area long, accounting



for slightly less than half of crandial length. Anterior border furrow is shallow, forwardly curved groove. Preglabellar field slopes downward to anterior border; very short, equal to 8% (7-10) of preoccipital glabellar length. Anterior border long, slightly longer than preoccipital glabellar length (103%; 101-104) and with spatulate anterior projection; width at mid-length of anterior projection is 82% (74-88) of glabellar width at SO. Lateral profile of border initially downsloping but projection curved gently upward. Anterior end of border curved under to form flattened 'pocket' that is floored by exoskeleton (e.g. Fig. 8A, C). Palpebral area of fixigena nearly flat and broad, width equal to 33% (31-36) of glabellar width at SO. Palpebral lobe is long, arcuate band, length (exsag.) approximately 33% of glabella length; palpebral furrow narrow, welldefined groove. Palpebral ridge weakly convex, extending obliquely forward to intersect axial furrow in front of S2 furrow. Anterior branches of facial sutures bowed gently outwards between palpebral lobe and anterior border furrow; converge gently forward at border with well defined inflexion at point 25% of distance between border furrow and anterior tip of border; full anterior extent of sutures unknown but they do not reach the anterior margin of anterior projection. Posterior branches of facial suture diverge backward. Posterior border is convex, narrow and slightly curved backward; posterior border furrow gently impressed on both internal mould and external surface. Glabellar lobes with coarsely granulose to finely tuberculate sculpture. Fixigenae with granular sculpture; granules arrayed along caecal network on preglabellar and preocular fields; anterior border finely granulose. Internal mould is smooth.

Remarks. *Dokimocephalus extensus* is most similar to *D. lingula* (Resser, 1942; Fig. 9), from which it differs in the proportions of the anterior border. The border of *D. extensus* tapers more rapidly, so it has a relatively narrow, spatulate anterior projection that contrasts with the less tapered, tongue shaped border of *D. lingula. Dokimocephalus intermedius* (Resser; Figs 6, 7) also differs from *D. lingula* in this respect, and has a relatively longer preglabellar field. Other members of the genus (e.g. Figs 4, 9–12) have narrower spatulate to spinose anterior projections of the border than *D. extensus*.

The smallest cranidium of *D. extensus* (Fig. 8G) demonstrates that the anterior projection develops relatively late in the holaspid ontogeny. It exhibits a relatively shorter, subtriangular border (equal to 81% of preoccipital glabellar length, rather than slightly more than 100% as in larger holaspids) that tapers evenly to terminate at a bluntly rounded point.

Dokimocephalus lingula (Resser, 1942) (Figs 9A–F, 9G, H)

- 1942 Burnetia lingula Resser, 82, pl. 17, figs 32, 33.
- 1949 *Dokimocephalus intermedius* (Resser); Wilson: 37, pl. 9, fig. 1 only [figs 2, 4, 5 = D. sp. indet.].
- ?1951 Dokimocephalus intermedius (Resser); Wilson: 640, pl. 90, fig. 25.
- ?1971 Dokimocephalus intermedius (Resser); Stitt: 18, pl. 1, fig. 7.

Types. The holotype cranidium (USNM 108811; Fig. 9A–C) is from the Honey Creek Formation, Arbuckle Mountains, Oklahoma.

Diagnosis. Very long, gently tapered, tongue-shaped border that occupies 42% of cranidial length (41–43); border length is 68% (66–71) of maximum border width. Preglabellar field very short, equal to 9% (8–11) of preoccipital glabellar length. Occipital spine present.

Material. Available for study were Resser's type cranidium, one nearly complete figured cranidium (Fig. 9D–F), and two incomplete unfigured cranidia. A cranidium from Pennsylvania (Fig. 9G, H) assigned questionably to the species was also restudied.

Occurrence. New material collected during the course of this study is from the Honey Creek Formation on the Kimbell Ranch, Ring Top Mountain, northern Comanche County, collection KR1 12.7-14. A cranidium from the Morgan Creek Member of the Wilberns Formation (Wilson 1949, pl. 9, fig. 1; Wilson locality 42–8w.3, four miles north of Marble Falls, Burnet County, Texas) appears to represent to *D. lingula*, and a cranidium (Fig. 9G, H) from the Ore Hill Member, Gatesburg Formation, Pennsylvania (Wilson 1951 locality 47-5w.8a at Potter Creek) is assigned questionably to this species.

Figure 7. *Dokimocephalus intermedius* (Resser, 1942), Honey Creek Formation, Oklahoma. A–L, O, P, from Ring Top Mountain, Kimbell Ranch, northern Comanche County, Oklahoma; M, N, Q, R, from Frederickson (1948) locality 12, Arbuckle Mountains. A–C, exfoliated cranidium (OU 12254), collection KR2 49.2, \times 4: A, anterior view; B, lateral view; C, dorsal view. D–F, testate cranidium (OU 12253), collection KR2 49.2, \times 6: D, lateral view; E, dorsal view; F, anterior view. G, testate cranidium (OU 12415), collection KR2 49.4, \times 6, dorsal view; H–J, mostly exfoliated cranidium (OU 12416), collection KR2 48 (float), \times 7: H, lateral view; I, dorsal view; J, anterior view. K, L, mostly exfoliated cranidium (OU 12417), collection KR2 48 (float), \times 7: K, dorsal view; L, anterior view. M, N, exfoliated cranidium (OU 12418), collection KR2 49.4, \times 3.5: O, anterior-oblique view; P, dorsal view; Q, R, testate librigena (OU 4287); previously unfigured specimen on same rock samples as Fig. 7M, N), \times 4: Q, dorsal view; R, lateral view.



Figure 8. A–N, *Dokimocephalus extensus* (Resser, 1942), Honey Creek Formation Arbuckle Mountains, Oklahoma. A–C, holotype cranidium, partly exfoliated (USNM 108807a), \times 4 (arrows shows exoskeleton wrapping around beneath border): A, dorsal view; B, lateral view; C, anterior view. D–F, paratype cranidium, partly exfoliated (USNM 108807b), \times 4: D, lateral view; E, dorsal view; F, anterior view. G, paratype cranidium partly exfoliated (USNM 108807c), dorsal view, \times 6; H–J, paratype cranidium, mostly testate (USNM 108807d), \times 5: H, dorsal view; I, anterior view; J, lateral view. K, L, partly exfoliated cranidium (OU 4287), \times 4 (arrow shows exoskeleton wrapping around beneath border): K, lateral view; L, dorsal view. M–O, *Dokimocephalus* cf. *D. extensus* (Resser, 1942), Honey Creek Formation, Ring Top Mountain, Kimbell Ranch, northern Comanche County, collection KR3 25; testate cranidium (OU 12419), \times 6: M, dorsal view; N, lateral view; O, anterior view.



Figure 9. *Dokimocephalus lingula* (Resser, 1942). A–F, Honey Creek Formation, Oklahoma. A–C, holotype cranidium, exfoliated (USNM 108810), Arbuckle Mountains, \times 4: A, dorsal view; B, lateral view; C, anterior view. D–F, mostly exfoliated cranidium (OU 12252), Ring Top Mountain, Kimbell Ranch, northern Comanche County, collection KR1 12.7-14, \times 4: D, anterior view; E, dorsal view; F, lateral view. G, H, Ore Hill Member, Gatesburg Formation, Pennsylvania; mostly exfoliated cranidium (YPM 18489), \times 4 (arrow shows exoskeleton wrapping around beneath border): G, dorsal view; H, anterior-oblique view.

Description. Cranidium (excluding occipital spine) subrectangular in outline, width approximately 75% of length, well rounded anteriorly. Axial and preglabellar furrows are firmly impressed grooves on both external surfaces and internal moulds. Glabella convex, standing

well above adjacent fixigenae, gently tapered in front of S1 furrows and rounded anteriorly; width 75% (72–81) of length. Lateral profile of glabella flat between occipital spine and L2 lobe, curved downward beyond L2. SO transverse medially but curves forward near axial furrow and bifurcates, with very shallow furrow evident along posterior margin of lateral lobes on internal moulds. LO occupies 21% (18-25) of glabellar length and is weakly inflated near axial furrow to form lateral lobes; base of stout occipital spine preserved on some specimens. S1 furrow curves backward and inward, firmly impressed on external surface and internal mould; L1 slightly longer (exsag.) than LO. S2 furrow evident on external surface and internal mould, narrower (tr.) and shallower than S1; L2 subequal in length to L1. S3 expressed clearly only on internal mould as very shallow, nearly transverse furrow. Frontal area long, occupying 46% (45-48) of cranidial length. Anterior border furrow shallow but clearly defined; extends obliquely inward from cranidal margin but is bowed forward in front of glabella and parallels course of preglabellar furrow. Preglabellar field very short, equal to 9% (8-11) of preoccipital glabellar length; slopes forward from glabella. Anterior border very long, accounting for 42% (41–43) of cranidial length, and tongue-shaped, narrowing forward and well rounded anteriorly; border length is 68% (66-71) of maximum border width at border furrow. Lateral profile of border is initially downsloping, flattening anteriorly to become gently upsloping along anterior half of border. Anterior end of border curved under to form flattened 'pocket' floored by exoskeleton (e.g. Fig. 9G). Palpebral area of fixigena wide, equal to 33% of glabellar width at SO, and gently upsloping. Palpebral lobe is flat, arcuate band equal to 30% of glabellar length; centred opposite anterior end of L1. Palpebral furrow is well-incised groove on internal mould. Palpebral ridge well expressed on external surface and internal mould, extends obliquely forward across fixigena to reach axial furrow opposite S3. Anterior branches of facial sutures bowed gently outward between palpebral lobe and anterior border furrow, before converging inward along anterior border; distinct inflexion in lateral cranidial margin at about 25% of distance from border furrow to anterior tip of cranidium. Posterior branches of facial sutures not preserved on available specimens. Posterior border is short (exsag.), convex band; posterior border furrow is clearly defined groove, slightly shorter (exsag.) than border. External surface of glabellar lobes with sculpture of scattered coarse granules; fixigenae with finer, more closely packed granules that are arrayed along caecae on preglabellar field; anterior border finely granulose. Internal moulds smooth.

Remarks. Dokimocephalus lingula (Resser) is characterized by a relatively long, tongue-shaped anterior border, the length of which is about 68% (66–71) of maximum border width. To some degree this species is intermediate between *D. intermedius* (Resser), which has a relatively shorter and wider border, and *D. extensus* (Resser), which has a narrower border with a distinct, spatulate anterior projection (see discussions of these species above). Other species assigned to the genus (Figs 4, 10–12, 14) have substantially narrower, spatulate to spinose anterior projections of the anterior border.

Dokimocephalus lingula occurs in correlative strata of the Honey Creek Formation in central Texas (Wilson 1949, pl. 9, fig. 1). A single cranidium from Pennsylvania featuring proportions of the border in the range of values of cranidia from Oklahoma may also represent this species.

Dokimocephalus curtus (Resser, 1942) (Fig. 5F–H)

- 1942 Burnetia curta Resser: 83, pl. 17, figs 28, 29.
- non 1948 Dokimocephalus curta (Resser); Frederickson: 801, pl. 123, figs 4–8 [figs 4–6 = D. oliveri sp. nov.; figs 7–8 = D. sp. indet.].
- non 1971 Dokimocephalus curtus (Resser); Stitt: 19, pl. 1, fig. 8 [= D. sp. indet.].

Types. The holotype (USNM 108811; Fig. 5F–H) is from the Honey Creek Formation at Blue Creek Canyon, northern Comanche County, Oklahoma.

Remarks. Frederickson (1948) recognized that the anterior border of the holotype of *Dokimocephalus curtus* (Resser, 1942; Fig. 5F–H) from the Honey Creek Formation of Oklahoma was broken anteriorly, and argued that specimens with long, slender anterior projections (Fig. 14I–N) represented completely preserved cranidia of this species. This suggestion was followed by Stitt (1971), but the discovery in the Honey Creek Formation of at least two other species with narrow anterior projections of the border (Figs 10–12, 14) complicates interpretation of *D. curtus*. The species name is best restricted to the holotype because other specimens can no longer be assigned to *D. curtus* with any certainty. Incomplete cranidia figured by Frederickson (1948, pl. 123, figs 7–8) and Stitt (1971, pl. 1, fig. 8) cannot be identified to the species level. The two nearly complete

Figure 10. Dokimocephalus stewarti sp. nov., Honey Creek Formation, Ring Top Mountain, Kimbell Ranch, northern Comanche County, collection KR1 19.0. A–C, cranidium, exfoliated (OU 12420), \times 4: A, dorsal view; B, anterior view; C, anterior-oblique view. D–F, holotype cranidium, exfoliated (OU 12421), \times 4: D, anterior view; E, anterior-oblique; F, dorsal view, G, paratype cranidium, mostly exfoliated (OU 12422), dorsal view; \times 4; H, paratype cranidum, mostly testate (OU 12423), dorsal view, \times 4; I–K, paratype cranidium, testate (OU 12424), \times 8: I, dorsal view; J, lateral view; K, anterior view. L–N, paratype pygidium, partly exfoliated (OU 12425), \times 5: L, dorsal view; M, posterior view; N, lateral view. O, paratype pygidium, partly exfoliated (OU 12426), dorsal view, \times 8; P, Q, paratype pygidium, partly exfoliated (OU 12427), \times 5: P, posterior view; Q, dorsal view; R, paratype cranidium, partly exfoliated (OU 12428), dorsal view, \times 6.



cranidia illustrated by Frederickson (1948, pl. 123, figs 4–6; Fig. 14I–N) are assigned below to *D. oliveri* sp. nov.

Dokimocephalus stewarti sp. nov. (Fig. 10)

Types. The holotype (OU 12421) is a cranidium (Fig. 10D–F); paratypes include five cranidia (OU 12420, OU 12422, OU12423, OU12444, OU 12428) and three pygidia (OU 12425, OU 12426, OU 12427). All sclerites are from the Honey Creek Formation, Kimbell Ranch, Ring Top Mountain, northern Comanche County, collection KR1 19.

Diagnosis. Broad, parallel-sided, spatulate projection of anterior border, minimum width equal to 57% (51–62) of glabellar width at SO. Surface of projection is weakly concave. Preglabellar field short, equal to 9% (8–9) of preoccipital glabellar length. Occipital spine present.

Etymology. Named for Jon Stewart.

Material. Six cranidia and three pygidia.

Occurrence. Honey Creek Formation, Kimbell Ranch, Ring Top Mountain, northern Comanche County, collection KR1 19.1

Description. Excluding anterior projection of anterior border and occipital spine, cranidium is subhexagonal in outline. Glabella convex, standing well above level of fixigenae, tapers forward from S1 and well rounded anteriorly; length (excluding occipital spine) is 73% (70-77) of width at SO; occupies half of cranidial length (including anterior projection of anterior border) and accounts for half of cranidal width across palpebral lobes. SO shallow and transverse medially but curves forward and deepens near axial furrow. LO comprises 26% (23-29) of glabellar length and is weakly inflated near axial furrows to form lateral lobes; base of stout occipital spine preserved on some specimens. S1 oblique to gently curved inward; slit-like on external surface but is broader groove on internal mould. L1 subequal in length to LO. S2 expressed on external surface as oblique band that lacks sculpture but forms distinct groove on internal mould (compare Fig. 10G and 10H). L2 slightly shorter than L1. S3 also expressed on external surface as band without sculpture, but is faint, nearly transverse furrow on internal mould. Frontal area long, occupying half of cranidial length. Preglabellar field very short,

equal to 9% (8-9) of preoccipital glabellar length; slopes steeply forward from preglabellar field. Anterior border long, accounting for 93% of frontal area length, with broad, parallel-sided, spatulate projection, minimum width equal to 57% (51-62) of glabellar width at SO; surface of projection weakly concave. Slope of border initially follows slope of preglabellar field but flattens, becoming upturned at anterior projection. Palpebral area broad and nearly flat, width equal to 30% (27-33) of glabellar width at SO. Palpebral lobe long, flat, arcuate band, length equal to 40% (38–43) of glabellar length; centred opposite anterior third of L1. Palpebral furrow is finely etched groove on external surface but more deeply impressed on internal mould. Palpebral ridge weakly convex, oblique, and reaches axial furrow opposite anterior tip of L3. Anterior branches of facial sutures bowed gently outward between palpebral lobe and anterior border furrow, then converge forward along nearly straight path between border furrow and base of anterior projection. Anterior limit of dorsal sutures unknown and projection may be floored by exoskeleton; projection is parallel-sided. Posterior branches diverge sharply backward. Posterior border is short, convex band that curves gently backward; posterior border furrow is firmly impressed. External surface of glabellar lobes with coarsely granulose to finely tuberculate sculpture that is not present in, and adjacent to, glabellar furrows; fixigenae with coarse granules that become arrayed along caecal markings on preglabellar and preocular fields; anterior border with fine granules; posterior border and palpebral lobe are smooth. Internal moulds are smooth.

Pygidium sub-semielliptical in outline, length about 40% of width. Axis strongly convex, standing well above pleural field, and parallel-sided but rounded posteriorly; long, occupying more than 80% of pygidial length, and wide, accounting for about 30% of pygidial width. Axial furrows are gently impressed but clearly defined. Axis composed of four segments; three transverse axial rings at anterior are roughly equal in length, with terminal piece somewhat longer than others; articulating half-ring semielliptical in outline and short, length equal to about half of length of anteriormost axial ring. Axial ring furrows transverse and all but posteriormost reach axial furrows. Pleural field gently inflated and slopes down to narrow border defined largely by absence of pleural furrows. Anteriormost pair of pleural furrows firmly impressed, broad, and unequally divide pleura into short posterior bands and longer anterior bands; two additional pairs of shallower pleural furrows present. Interpleural furrow shallow but clearly defined on internal moulds. External surface of pygidium except

Figure 11. Dokimocephalus blacki sp. nov., Honey Creek Formation, Royer Ranch section (Stitt 1971), Murray County, Oklahoma, collection RR140 (float). A–C, paratype cranidium, exfoliated (OU 12265), \times 4: A, dorsal view; B, lateral view; C, anterior view. D, E, paratype cranidium, partly exfoliated (OU 12261), \times 4: D, dorsal view; E, lateral view. F–H, holotype cranidium, mostly exfoliated (OU 12263), \times 4: F, dorsal view; G, anterior view; H, lateral view. I, J, paratype librigena, exfoliated (OU 12268), \times 3: I, lateral view; J, dorsal view.



for furrows is finely granulose; internal mould is finely punctate.

Remarks. Among species with an anterior projection of the anterior border, Dokimocephalus stewarti sp. nov. is most similar to D. blacki sp. nov. The former species differs in having a much broader anterior projection whose minimum width is equal to 57% (51-62) of glabellar width at SO, rather than 37% (31-42) of glabellar width as in D. blacki. In addition, the upper surface of the anterior projection of D. stewarti is concave, whereas D. blacki has a flat upper surface. Dokimocephalus oliveri sp. nov. also has a concave upper surface to the anterior projection. However, this species shows a distinct anterior expansion of the projection, which gives it a spoon-shaped appearance (e.g. Fig. 14A–C, I–N). In contrast, the anterior projection of D. oliveri is parallel-sided (e.g. Fig. 10A-F). Dokimocephalus extensus (Resser; Fig. 8A-F, K, L) has a relatively wider anterior projection than D. stewarti, with width equal to 82% (74-88) of glabellar width, and has a flat upper surface. Both D. pernasutus (Walcott; Fig. 4D-N) and D. gregori (Walcott; Fig. 4A-C) are clearly differentiated from D. stewarti in possessing anteriorly tapered, spinose anterior projections whose distal tips curve downward, whereas projections are not developed in both D. intermedius (Resser; Figs 6, 7) and D. lingula (Resser; Fig. 9).

Dokimocephalus blacki sp. nov. (Figs 11, 12)

Types. The holotype (OU 12263) is an incomplete cranidium (Fig. 11F–H) from the Royer Ranch section (float collection at RR140), Arbuckle Mountains, Oklahoma. Paratypes include three cranidia (OU 12265, OU 12261, OU 12429) and one librigena (OU 12268) from collection RR 140; five cranidia (OU 12430, OU 12431, OU 12432, OU 12433, OU 12434) and one pygidium (OU 12435) from Ring Top Mountain, Kimbell Ranch, northern Comanche County, collection KR1 20.5. All sclerites are from the Honey Creek Formation.

Diagnosis. Anterior border extended into narrow, flat, spatulate projection, minimum width equal to 37% (31–42) of glabellar width at SO. Preglabellar field short, equal to 8% (6–10) of preoccipital glabellar length. Occipital spine present.

Etymology. Named for Lewis Black.

Material. Nine figured cranidia, one figured librigena and one figured pygidium; two incomplete, unfigured cranidia were also available for study.

Occurrence. Honey Creek Formation, Oklahoma; Royer Ranch section (Stitt 1971), Murray County, collection RR 140 (float) and Kimbell Ranch, Ring Top Mountain, northern Comanche County, collection KR1 20.5.

Description. Cranidium (excluding occipital spine and anterior projection) subpentagonal in outline, width across papebral lobes approximately 70% of length (including projection). Glabella convex, tapered forward beyond S1 and rounded anteriorly; occupies 50% (49-50) of cranidial length and 53% (52-54) of cranidial width at palpebral lobes. Axial and preglabellar furrows narrow and shallow, but well defined. SO shallow medially but deepens laterally and curves forward; bifurcates near axial furrow, with faint posterior branch, to outline weakly inflated lateral lobes on LO. LO accounts for 24% (22-26) of glabellar length and carries long, stout occipital spine. Oblique S1 lateral furrows are narrow, shallow grooves on external surface but are somewhat broader and deeper on internal mould. S2 furrows very shallow on external surface and marked largely by oblique bands that lacks sculpture; form shallow grooves on internal mould. S3 furrows nearly transverse and identifiable on external surface only as bands that lack sculpture; form very shallow to barely perceptible grooves on internal moulds. Frontal area very long and comprises 50% (50-51) of cranidial length. Preglabellar field short, length (sag.) equal to 8% (6-10) of preoccipital glabellar length, and slopes steeply down to anterior border furrow. Anterior border furrow is narrow, gently impressed and bowed forward. Anterior border is long, occupying 94% of frontal area length, and extended into a narrow, upsloping, flattened, spatulate projection; minimum width of projection is equal to 37% (31-42) of glabellar width at SO. Palpebral area of fixigena broad, width equal to 31% (29-34) of glabellar width, and slopes gently upward from axial furrow. Palpebral lobe long, flat, arcuate band, length equal to 35% (31-38) of glabellar length, and centred opposite anterior end of L1 glabellar lobe. Palpebral furrow shallow but well-defined groove; somewhat deeper on internal mould. Palpebral ridge is well

Figure 12. Dokimocephalus blacki sp. nov., Honey Creek Formation, Oklahoma. A–C, Royer Ranch section (Stitt 1971), Murray County, Oklahoma, collection RR140 (float); paratype cranidium, mostly exfoliated (OU 12429), \times 4: A, lateral view; B, anterior view; C, dorsal view. D–L, Ring Top Mountain, Kimbell Ranch, northern Comanche County, collection KR1 20.5: D, paratype cranidium, partly exfoliated (OU 12430), dorsal view, \times 4; E, paratype cranidium, partly exfoliated (OU 12431), dorsal view, \times 5; F–H, paratype cranidium, mostly testate (OU 12432), \times 4: F, anterior view; G, dorsal view; H, lateral view; I, paratype cranidium, testate (OU 12433), dorsal view, \times 6; J, paratype cranidium, partly exfoliated (OU 12434), dorsal view; \times 4; K, L, paratype pygidium, testate (OU 12435), \times 5; K, dorsal view; L, posterior view.





Figure 13. External surface of left preocular field of *Dokimocephalus blacki* sp. nov. (OU 12430; Fig. 12D), showing sculpture of coarse granules arrayed along caecal markings, \times 13.

expressed on external surface and internal mould; extends obliquely forward from palpebral lobe to reach axial furrow opposite S3 furrow. Anterior branches of facial suture bow gently outward from between the palpebral lobe and anterior border furrow, then converge forward; anterior limit of dorsal sutures unknown and projection may be at least partly floored by exoskeleton; projection is parallel-sided to very slightly expanded anteriorly. External surface of glabellar lobes with coarsely granulose to finely tuberculate sculpture that is not present in, and adjacent to, glabellar furrows; fixigenae with coarse granules that become arrayed along caecal markings on preglabellar and preocular fields (Fig. 13); anterior border with fine granules, posterior border and palpebral lobe are smooth. Internal moulds are smooth.

Librigena incomplete and preserves only base of genal spine. Librigenal field broad, accounting for more than half of librigenal width; inflated with convex lateral profile. Lateral and posterior border furrows are shallow grooves on internal mould and join near base of genal spine. Lateral border is wide, expanding slightly posteriorly, and downsloping; inflated at base of genal spine, which is bounded adaxially by very shallow furrow. Posterior border gently convex and narrow, equal to less than half of width of lateral border. Internal mould of librigenal field carries caecal markings; remainder of librigena is smooth. Pygidium (Fig. 12K, L) is virtually identical to the pygidium of *D. stewarti* (Fig. 10I, M–Q) so that description is unnecessary. It differs only in having shallower pleural furrows and a slightly shorter axis.

Remarks. *Dokimocephalus blacki* sp. nov. and *D. oliveri* sp. nov. are closely similar species that differ in the morphology of the anterior projection of the anterior border. In *D. oliveri*, the projection is relatively longer with a concave dorsal surface, and expands conspicuously to produce a spoon-shaped termination. The anterior projection of *D. blacki* is relatively shorter with a flat dorsal surface, and is only slightly expanded distally to produce a spatulate termination. The librigena of *D. oliveri* possesses a narrow rim on the lateral border (Fig. 14D–F) that is not present in *D. blacki* (Fig. 11I, J).

Dokimocephalus oliveri sp. nov. (Figs 5I–K, 14)

1948 *Dokimocephalus curta* Resser; Frederickson: 801, pl. 123, figs 4–6 only [figs 7, 8 = *Dokimocephalus* sp. indet.].

Types. The holotype is a cranidium (OU 12255; Fig. 14A–C) from the Dotson Ranch section, Murray County, Oklahoma, collection DR 11.77-12. Paratypes include one cranidium (OU 12437), one librigena (OU 12257) and one pygidium (OU 12256) from collection DR11.77–12; one cranidium (OU 4284) from Frederickson's (1948) locality 11; one cranidium (OU 4283) from Frederickson's (1948) locality 12; one librigena (OU 12257) from Ring Top Mountain, Kimbell Ranch, northern Comanche County, collection KR1 21.9. All sclerites are from the Honey Creek Formation.

Diagnosis. Anterior border extended into narrow, spoonshaped projection with concave dorsal surface. Preglabella field very short, length equal to 8% (6–9) of preoccipital glabellar length. Occipital spine present. Lateral border of librigena with narrow (tr.) rim.

Etymology. Named for John Oliver.

Material. Four figured cranidia, two figured librigenae and one figured pygidium; three additional unfigured cranidia.

Figure 14. *Dokimocephalus oliveri* sp. nov., Honey Creek Formation, all Murray County Oklahoma, except **D** (northern Comanche County). **A–C**, holotype cranidium, partly exfoliated (OU 12255), Dotson Ranch, collection DR 11.77-12, \times 4: **A**, dorsal view; **B**, anterior view; **C**, lateral view. **D**, paratype librigena, partly exfoliated (OU 12436), Ring Top Mountain, Kimbell Ranch, collection KR1 21.9, dorsal view, \times 3; **E**, **F**, paratype librigena, testate (OU 12257), Dotson Ranch, collection DR 11.77-12, \times 3: **E**, dorsal view; **F**, lateral view. **G**, paratype cranidium, partly exfoliated (OU 12437), Dotson Ranch, collection DR 11.77-12, \times 3: **E**, dorsal view; **F**, lateral view. **G**, paratype cranidium, partly exfoliated (OU 12437), Dotson Ranch, collection DR 11.77-12, dorsal view, \times 3; **H**, pygidium, testate (OU 12256), Dotson Ranch, collection DR 11.77-12, dorsal view, \times 5; **I–K**, cranidium, partly exfoliated (OU 4283), Frederickson (1948) locality 12, \times 4: **I**, anterior view; **J**, lateral view; **K**, dorsal view. **L–N**, cranidium, testate (OU 4284), Frederickson (1948) locality 11, \times 4: **L**, dorsal view; **N**, anterior view.



Occurrence. Honey Creek Formation, Ring Top Mountain, Kimbell Ranch, collection KR1 21.9; Dotson Ranch, Murray County, Oklahoma, collection DR 11.77-12. Specimens (Fig. 14I–N) illustrated previously by Frederickson (1948) under the name *D. curta* (sic) are also from his localities 11 and 12.

Description. Cranidium (excluding occipital spine and anterior projection of anterior border) is subpentagonal in outline. Convex glabella is raised well above fixigena and occupies 47% (46-47) of cranidial length (including anterior projection) and 55% (55-56) of cranidial width at palpebral lobes; tapers forward, particularly beyond S1 and well rounded anteriorly; glabellar width at SO equal to 77% (75-80) of length. Axial and preglabellar furrows are shallow grooves on both external surface and internal mould. SO transverse medially and finely etched on external surface (deeper on internal mould) but deepens abaxially and bifurcates, with short posterior branch on inner edge of lateral occipital lobe and anterior branch that curves forward. LO accounts for 24% (23-25) of glabellar length; weakly inflated near axial furrows to form lateral lobes; some specimens preserve base of stout occipital spine. S1 lateral furrows oriented obliquely backward, firmly impressed on external surface and internal mould. S2 lateral furrows oblique and subparallel to S1; very shallow on external surface and expressed largely as smooth bands that interrupt sculpture, but form deep groove on internal mould. S3 furrows nearly transverse, expressed only as smooth areas on external surface and as barely perceptible grooves on internal moulds. Frontal area long and accounts for 53% (53-54) of cranidial length. Preglabellar field very short, equal to 8% (6-9) of preoccipital glabellar length and slopes steeply downward to anterior border furrow. Anterior border furrow shallow but well defined on both external surface and internal mould; bowed forward with slight increase in curvature in front of glabella. Anterior border very long and comprises 95% (94-95) of frontal area length; extended into a narrow, concave, spoon-shaped projection whose maximum width is 143% (142–144) of minimum width; sloping near border furrow but becomes upturned along most of length, eventually decreasing slope near anterior margin; anterior margin curved under to form flap-like 'pocket' of uncertain length. Palpebral area of fixigena wide, equal to 30% (29-31) of glabellar width at SO, and slopes gently upward. Palpebral lobe long, flat, arcuate band, length equal to 40% (33-46) of glabellar length; centred opposite anterior end of L1. Palpebral furrow well defined groove on both external surface and internal mould. Convex, oblique palpebral ridge extends forward from palpebral lobe, reaching axial furrow opposite S3 furrow. Anterior branches of facial suture bow gently outward between palpebral lobe and anterior border furrow, then converge forward; anterior limit of dorsal sutures unknown but, judging from width of doublure at the anterior end of the librigena (Fig. 14E) projection is at least partly floored by exoskeleton. Posterior branches of the facial suture diverge sharply backward. Posterior border is short, strongly convex and curved slightly backward. Posterior border furrow firmly impressed groove on external surface and internal mould. External surface of glabellar lobes with coarsely granulose to finely tuberculate sculpture that is not present in, and adjacent to, glabellar furrows; fixigenae with coarse granules that become arrayed along caecal markings on preglabellar and preocular fields; anterior border with fine granules, posterior border with very fine granules and palpebral lobe smooth. Internal moulds are smooth.

Librigena with long, stout genal spine directed outward and backward. Librigenal field broad, accounting for more than half of librigenal width; inflated with convex lateral profile. Lateral and posterior border furrows are shallow grooves on internal mould and join near base of genal spine; posterior border furrow extends along inner edge of base of genal spine. Lateral border is wide, expanding slightly posteriorly and downsloping; inflated at base of genal spine; narrow rim runs along outer edge of border and is bounded by a shallow furrow. Doublure beneath lateral border is broad (tr.) and extends inward as far as border furrow. Posterior border gently convex and narrow, equal to less than half of width of lateral border. External surfaces of borders and base of spine with sculpture of fine granules; librigenal field with coarser granules arrayed along caecal markings. Internal mould of librigenal field carries caecal markings; remainder of mould is smooth.

Strongly convex hypostome subrectangular in outline, width equal to about 75% of length, with conspicuous triangular anterior wings; wing with low, ventrally directed rim extending along anterior margin. Median body subelliptical in outline and occupies about 96% of hypostome length; divided into long anterior lobe and shorter posterior lobe by u-shaped middle furrow that is shallow medially but deepens abaxially into large macculae; anterior lobe accounts for about 85% of median body length. Borders incompletely preserved but form narrow rims; posterior border slightly shorter than lateral border; border furrows gently impressed. Anterior wings and flanks of median body with granulose sculpture; crest of median body is smooth.

Pygidium semielliptical in outline, length equal to about 45% of width. Axial furrows are very shallow grooves. Dorsal surface of axis incompletely preserved on available material; long, occupying about 90% of pygidial length, and width at anteriormost ring equal to about 33% of pygidial width; tapers backward and is well rounded posteriorly. Pleural field gently inflated and crossed by broad (exsag.), firmly impressed pleural furrows that divide pleurae into short, ridge-like posterior pleural band and somewhat longer anterior band. Pleural field slopes down to nearly flat border; border widest anteriorly, width normal to border furrow equal to about 20% of maximum width of axis, but is reduced in width by more than 50% posteriorly.

pleural field and border. External surface of pleural bands and border with finely granulose sculpture.

Remarks. Some of sclerites of *Dokimocephalus oliveri* sp. nov. were assigned previously to *Dikelocephalus curtus* by Frederickson (1948) but, as noted above, the latter name is best restricted to the incompletely preserved holotype. *Dokimocephalus oliveri* is differentiated from all other members of the genus by the distinctly spoon-like shape of the concave anterior projection. It is the youngest species of *Dokimocephalus* in Honey Creek Formation, and occurs immediately below the base of the Sunwaptan Stage at both the Dotson Ranch and Kimbell Ranch sections.

Dokimocephalus cf. D. extensus (Resser, 1942) (Fig. 8M–O)

cf. 1942 Burnetia extensa (Resser); Resser: 81, pl. 17, figs 15–22.

Occurrence. Honey Creek Formation at Ring Top Mountain, Kimbell Ranch, northern Comanche County, Oklahoma (collection KR3 25).

Remarks. A single cranidium from the Honey Creek Formation resembles *Dokimocephalus extensus* (Resser; Fig. 8A–L), differing only in the outline of the anterior border. The latter has a relatively shorter and wider border, whose margins become subparallel along the anterior projection. The border tapers more evenly in the former, and the anterior termination is relatively narrow and less rounded. Although it may well represent a new species, the Honey Creek cranidium is best placed in open nomenclature until more material becomes available.

> Dokimocephalus sp. indet. 1 (Fig. 5B–D)

Occurrence. Sneakover Member of the Orr Formation, Orr Ridge, northern House Range, Millard County, Utah, collection ORR 59.4.

Remarks. An incomplete cranidium and associated librigena demonstrate the presence of *Dokimocephalus* in latest Steptoean strata in Utah, above the range of *D. pernasutus* (Walcott) and immediately below the first occurrences of *Comanchia* Frederickson, in Wilson & Frederickson, 1950, and *Bartonaspis* Westrop & Adrain, 2007. Although it cannot be identified to the species level, both the very short preglabellar field and anterior branches of the facial sutures that converge rapidly forward beyond the border furrow ally the cranidium with species from Oklahoma that possess a narrow spatulate to spoon-shaped anterior projection of the border (e.g. Figs 10–12, 14). The preglabellar field is noticeably shorter than in all previously described species, so that the preglabellar furrow is barely separated from the anterior border furrow.

Dokimocephalus sp. indet. 2 (Fig. 5E)

Occurrence. Open Door Limestone, Warm Springs Creek, Wind River Range, Fremont County, Wyoming.

Remarks. An incomplete cranidium from Wyoming appears to record the presence of *Dokimocephalus* in the upper *Elvinia* Zone of the Open Door Limestone. The occipital ring is incomplete medially but shows a roughly circular break suggestive of the presence of an occipital spine. The preglabellar field is relatively short (equal to 11% of preoccipital glabellar length) and falls within the range of variability of such species as *D. lingula* (Resser; Fig. 9).

The cranidium was recovered from the base of a bioclastic pack to rudstone at Warm Springs Creek that includes orthid brachiopods. Saltzmann (1999, fig. 3) assigned the brachiopod-bearing interval to the Sunwaptan *Taenicephalus* Zone, but the occurrence of *Dokimocephalus*, along with such genera as *Camaraspis* Ulrich & Resser, in Ulrich, 1924 and *Elvinia* Walcott, 1924 (Westrop & Adrain unpublished), demonstrates that much of this interval is latest Steptoean in age.

Genus Iddingsia Walcott, 1924

Type species. *Ptychoparia similis* Walcott, 1884, from the Dunderberg Formation, Eureka District, Nevada, by original designation.

Diagnosis. Steeply upsloping palpebral area of fixigena in larger holaspids so that palpebral lobe is elevated well above axial furrow.

Remarks. *Iddingsia* emerged from the phylogenetic analysis as a grouping of species that share a single apomorphy, a steeply upsloping palpebral area of the fixigena which results in the palpebral lobe being elevated well above the axial furrow (e.g. Figs 15B, N; 16B, F, J). Other genera of the Dokimocephalidae *s.s.* are characterized by gently sloping palpebral areas (e.g. Figs 6C, 7A, 8C, 4B, 12F–H, 19E, L, 23B, I, 29A, F).

Iddingsia similis (Walcott, 1884) (Figs 15, 16G–L)

1884 Ptychoparia similis Walcott: 52, pl. 10, fig. 10.
1965 Iddingsia similis (Walcott); Palmer: 36, figs 1–4 (synonymy to date).

Types. The lectotype (USNM 24641a; Fig. 150–Q), and paralectotype (USNM 24641b; Fig. 15L–N) are



incomplete cranidia and from the Dunderberg Formation, Eureka Mining District, Eureka County, Nevada.

Diagnosis. Sculpture of coarse granules on glabella (exclusive of furrows and narrow bands surrounding furrows) and very fine granules on crests of palpebral and posterior areas of fixigena; remainder of cranidium smooth. Granulose sculpture of glabella barely perceptible on internal mould.

Material. In addition to Walcott's (1884) types, figured material includes five cranidia, one hypostome, one librigena, one thoracic segment and one pygidium. Several additional cranidia were available for study.

Occurrence. Dunderberg Formation, Eureka Mining District, Nevada (Walcott 1884; Palmer 1960). Corset Spring Shale, Patterson Pass, Lincoln County, Nevada, collections PP 310, PP310.5, 310.55.

Description. Cranidium, subrectangular in outline, width across palpebral lobes approximately equal to 90% of length, and well rounded anteriorly. Convex glabellar suboval in outline, width equal to 75% (67-80) of length, with rounded anterior and posterior margins; occupies 70% (69–71) of cranidial length and 54% of cranidial width at palpebral lobes. SO firmly impressed on external surface and internal mould; transverse medially but curves forward near axial furrow and becomes deeper. LO accounts for 20% (19-23) of glabellar length and is inflated near axial furrows to form lateral lobes. S1 is oblique and nearly straight, well incised on external surface and internal mould. S2 also oblique, but shallower, and directed inward at a lower angle, than S1. S3 nearly transverse, expressed only as a smooth band on external surface but may form finely-etched groove on internal mould (e.g. Fig. 16H). Frontal area occupies 30% (29-31) of cranidial length. Preglabellar field relatively long, equal to 21% (19-23) of preoccipital glabellar length, gently inflated and slopes steeply forward. Anterior border furrow curved forward, shallow on both external surface and internal mould. Anterior border longer than preglabellar field, comprising 61% (56-63) of frontal area length and slopes gently forward. Palpebral area of fixigena broad, width equal to 24% (23-26) of glabellar width at SO, and slopes strongly upward. Palpebral lobe is long curved band, equal to about one-third of glabellar length,

centred opposite anterior end of L1; palpebral furrow is well defined on external surface and internal mould. Anterior branches of facial sutures diverge forward between palpebral lobe and anterior border furrow, so that cranidial width increases by 10%, before curving inward along anterior cranidial margin. Posterior branches of sutures diverge abruptly backward along weakly sigmoidally curved paths. Posterior border furrow well incised on external surface and internal mould; posterior border convex, curves gently backward. Sculpture of coarse granules on glabella (exclusive of furrows and narrow bands surrounding furrows) and very fine granules on crests of palpebral and posterior areas of fixigena; remainder of cranidium smooth. Granulose sculpture of glabella barely perceptible on internal mould.

Incomplete librigena preserves base of stout genal spine; librigena illustrated by Palmer (1965, pl. 2, fig. 1) has long, outwardly curved spine. Convex librigenal field occupies about 60% of maximum width of librigena. Lateral and posterior border furrows well defined, confluent; single furrow extends from junction onto adaxial side of base of genal spine. Lateral border downsloping but inflated at base of genal spine; posterior border weakly convex, width equal to about half of lateral border. Librigenal field with granules arrayed on caecal markings; base of genal spine with granules that extend onto lateral border, becoming finer anteriorly.

Hypostome suboval in outline with width at anterior end of anterior furrow equal to slightly more than threequarters of length; short (tr., exsag.) anterior wing present. Median body strongly convex and stands well above borders. Median furrow expressed only abaxially as shallow, oblique groves at maculae. Anterior lobe long, occupying about 80% of hypostomal length, and elliptical in outline. Posterior lobe is crescentic in outline; in lateral view, continues slope of posterior end of anterior lobe without break. Anterior border short and flat to gently concave. Lateral border convex and narrow (tr.) decreasing in width towards rear; posterior border very short. Lateral border furrows firmly impressed; posterior border is finely etched groove.

Associated, incomplete thoracic segment is macropleural with long spine that is directed outward and gently downward. Axis convex and narrow (tr.), accounting for slightly more than 25% of segment width (excluding spine); articulating half-ring comprises a little more than one-third of ring length; articulating furrow nearly transverse medially

Figure 15. *Iddingsia similis* (Walcott, 1884). A–K, Corset Spring Shale, Patterson Pass, Schell Creek Range, Lincoln County, collection PP 310.55 except A–D (PP 310.50). A–C, mostly exfoliated cranidium (OU 12438), \times 5: A, dorsal view; B, anterior view; C, lateral view. D, partly exfoliated cranidium (OU 12439), dorsal view, \times 5; E, F, partly exfoliated pygidium (OU 12440), \times 8: E, dorsal view; F, posterior view. G–I, testate hypostome (OU 12441), \times 8: G, posterior view; H, lateral view; I, dorsal view. J, K, testate thoracic segment (OU 12442), \times ??: J, dorsal view; K, lateral view. L–Q, Dunderberg Formation, Eureka Mining District, Eureka County, Nevada. L–N, paralectotype cranidium, testate (USNM 24641b), \times 3.5: L, dorsal view; M, lateral view; N, anterior view. O–Q, lectotype cranidium, partly exfoliated (USNM 24641a), \times 3.5; O, lateral view; P, dorsal view; Q, anterior view.

but curved forward near axial furrow. Axial furrow shallow, defined largely by change in slope between axis and pleura. Pleura crossed by pleural furrow that is nearly transverse and deep between axial furrow and fulcrum but narrows and curves distally, extends onto base of pleural spine; furrow equally divides pleura into convex anterior and posterior pleural bands that curve backward distally. Anterior margin of pleura transverse between axial furrow and fulcrum; narrow articulating flange runs along margin, becoming longer near fulcrum and extends along lateral margin as far back as point opposite distal tip of pleural furrow.

Pygidium strongly arched in posterior view, and semielliptical in outline, length equal to about 45% of maximum width. Axial furrows very shallow and expressed posteriorly only by change in slope between terminal piece and pleural field. Axis convex, raised well above pleural field and relatively wide, with width equal to slightly more than 80% of length; occupies about 85% of pygidial length and one-third of pygidial width; initially parallel-sided but tapers beyond second axial ring furrow and is well rounded posteriorly. Axis divided into four segments, with two posteriormost forming terminal piece and clearly differentiated from eachother only on internal mould. Articulating furrow and two pairs of transverse axial ring furrows expressed on external surface. Articulating half-ring is semielliptical in outline and accounts for slightly less than 20% of axis length. First and second axial rings roughly equal in length and each are about 30% longer than articulating half-ring. Terminal piece long, equal to nearly half of axis length. Pleural field near flat at axis but flexed downward distally; crossed by three pairs of pleural furrows that become progressively shallower towards the rear and extend onto lateral border. Anterior and posterior pleural bands convex, although convexity is reduced in successive pairs; extend onto border. Interpleural furrows not expressed on external surface. Lateral border furrow very shallow and expressed largely as change in slope between pleural field and border. Border slopes gently down to pygidial margin; widest at anterior, with width normal to border equal to about 8% of maximum pygidial width, but narrows posteriorly, particularly behind axis. External surface of axis except for furrows is covered with closely spaced granules; pleural field and border also granulose; internal mould of pleural field is very finely punctate.

Remarks. Palmer (1965, p. 36) diagnosed *Iddingsia similis* (Walcott) largely on the basis of cranidial sculpture.

The larger sample available here, including the lectotype and paralectotype (Fig. 15L-Q), confirms that this species is characterized by granulose sculpture on the glabella and, to a lesser extent, fixigena, whereas frontal area is smooth. In terms of cranidial proportions, including the relative lengths of the preglabellar field and anterior border, I. similis is most similar to I. utahensis Resser (Fig. 5L-O). Although Resser (1942 p. 86) described the external surface of the latter as "granulose, as usual", there is no trace of sculpture on testate surfaces of the holotype (Fig. 2L–O) and none is evident on the paratype (Resser, 1942. pl. 16, fig. 20). We concur with Palmer (1965, p. 37) that I. utahensis is characterized by smooth cranidial surfaces. The poorly known I. robusta (Walcott, 1884), also from the Great Basin, apparently possesses a cranidium that is entirely granulose (Palmer 1965, p. 36). As noted above, both the librigena and pygidia attributed to I. intermedia Palmer (1965, pl. 2, figs 6, 8) are probably misidentified. The cranidia (Palmer 1965, pl. 2, figs 5, 7) have a relatively short border that occupy about one third of frontal area length, whereas the border of I. similis accounts for about 60% of the frontal area.

Iddingsia missouriensis Resser, 1942 (Fig. 16A-F)

1942 *Iddingsia missouriensis* Resser: 6, pl. 16, figs 21–26. 1975 *Iddingsia missouriensis* Resser; Kurtz: 1026, pl. 1, figs 13–14 (synonymy to date).

Types. The holotype and paratypes (USNM 108798a-d; Resser 1942, pl. 16, figs 21–26) are from the Davis Formation at Flat River, Missouri. According Kurtz (1975, p. 1022, plate caption), the specimens illustrated herein (Fig. 16A–F) may be topotypes.

Diagnosis. Broad, strongly upsloping palpebral area of fixigena, width equal to 42% (42–43) of glabellar width at LO; consequently, cranidium relatively wide, so that glabella accounts for less than half (45%; 42–47) of cranidial width across palpebral lobe. Frontal area long, occupying 33% (32–35) of cranidial length. Internal mould of cranidium with granular sculpture on glabella and palpebral and postocular fixigena; frontal area with well developed caecal markings.

Occurrence. Unit C, Davis Formation, Missouri (Kurtz 1975).

Figure 16. A–F, *Iddingsia missouriensis* Resser, 1942, Member B, Davis Formation section 9 of Kurtz (1975), St Francois County, Missouri. A–C, exfoliated cranidium (OU 3529b), \times 3: A, dorsal view; B, anterior view; C, lateral view; note that the left palpebral lobe was restored by Kurtz (although not acknowledged in his 1975 paper) using a plaster cast from the counterpart mould. D–F, exfoliated cranidium (OU 3529a), \times 4: D, dorsal view; E, lateral view; F, anterior view; note that the right palpebral lobe was restored by Kurtz using a plaster cast from the counterpart mould. G–L, *Iddingsia similis* (Walcott, 1884), Corset Spring Shale, Patterson Pass, Schell Creek Range, Lincoln County, collection PP 310.55. G, partly exfoliated cranidium (OU 12443), dorsal view, \times 5; H, exfoliated cranidium (OU 12444), dorsal view, \times 3.5; I–K, mostly exfoliated cranidium (OU 12445), \times 3.5; I, dorsal view; K, lateral view; L, testate librigena (OU 12446), dorsal view, \times 4.



Description. Description based on internal mould only; external surface unknown. Cranidium strongly arched in lateral and anterior views, subquadrate in outline and well rounded anteriorly, length equal to 97% (92-104) of width across palpebral lobes. Axial and preglabellar furrows shallow but clearly defined grooves. Glabella subtrapezoidal in outline with conspicuous anterior taper beyond S1, with width at SO equal to 73% (71–74) of length; occupies 67% (65-68) of cranidial length and 47% of cranidial width across palpebral lobes. SO deep, nearly transverse medially but curved forward near axial furrow. LO accounts for 17% (16–19) of glabellar length and inflated near axial furrows to form small lateral lobes; median node present near anterior margin. S1 firmly impressed, oblique and gently curved to geniculate; L1 slighly longer than LO. S2 shorter (tr.) and shallower than S1, and curved gently backwards; L2 equal in length to L1. S3 very faint and nearly transverse. Frontal area long, comprising 33% (32-35) of cranidial length. Anterior border furrow shallow and defined in part by change in slope between preglabellar field and anterior border; proceeds obliquely inward from cranidial margin but becomes bowed forward in front of glabella, particularly in larger specimen (Fig. 16A-C). Steeply sloping preglabellar field comprises 41% (41-42) of frontal area length; anterior border gently sloping, with weakly depressed area along posterior edge, in front of glabella. Palpebral area of fixigena wide, width equal to 42% (42-43) of glabellar width at LO, and steeply upsloping. Palpebral lobe is long, gently upsloping, arcuate band, length equal to 34% (31-36) of glabellar length, and centred opposite anterior end of L1. Palpebral furrow is firmly impressed groove. Palpebral ridge convex, strongly oblique and extends forward and inward from palpebral lobe to intersect axial furrow in front of S3. Anterior branches of facial sutures diverge forward, so that cranidial width at anterior tip of palpebral lobe is 81% (80-82) width at anterior border furrow; in front of border furrow, sutures swing inward along anterior cranidial margin. Posterior branches diverge in a faintly sigmoid curve. Posterior border furrow is well incised and becomes somewhat longer (tr.) abaxially. Posterior border convex, nearly transverse along postocular field, but curves backward along posterolateral projection. Internal mould with granular sculpture on glabella and palpebral and postocular fixigena; frontal area with well developed caecal markings.

Remarks. The broad palpebral area and, consequently, relatively wide cranidium, together with the sculpture of conspicuous caecal markings on the frontal area, differentiates *Iddingsia missouriensis* from all other members of the genus. Compared to the type species, *I. similis* (Walcott), *I. missouriensis* posseses more divergent anterior branches of the facial sutures, so that the cranidium is relatively wider at the anterior border furrow.

Cranidia from the Wonowoc Formation of Minnesota that were attributed to *I. missouriensis* by Bell *et al.* (1952, pl. 31, figs 4a–b) have relatively longer papebral lobes that extend farther forward than those illustrated herein, so that the palpebral ridges are more transverse. In addition, cranidia from Minnesota appear to have a somewhat shorter preglabellar field. The significance of these differences is impossible to evaluate with the available material. Bell *et al.* (1952, pl. 31, fig. 4c) assigned a pygidium to *I. missouriensis*, and this was used as a coding source in the phylogenetic analysis. It differs from the pygidium of *I. similis* (Fig. 15E, F) in having a relatively longer axis that appears to be composed of five, rather than four segments.

Iddingsia utahensis Resser, 1942 (Fig. 5L–O)

1942 *Iddingsia utahensis* Resser: 85, figs 18–20. 1965 *Iddingsia utahensis* Resser; Palmer: 37, pl. 2, fig. 9

Types. The holotype of *I. utahensis* (Fig. 5L–O) is from the Orr Formation, Fandango Canyon, Dugway Range, Tooele County, Utah.

Diagnosis. Smooth external surface and external mould.

Occurrence. Orr Formation, Utah. The cranidium assigned to this species by Palmer (1965, pl. 2, fig. 9) is from the uppermost Dunderberg Formation at McGill, White Pine County, Nevada.

Remarks. As noted above, cranidial proportions of *Iddingsia utahensis* and *I. similis* are closely comparable and discrimination of these species hinges upon persistent differences in sculpture of the external surface (see also Palmer 1965).

Genus Plataspella Wilson, 1949

Type species. *Plataspella anatina* (Resser, 1942), from the Honey Creek Formation, Blue Creek Canyon, Wichita Mountains, Oklahoma (by original designation).

Diagnosis. Gently inflated bacculae on fixigenae. Lateral glabellar furrows barely perceptible to absent on both external surface and internal mould.

Remarks. Wilson (1949) named *Plataspella* for species from the Honey Creek Formation that Resser (1942) assigned to *Iddingsia*. Wilson separated this genus from *Iddingsia* Walcott on the basis of a less convex and broader frontal area, wider anterior border furrow, very faint lateral glabellar furrows and the presence of an occipital spine. Over the ensuing 40 years, various authors have either

accepted Wilson's conclusions (e.g. Stitt 1971), or have considered *Plataspella* to be a junior subjective synonym of *Iddingsia* (e.g. Bell *et al.* 1952; Lochman 1953; Westrop 1986). Study of Resser's type material and new specimens from the Honey Creek Formation (Figs 17–20) revealed the presence of a previously overlooked synapomorphic character state, the presence of bacculae on the fixige-nae, which supports monophyly of *Plataspella*. Efface-ment of lateral glabellar furrows occurs in all species of *Plataspella*, but is also shared with *Edithiella*. Most species of *Plataspella* possess occipital spines but *P*. sp. nov. from the Honey Creek Formation of Oklahoma is characterized by an aspinose occipital ring.

Plataspella is most similar to *Iddingsia*, but the latter possesses strongly upsloping palpebral areas of the fixigenae (e.g. Figs 15B, N, 16B), whereas *Plataspella* retains the plesiomorphic state of gently sloping palpebral areas (e.g. Fig. 19E, L).

Plataspella was reduced to a monotypic genus by Palmer (1960). However, restudy of Resser's (1942) type material reveals two distinct species in the Honey Creek Formation, and new sclerites collected during this study indicate that an additional species with an aspinose occipital ring is also present. As discussed below, specimens from the Bison Creek Formation of Alberta that were identified by Westrop (1986, pl. 29, figs 2–6) as *Iddingsia anatina* Resser may represent a fourth species.

Plataspella simplicitas (Resser, 1942) (Figs 17A–I, ?17M–O, 18A–I, ?18J–L, 19A–E, I–N, 20A–J)

1942 *Iddingsia alpersensis* Resser: 88, pl. 16, figs 33–38. 1942 *Iddingsia simplicitas* Resser; Resser: 89, pl. 17, figs 3–9.

1949 *Plataspella anatina* (Resser); Frederickson: 355, pl. 68, figs 10–13.

1951 *Plataspella anatina* (Resser); Wilson: 647, pl. 92, fig.6.

1971 Plataspella anatina (Resser); Stitt: 20, pl. 1, fig. 10.

Types. The holotype cranidium (USNM 108804a, Fig. 18A–C), two paratype cranidia (USNM 108804b, c; Fig. 18F–I), and a librigena (USNM 108804d; Fig. 18D, E) are from the Honey Creek Formation at Resser's (1942) locality 89y, West Timbered Hills, Arbuckle Mountains, Oklahoma.

Diagnosis. Preglabellar field is slightly shorter (87% of length; 72–104) than anterior border. Long occipital spine present.

Material. In addition to the types, figured material includes 12 cranidia, one librigena, an incomplete thoracic

segment and two pygidia. Several additional, mostly incomplete cranidia were available for study.

Occurrence. Honey Creek Formation, Oklahoma: four miles east of Alpers, Murray County; Dotson Ranch, Murray County, collections DR 5.75, 8.55; Kimbell Ranch, Ring Top Mountain, northern Comanche County, collections KR1 9.25; KR2 48.2–48.5; KR3 20.5. ?Ore Hill Member, Gatesburgh Formation, Pennsylvania (Wilson 1951).

Description. Cranidium subquadrate in outline, width across palpebral lobes equal to 96% (95-97) of length (excluding occipital spine) and well rounded anteriorly; strongly arched in anterior and lateral views. Glabella strongly convex, raised well above fixigena; occupies 64% (60-68) of cranidial length and 44% (42-46) of cranidial width across palpebral lobes. Axial and preglabellar furrows are shallow but clearly defined grooves. Glabella subrectangular in outline, width at SO equal to 67% (62–73) of length (excluding occipital spine); tapers forward in front of mid-length and rounded anteriorly; in front of LO, glabella is roughly barrel-shaped in outline. SO shallow on external surface, but deeper and longer (sag., exsag.) on internal mould; transverse to bowed gently backward medially; curves forward near axial furrow and deepens. LO accounts for 21% (17–24) of glabellar length (excluding spine) and has long, occipital spine that curves steeply upward and backward (Fig. 19J-L); inflated abaxially to form gently convex lateral lobes; lateral lobes bounded anteriorly by SO but defined posteriorly largely by change in slope. S1 and S2 furrows largely effaced; barely perceptible on external surface (Fig. 19I-L) but slightly deeper on internal mould (e.g. Fig. 18A-C). Frontal area divided into preglabellar field and somewhat longer anterior border by shallow border furrow that is bowed evenly forward. Preglabellar field long, equal to 87% (72-107) of anterior border length, gently inflated and slopes steeply forward. Anterior border comprises 54% (48-58) of frontal area length (sag.) but narrows laterally, and slopes gently upward from border furrow. Palpebral area of fixigena wide, equal to 41% (34-46) of glabellar width at SO and slopes gently upward. Palpebral lobe long, equal to 41% (40–43) of glabellar length, arcuate band that slopes very gently upward from palpebral furrow; centred opposite anterior end of L1. Palpebral furrow is shallow groove on external surface but more firmly impressed on internal mould. Palpebral ridge weakly convex on external surface but better expressed on internal mould; oblique, extending forward and inward to intersect axial furrow near anterior end of glabella. Anterior branches of facial sutures diverge forward between palpebral lobe and anterior border furrow, so that cranidial width at anterior tip of palpebral lobe is 83% (79-85) of width at border furrow, then curving inward along anterior cranidial margin. Posterior branches diverge



abruptly backwards in faintly sigmoid curve. Postocular area of fixigena with weakly inflated, oval baccula opposite L1. Posterior border short (exsag.), convex and nearly transverse; posterior border furrow shallow near glabella but deepens at posterolateral projection. Apart from network of anastomosing caecal markings on preocular and preglabellar fields and posterior part of anterior border, external surface is smooth; internal mould also smooth and caecal markings are less clearly defined.

Librigena with long, flat genal spine curved backwards and outward. Librigenal field gently inflated and slopes steeply down from eye. Lateral border curved gently upward with width equal to about half of librigenal field; becomes inflated at intersection with base of genal spine. Lateral border furrow well defined anteriorly but becomes effaced posteriorly. Posterior border furrow shallow and curves down along inner edge of proximal part of genal spine without intersecting lateral border; posterior border flat. Librigenal field with well-defined caecal markings that are also weakly expressed on lateral border; small areas of exoskeleton adhering to genal spine are smooth.

Incomplete thoracic segment preserves outermost part of pleura. Distal tip of deep pleural furrow divided pleural into long, convex anterior pleural band and shorter posterior pleural band. Anterior pleural band extended into long, stout pleural spine curved outward and backward.

Pygidium sub-semielliptical in outline (although smaller specimen, see Fig. 19M, N, is less rounded posteriorly than larger pygidium, see Fig. 20C), with length 43% (42-44) of maximum width. Axial furrow gently impressed and defined largely by change in slope between axis and pleural field. Axis strongly convex and wide, maximum width equal to length; tapered very gently backward and well rounded posteriorly; occupies 75% of pygidial length and 33% of pygidial maximum width. Articulating half-ring semielliptical in outline, comprises less than one-fifth of axis length; articulating furrow firmly impressed and transverse. Axis composed of four segments. First and second axial rings convex, roughly equal in length, and bounded by well defined transverse ring furrows; first ring accounts for 18% (17-19) of axis length. Terminal piece comprises two segments separated by faint transverse furrow that does not reach axial furrow. Pleural field nearly flat next to axis but is flexed gently downward distally; post axial area inflated and slopes more steeply backward. Anteriormost pleural furrow long (exsag.) but shallow, and defines short

anterior and posterior pleural bands; interpleural furrow shallow and short (exsag.); one or two additional pairs of very shallow pleural furrow present. Border furrow faint and defined largely by change in slope between pleural field and border. Border nearly flat, equal to 23% (22–24) of axis length at maximum width (normal to pygidial margin), but narrows rapidly posteriorly, particularly on smaller specimen. External surface and internal mould are smooth.

Remarks. Wilson (1949) considered Plataspella alpersensis (Resser, 1942) and P. simplicitas (Resser, 1942) to be synonyms of the type species, P. anatina (Resser, 1942), and subsequent authors (e.g. Frederickson 1949; Stitt 1971) have followed his interpretation. However, examination of type material and new specimens from the Honey Creek Formation suggests that synonymy of all three species is premature. All new cranidia from our collections have a relatively long preglabellar field that is only slightly shorter than the anterior border (87%; 72–107) and, in this respect, they closely resemble the types of both P. alpersensis and P. simplicitas (87%; 72–98). The latter two species do not differ any any discernable attribute (compare Fig. 17A-I and Fig. 18A-I) and are regarded as synonyms. Although P. alpersensis has page priority, we prefer to retain the name P. simplicitas because the type cranidia are more completely preserved and one of the paratypes is a librigena (note that I. bicinta Resser, 1942 also has page priority, but this species is based on an incomplete external external mould and the name is best restricted to the type). In contrast, the holotype of Plataspella anatina is a distinct outlier, with a preglabellar field that is equal to less than 60% of anterior border length. Among specimens from Oklahoma that we have examined only the holotype is assignable to P. anatina using this criterion.

The single specimen from the Ore Hill Member of the Gatesburgh Formation (Fig. 18J–L) that Wilson (1951) identified as *P. anatina* falls within the range of variability of the cranidia illustrated here and is assigned tentatively to *P. simplicitas*. Like *P. simplicitas*, cranidia of *Plataspella* from the Bison Creek Formation, Alberta (Westrop 1986, pl. 29, figs 2, 3) possess a relatively long preglabellar field that is roughly equal to the border. However, they also display long, stout genal spines that contrast with the relatively slender spines of the cranidia from Oklahoma, and the associated pygidium (Westrop 1986, pl. 29, fig. 6) is relatively shorter and wider than those of *P. simplicitas*. The status

Figure 17. A–O, *Plataspella simplicitas* (Resser, 1942), Honey Creek Formation, Arbuckle Mountains, Oklahoma. A–C, cranidium, partly exfoliated (USNM 108801b; paratype of *P. alpersensis* Resser, 1942), × 4; A, dorsal view; B, lateral view; C, anterior view. D–F, cranidium, partly exfoliated (USNM 108801a; holotype of *P. alpersensis* Resser, 1942), × 4: D, anterior view; E, lateral view; F, dorsal view. G–I, cranidium, mostly exfoliated (USNM 108801c; paratype of *P. alpersensis* Resser, 1942), × 5: G, dorsal view; H, lateral view; I, anterior view. M–O, cranidium, partly exfoliated (OU 40304), × 5: M, dorsal view; N, anterior view; O, lateral view. J–L, *Plataspella anatina* (Resser, 1942), Honey Creek Formation, Blue Creek Canyon, northern Comanche County, Oklahoma; holotype cranidium, testate (USNM 108803), × 5: J, dorsal view; K, lateral view; L, anterior view.



Figure 18. A–I, *Plataspella simplicitas* (Resser, 1942), Honey Creek Formation, Honey Creek Formation, Arbuckle Mountains, Oklahoma. A–C, holotype cranidium, exfoliated (USNM 108804a), \times 3.5: A, dorsal view; B, anterior view; C, lateral view. D, E, paratype librigena, exfoliated (USNM 108804d), \times 4: D, dorsal view; E, lateral view. F–H, paratype cranidium, exfoliated (USNM 108804c), \times 4: F, dorsal view; G, anterior view; H, lateral view. I, paratype cranidium, exfoliated (USNM 108804b), \times 3.5, dorsal view; J–L, *Plataspella simplicitas* (Resser, 1942), Ore Hill Member, Gatesburg Formation, Pennsylvania; partly exfoliated cranidium (YPM 18533), \times 4: J, lateral view; K, anterior view; L, dorsal view.

of these sclerites is uncertain but they could well represent a distinct species. They were included in the phylogenetic analysis as *P*. sp. indet. (Figs 2, 3; Table 1).

> Plataspella anatina (Resser, 1942) (Fig. 17J–L)

- 1942 Iddingsia anatina Resser: 89, pl. 17, figs 1-2.
- ?1949 *Plataspella anatina* (Resser); Wilson: 42, pl. 9, figs 20–22, 25, 26.
- non 1949 Plataspella anatina (Resser); Frederickson: 355, pl. 68, figs 10–13 [= Plataspella simplicitas].
- *non* 1951 *Plataspella anatina* (Resser); Wilson: 647, pl. 92, fig. 6 [= *Plataspella simplicitas*].
- *non* 1971 *Plataspella anatina* (Resser); Stitt: 20, pl. 1, fig. 10 [= *Plataspella simplicitas*].
- *non* 1986 *Iddingsia anatina* (Resser); Westrop: 61, pl. 29, figs 2–6 [= *Plataspella* sp. indet.].

Types. The holotype is an incomplete cranidium (USNM 108803; Fig. 17J–L) from the Honey Creek Formation, Blue Creek Canyon, northern Comanche County, Oklahoma.

Diagnosis. Preglabellar field equal to less than 60% of preglabellar field. Occipital ring preserves base of slender occipital spine.

Occurrence. Honey Creek Formation, Blue Creek Canyon, northern Comanche County, Oklahoma; ?Morgan Creek Member, Wilberns Formation, central Texas (Wilson 1949).

Remarks. As noted above, under the remarks on *P. simplicitas, Plataspella anatina* (Resser, 1942) has a relatively short preglabellar field that is equal to less than 60% of the length of the anterior border. As diagnosed herein, almost all of the sclerites attributed to *P. anatina* by previous workers are better assigned to *P. simplicitas.* Mostly incomplete cranidia from the Wilberns Formation of Texas that were figured by Wilson (1949, pl. 9, figs 20–22, 25, 26) may be an exception. The best preserved of these (Wilson 1949, pl. 9, fig. 22) has a short preglabellar field comparable to *P. anatina*, although the posterior end of LO is incomplete and it is not clear whether this sclerite possessed an occipital spine. For this reason, Wilson's material is only questionably assigned to *P. anatina.*

Occurrence. Honey Creek Formation, Dotson Ranch, Murray County, collection DR 5.75

Discussion. A single cranidium from the Honey Creek Formation at the Dotson Ranch section lacks an occipital spine and likely represents a new species. In other respects, including the relatively long preglabellar field that is almost equal in length to the preglabellar field, it is similar to cooccurring specimens of *P. simplicitas*. Wilson (1949, p. 42) reported that half of the cranidia in his collections from the Wilberns Formation lacked occipital spines, so it is possible that *P.* sp. nov. 1 also occurs in Texas.

Genus Burnetiella Lochman, 1958

Type species. *Ptychoparia? urania* Walcott, 1890, from the Cap Mountain Member, Riley Formation, Texas (by original designation).

Diagnosis. Very short preglabellar field, so that anterior border furrow is barely separated from preglabellar furrow. Pygidium with relatively narrow (tr.) axis composed of five, rather than four, segments, and concave border.

Remarks. *Burnetiella* is diagnosed by apomorphic pygidial characters, including a relatively narrow (tr.) axis composed of five, rather than four, segments, and a concave border. Most characters of the cranidium, including the glabellar outline, size and position of the palpebral lobes, the very short preglabellar field, and tuberculate sculpture, are shared with speices of *Dokimocephalus*. The most conspicuous cranidial difference lies in the orientation of the anterior branches of the facial sutures, which are strongly divergent, rather than bowed gently outward, in *Burnetiella*. However, this is a plesiomorphic condition that is shared with *Iddingsia, Plataspella* and such outgroups as *Dunderbergia* (e.g. Figs 16A–F, 18A–C, F–L; Palmer 1965, pl. 4, fig. 8).

Burnetiella urania (Walcott, 1890) (Fig. 21E–G)

- 1890 Ptychoparia? urania (Walcott); Walcott: 274, pl. 21, figs 10, 11.
- 1924 Burnetia urania (Walcott); Walcott: 54, pl. 10, fig. 2.
- 1925 Burnetia urania (Walcott); Walcott: 77, pl. 17, figs 1–3.
- 1944 Burnetia urania (Walcott); Shimer & Shrock: 263, figs 25–26.
- non 1949 *Burnetia urania* (Walcott); Wilson: 32, pl. 9, figs 3, 9, 10 [= *Burnetiella* sp. indet].
- non 1949 *Burnetia urania* (Walcott); Frederickson: 348, pl. 70, figs 12–13 [? = *Burnetiella* sp. nov. 1].
- non 1951 *Burnetia urania* (Walcott); Wilson: 625, pl. 89, figs 13–18 [= *Burnetiella* sp. nov. 1].
- 1958 Burnetiella urania (Walcott); Lochman:e 417.

Types. The holotype is a cranidium (USNM23861a) from the Morgan Creek Member of the Wilberns Formation, Packsaddle Mountain, Llano County, Texas (Fig. 21E–G).



Occurrence. Morgan Creek Member of the Wilberns Formation, Texas.

Remarks. Restudy of the large holotype cranidia of Burnetiella urania (Walcott; Fig. 21E-G) shows that the frontal is incompletely preserved and the true length of the anterior border cannot be determined. This is unfortunate because cranidia from the Honey Creek Formation fall into two species that are readily discriminated on border length. Burnetiella exilis (Resser, 1942) (Fig. 22A-I, 21) has a relatively long border that is equal to 61% (57–66) of glabellar length, whereas cranidia assigned questionably to B. sp. nov. 1 (Fig. 25G-J) have much shorter borders that are equal to 47% (42-51) of glabellar length. Critical comparison between B. urania and the Oklahoman species is impossible on this basis, and other supposedly diagnostic characters proposed for the former, including glabellar convexity and the expression of the preglabellar field (Frederickson 1949, p. 348) fall within the range of variation of B. exilis. The portion of the border that is preserved on the holotype of B. urania is equal to about 45% of glabellar length and the lateral profile is evenly sloping (Fig. 21G). In contrast, both B. exilis and B. sp. nov. 1 possess variably sloping lateral profiles that flatten distally (e.g. Figs 22B, D, H; 25I). Cranidia identified as B. urania from the type area in central Texas (Wilson 1949, pl. 9, figs 2, 9–10) also appear to be broken anteriorly and offer no additional information. We conclude that the status of B. urania is impossible to evaluate at present, and we recommend that the name be restricted to the holotype.

Burnetiella exilis (Resser, 1942) (Figs 22A–I, 23A–E, G–I)

1942 Burnetia exilis Resser: 81, pl. 17, figs 23-27.

1942 Burnetia ectypa Resser; Resser: 82, pl. 17, figs 30–31.

non 1949 *Burnetia exilis* Resser; Frederickson: 348, pl. 70, figs 9–11 [fig. 9 = *Burnetiella* sp indet; 10–11 = *Burnetiella* sp. nov. 1?].

?1965 *Burnetiella ectypa* Resser; Grant: 110, pl. 8, figs 22 only [fig 24 = *Burnetiella* sp. nov. 1?].

non 1975 *Burnetiella exilis* Resser; Kurtz: 1022, pl. 2, fig. 21, pl. 4, fig. 30 [? = *Burnetiella* sp. nov. 1].

Types. The holotype cranidium (USNM108808a; Fig. 22A–C) and two paratype cranidia (USNM 108808b, c; Fig. 22D–I) are from the Honey Creek Forma-

tion, West Timbered Hills, Arbuckle Mountains, Oklahoma.

Diagnosis. Very long, roughly tongue-shaped border, length equal to 61% (57–66) of glabellar length, and strongly rounded anteriorly; border length equal to 43% (41–45) of maximum width; slopes steeply forward from preglabellar furrow but flattens along anterior half of length.

Material. Sclerites available for study includes Resser's (1942) types, and three additional figured cranidia.

Occurrence. Honey Creek Formation, Kimbell Ranch, Ring Top Mountain, northern Comanche County, collections KR1 20.5, ?KR3 25.

Description. Cranidium elongate, with width at palpebral lobes about 75% of length; sub-semielliptical in outline and well rounded anteriorly: strongly arched in lateral and anterior views. Axial furrows are very shallow grooves on both external surface and internal mould; preglabellar furrow shallows medially but deepens somewhat laterally. Glabella convex, raised well above fixigena and occupies 60% (59-61) of cranidial length, and about half of cranidial width at the palpebral lobes; tapers forward, particularly in front of S1, and rounded anteriorly. SO nearly transverse medially but curves forward abaxially; well defined on both external surface and internal mould; shallow medially but deepens in front of lateral lobe of LO. LO accounts for 16% (15-18) of glabellar length; inflated abaxially to form convex lateral lobes. S1 curved to geniculate, well incised on internal mould and external surface; on latter, also expressed as smooth band that lacks sculpture. L1 slightly longer than LO. S2 shallower and less strongly defined than S1, expressed on external surface largely as smooth band that lacks sculpture; S3 recognizable only as smooth, nearly transverse band that interrupts sculpture. Preglabellar field very short, equal to 7% (5-9) of frontal area length, and slopes steeply forward. Anterior border furrow shallow but clearly defined groove on both external surfaces and internal moulds; proceeds obliquely inward from cranidial margin, becoming bowed forward to varying extent in front of glabella (compare Fig. 22A and Fig. 23A). Anterior border very long, roughly tongue-shaped, with length equal to 61% (57–66) of glabellar length, and strongly rounded anteriorly; border length equal to

Figure 19. A–E, I–N, *Plataspella simplicitas* (Resser, 1942), Honey Creek Formation, Arbuckle Mountains, Oklahoma; Dotson Ranch, Murray County, collection DR 5.75, except I (collection DR 8.55). A, B, testate cranidium (OU 12447), \times 4: A, dorsal view; B, anterior-oblique view. C–E, exfoliated cranidium (OU 12448), \times 5: C, dorsal view; D, lateral view; E, anterior view. I, testate cranidium (OU 12449), \times 5, dorsal view; J–L, testate cranidium (OU 12450), \times 5: J, dorsal view; K, lateral view; L, anterior view. M–N, testate pygidium (OU 12283), \times 6: M, dorsal view; N, posterior view. F–H, *Plataspella* sp. nov., Honey Creek Formation, Dotson Ranch, Arbuckle Mountain, Murray County, Oklahoma, collection DR 5.75; partly exfoliated cranidium (OU 12282), \times 5: F, dorsal view; G, anterior view; H, lateral view.



Figure 20. *Plataspella simplicitas* (Resser, 1942), Honey Creek Formation, Dotson Ranch, Arbuckle Mountain, Murray County, Oklahoma, collection DR 5.75. A–B, partly exfoliated librigena (OU 12451), \times 4: A, lateral view; B, dorsal view. C, mostly testate pygidium (OU 12452), \times 6, dorsal view; D, tip of thoracic segment, mostly testate, showing long, backwardly curved spine (OU 12453), \times 4, dorsal view; E–G, partly exfoliated cranidium (OU 12454), \times 4: E, dorsal view; F, lateral view; G, anterior view. H, I, cranidium (OU 12455), \times 4: H, dorsal view; I, anterior-oblique view. J, incomplete exfoliated cranidium (OU 12482), \times 4, dorsal view.



Figure 21. A–D, H, I, *Burnetiella* cf. *B. urania* (Walcott, 1890), Honey Creek Formation, Ring Top Mountain, Kimbell Ranch, northern Comanche County. A–C, partly exfoliated cranidium (OU 12220), collection KR2 37.0, \times 3: A, dorsal view; B, anterior view; C, lateral view. D, exfoliated cranidium (OU 12223), collection KR2 48.2–48.5, dorsal view, \times 1.5; H, I, partly exfoliated pygidium (OU 12221), collection KR2 37.0, \times 6: H, dorsal view; I, posterior view. E–G, *Burnetiella urania* (Walcott, 1890), Morgan Creek Member, Wilberns Formation, Burnet County, Texas; holotype cranidium, exfoliated (USNM 23861a), \times 3.5: E, anterior view; F, dorsal view; G, lateral view.

Downloaded By: [The University of Iowa] At: 19:51 28 November 2010



Figure 22. A–I, *Burnetiella exilis* (Resser, 1942), Honey Creek Formation Arbuckle Mountains, Oklahoma. A–C, holotype cranidium, exfoliated (USNM 108808a), \times 4: A, dorsal view; B, lateral view; C, anterior view. D–F, exfoliated paratype cranidium (USNM 108808x), \times 5: D, lateral view; E, anterior view; F, dorsal view; G–I, paratype cranidium, exfoliated (USNM 108808x), \times 5: G, dorsal view; H, lateral view; I, anterior view. J, K, *Burnetiella* cf. *B. urania* (Walcott, 1890), Honey Creek Formation, Ring Top Mountain, Kimbell Ranch, northern Comanche County, collection KR2 37.0; mostly exfoliated librigena (OU 12222), \times 1.5: J, dorsal view; K, lateral view. L–N, ?*Burnetiella* sp. nov. 1, Ore Hill Member, Gatesburg Formation, Drab, Pennsylvania, Wilson (1951) collection 47–3w.22; librigena (YPM, 18537), cast from an external mould, \times 2: L, dorsal view; M, lateral view; N, anterior view.

43% (41-45) of maximum width; slopes steeply forward from preglabellar furrow but flattens along anterior half of length. Internal moulds show distinct but very shallow furrow on flattened half of anterior border (e.g. Fig. 22A-C). Palpebral area of fixigena broad, width equal to 35% (34-36) of glabellar width at SO, and slopes gently upward from axial furrow. Palpebral lobe long, nearly flat, curved band equal to 34% (32-37) of glabellar length; palpebral furrow is firmly impressed, arcuate groove on both external surface and internal mould. Palpebral ridge oblique, gently convex and preceeds forward and inward from palpebral lobe to reach axial furrow opposite S3. Anterior branches of sutures diverge forward to reach maximum separation just behind mid-length of anterior border, so that cranidial width at anterior tip of palpebral lobe is about 70% of maximum width of frontal area; then curves inward along cranidial margin. Posterior branches diverge abruptly backward; directed nearly transversely before curving backward to intersect posterior cranidial margin. Posterior border furrow is well defined, nearly transverse near glabella but curved backward along posterolateral projection; posterior border short (exsag.), convex, also nearly transverse near glabella but curved backward along posterolateral projection. External surface of glabella (except for smooth bands associated with glabellar furrows), preocular and preglabellar fields, palpebral and posterior areas with scattered fine tubercles separated by finer granules; only the tubercles are expressed on internal moulds. Frontal area with coarse granules arrayed along caecal markings; fine granules scattered through areas between caecal ridges; caecae become indistinct and granules smaller on anterior third of border; internal mould of frontal area is smooth.

Discussion. Kurtz (1975, p. 1022) considered Burnetiella exilis, B. ectypa (Resser, 1942), B. cava (Resser, 1942) and B. pennsylvanica (Resser, 1942) to represent a single species that was diagnosed by the granulose sculpture of the anterior border. He regarded B. urania as a second species that lacked sculpture on the border. Unfortunately, this simple approach hinders, rather than helps, development of species diagnoses. Comparision of their respective types (Figs 22A–I, 23G–I) supports synonymy of B. exilis and B. ectypa but these and other specimens from Oklahoma also demonstrate that the sculpture of the external surface of the border is not expressed on the internal mould. Although the exfoliated holotype of B. urania (Walcott, 1890) has a smooth border, the nature of the external surface is unknown. Thus, the apparent differences in border sculpture between species are likely to be a function of preservation rather than any meaningful biological difference.

Examination of both type and new material shows that *Burnetiella exilis* is diagnosed by a very long (equal to 61% [57–66] of glabellar length), roughly tongue-shaped

anterior border that initially slopes forward but flattens anteriorly. Even a casual glance at the anterior border of the holotype of *B. pennsylvania* (Fig. 24A) shows that it is considerably shorter than the border of *B. exilis*. The single cranidium of *B. cava* (Resser, 1942, pl. 20, figs 1-3) is incomplete and cannot be evaluated adequately. As noted earlier, *B. urania* is best restricted to the holotype.

At present, Burnetiella exilis can only be identified with confidence from the Honey Creek Formation of Oklahoma. One of Grant's (1965, pl. 8, fig. 22) specimens from Wyoming that he identified as *B. ectypa* appears to have a long anterior border and might be conspecific with B. exilis, but the other (Grant 1965, pl. 8, fig. 24) has a relatively short border that is similar to that of B. sp. nov. 1 (e.g. Fig. 25D-F). Kurtz (1975) assigned two cranidia from the Davis Formation of Missouri to B. exilis. The best preserved of these (Kurtz 1975, pl. 2, fig. 21) has a shorter, less strongly rounded border than B. exilis and may represent B. sp. nov. 1. The other specimen (Kurtz 1975, pl. 4, fig. 30), which is flattened in shale, has similar proportions of the frontal area and may also be assigned questionably to B. sp. nov. 1. Similarly, a specimen attributed to B. ectypa by Stitt (1971, pl 1, fig. 9) also differs from B. exilis in having a shorter anterior border with a less strongly curved anterior margin, and may also represent B. sp. nov. 1.

A small cranidium (less than 1 cm sag.) from collection KR3 25 (Fig. 23F) is assigned questionably to *B. exilis*. The anterior border is relatively short compared to larger cranidia (equal to 47% of gleballar length versus an average of 61% for large sclerites) but resembles the latter in having a well-rounded anterior margin. A slightly larger cranidium of *B.* sp. nov. 1? (Fig. 28F, G) possesses a relatively shorter and wider (length is 30% of width, rather than 38%) border with less curved anterior margins. If the identification of the cranidium from KR3 25 is correct, the relative length of the frontal area and anterior border increases during holaspid ontogeny of *B. exilis*.

Burnetiella alta (Resser, 1942) (Fig. 28J, K, ?L)

1942 *Burnetia alta* Resser: 80, pl. 17, figs 12–14. non 1956 *Burnetia alta* Resser; Deland & Shaw: 548, pl. 65, figs 1–3 [= *Burnetiella* sp. indet.].

?1975 Burnetiella alta Resser; Kurtz: 1021, pl. 4, fig. 31.

Types. The holotype (USNM 108806; Fig. 28J, K) is an incomplete cranidium from Davis Formation, Flat River, St. Francois County, Missouri.

Occurrence. Kurtz (1975, p. 1021) claimed to have found "probable topotypes" of *Burnetiella alta* from Member C of the Davis Formation. The holotype is on a small piece of bio-oolitic wackestone.



Remarks. Kurtz (1975, p. 1021) stated that Burnetiella alta was diagnosed by a short border and and a border furrow that "nearly touches the preglabellar furrow". The holotype (Fig. 28J, K) does appear to have a relatively short border, although the anterior margin is broken and ragged, so that its true extent is unclear. However, as recognized by Kurtz, there is a distinct preglabellar field separating the anterior border furrow from the preglabellar field (Fig. 28K). The small cranidium attributed to this species by Kurtz (Fig. 28L) is flattened in shale. It possesses a relatively long preglabellar field, although is possible that this feature is accentuated by compaction. There is no trace of sculpture on the glabella and fixigena, which differentiates this specimen from all other known cranidia of Burnetiella, including the holotype of B. alta. It is far from clear as to whether Kurtz's specimen is conspecific with the holotype, and it could be equally well assigned to Iddingsia. We conclude that there is too little information to characterize B. alta, and the name is best restricted to the type.

The incomplete cranidium assigned to *B. alta* by Deland & Shaw (1956, pl. 65, fig. 1) cannot be indentified with confidence. The anterior border appears to be longer than those of both *B. alta* and *B. pennsylvanica* (Resser, 1942) (Fig. 24A–D) but shorter than in *B.* sp. nov. 1 (e.g. Fig. 25F).

Burnetiella pennsylvanica (Resser, 1942) (Fig. 24A–D)

1942 Burnetia pennsylvanica Resser: p. 84, pl. 21, figs 29–30 only [fig 31 = Burnetiella sp. indet.].

Types. The holotype (USNM 108842a) is an internal mould of a cranidium that preserves only a small part of the frontal area (Fig. 24C, D), and an external mould of the anterior part of the glabella and almost all of the frontal area (Fig. 24A, D). Resser's figure (1942, pl. 21, figs 29, 30) of this specimen is a composite; small patches of plaster adhering to the broken face of the small piece of limestone that houses the holotype indicates that the frontal area was reconstructed by attaching a plaster cast from the incomplete counterpart mould. The paratype cranidium (USNM 108842b; Fig. 24E–G) is an incomplete internal mould that may not be conspecific with the holotype (see below).

Diagnosis. Short anterior border equal to about 33% of glabellar length.

Occurrence. Ore Hill Member, Gatesburg Formation, one mile south of Ore Hill, Pennsylvania.

Remarks. The paratype cranidium of *Burnetiella pennsylvanica* (Fig. 24E–G) is broken anteriorly so that the length of the anterior border cannot be determined. Resser's (1942, pl. 21, fig. 31) image of this specimen is misleading because part of the border has been cropped out. Both images show the same fracture on the anterior border and there can be no doubt that they depict the same specimen. However, as is clear by comparison with our photograph (Fig. 24E), Resser's image underestimates the length of the border by about 50% and has been trimmed to suggest that the anterior margin is complete. The border of this specimen is clearly longer than that of the holotype (Fig. 24A), and they are unlikely to be conspecific.

Wilson (1951) treated *Burnetiella pennsylvanica* as a synonym of *B. urania* (Walcott; restricted herein to the holotype; see above). However, the preserved portion of the anterior border of the latter is longer than that of *B. pennsylvanica* (equal to 45% of glabellar length, rather than 33%) and slopes evenly forward instead of flattening anteriorly. Figured specimens from Pennsylvania which were identified as *B. urania* by Wilson (1951, pl. 89, figs 13|–18) (Figs 25A–F, K-M, ?25N, 25O) are assigned below to *B.* sp. nov. 1.

Burnetiella pennsylvanica is most similar to the holotype of *B. alta* (Resser, 1942; Fig. 28J, K) in proportions of the frontal area, with the border equivalent to about 33% of glabellar length in both cases. The incomplete nature of *B. alta* prevents detailed comparison, but it is conceivable that future work will demonstrate that these species are synonyms.

Burnetiella cf. *B. urania* (Walcott, 1890) (Figs 21A–D, H, I, 22J, K)

cf. 1890 *Ptychoparia? urania* (Walcott); Walcott: 274–275, pl. 21, figs 10–11.

cf. 1924 Burnetia urania (Walcott); Walcott: 54, pl. 10, fig. 2.

Material. Figured sclerites are two cranidia, a librigena and a pygidium.

Occurrence. Honey Creek Formation, Ring Top Mountain, Kimbell Ranch, collections KR2 37, KR2 48.2–48.5

Figure 23. *Burnetiella exilis* (Resser, 1942), Honey Creek Formation. A–F from Ring Top Mountain, Kimbell Ranch, northern Comanche County; G–I from Arbuckle Mountains, Oklahoma. A–E, partly exfoliated cranidium (OU 12456), collection KR1 20.5, × 4: A, dorsal view; B, anterior view; C, lateral view; D, dorsal view, latex cast from external mould of anterior border and anterior half of glabella; E, composite image from Fig. 1a and 1d. 23F, testate cranidium (OU 12457), collection KR3 25.0, × 9. G–I, cranidium, partly exfoliated (USNM 108809; holotype of *Burnetia ectypa* Resser, 1942), × 3.25: G, dorsal view; H, lateral view; I, anterior view.



Figure 24. A–D, *Burnetiella pennsylvanica* (Resser, 1942), Ore Hill Member, Gatesburg Formation, one mile south of Ore Hill, Pennsylvania. A, B, cast from partial counterpart mould of holotype cranidium (USNM 108842a), \times 3.5: A, dorsal view; B, anterior-oblique view. C, D, holotype cranidium, mostly exfoliated (USNM 108842a), \times 3.5 (the specimen illustrated by Resser (1942, pl. 21, figs 29–30) is a composite of A and B): C, dorsal view; D, anterior-oblique view. E–G, *Burnetiella* sp. indet., Ore Hill Member, Gatesburg Formation, one mile south of Ore Hill, Pennsylvania; exfoliated cranidium (USNM 108842b; paratype of *Burnetiella pennsylvanica* (Resser, 1942)), \times 4: E, dorsal view; F, lateral view; G, anterior view.

Description. Cranidium sub-semielliptical in outline, width across palpebral lobes approximately 75% of length, and strongly convex in lateral and anterior views. Axial furrows are shallow but clearly defined grooves; preglabellar furrow weakly expressed on external surface. Glabella strongly convex and rises well above fixgena; occupies

about 60% of cranidial length and slightly more than half of cranidial width across palpebral lobes; tapers forward from S1 and is well-rounded anteriorly. SO shallow and nearly transverse medially but curves forward and deepens in front of lateral occipital lobes. LO accounts for about 15% of glabellar length and is gently inflated near axial

9

furrows to form low lateral lobes. S1 expressed as firmly impressed furrow and patch of exoskeleton that lacks sculpture; L1 slightly longer than SO. S2 nearly transverse and expressed largely as band of exoskeleton that lacks sculpture. Frontal area long, equal to about 40% of cranidial length. Preglabellar field short, accounting for about 10% of frontal area length, and steeply sloping. Anterior border furrow shallow, defined in part by change in slope between preglabellar field and border, and curved evenly forward. Anterior border long, equal to slightly more than half of glabellar length, and slopes gently forward. Palpebral area of fixigena broad, equal to about 35% of glabellar width at SO, and gently upsloping from axial furrows. Palpebral lobe long, strongly curved band, length equal to about 25% of glabellar length, and centred slightly behind S1. Palpebral furrow is shallow but clearly defined groove. Palpebral ridge ill-defined, oblique, and intersects axial furrow in front of S2. Anterior branches of facial sutures diverge forward, reaching maximum separation just in front of anterior border furrow, so that cranidial width at anterior tip of palpebral lobe is about 70% maximum width of frontal area; sutures then curve inward along anterior margin of border. Much of posterior area of fixgena and course of posterior branch of sutures are not preserved. External surface of cranidium apart from furrows is covered with sculpture of fine tubercles and coarse granules; sculpture is not expressed on frontal area of internal mould.

Librigena preserves part of stout genal spine. Librigenal field broad, occupying more about two-thirds of maximum width of librigena, and inflated. Lateral and posterior border furrows are shallow, confluent grooves; from their intersection, a short, shallow furrow separates posterior border from inflated base of genal spine. Lateral border broad, occupying at maximum extent about one-third of librigenal width; slopes downward posteriorly but flattens anteriorly; narrow rim present. Posterior border weakly convex. On internal mould, librigenal field with fine tubercles arrayed along caecal markings; borders and genal spine are smooth. Patches of exoskeleton adhering to border are coarsely granulose.

Pygidium is semielliptical in outline, length slightly less than half of maximum width. Axial furrows are very shallow, finely etched grooves. Axis convex, long and relatively narrow, length (excluding post-axial ridge) equal to 70% of pygidial length and occupies 25% of axis width; axis width at first axial ring is about 75% of axis length. Axis with five segments; posterior pair incorporated into terminal piece; postaxial ridge prominent and inflated. Three anterior rings separated by firmly impressed, nearly transverse ring furrows that reach axial furrows; terminal piece divided by faint furrow that becomes obsolete abaxially. Pleural field inflated and gently sloping, passing almost imperceptibly into broad, concave border with upturned outer edge. Border widest anteriorly, equal to about 70% of axis width, but narrows posteriorly, so that width behind axis is about one-third maximum width. Anteriormost pleural and interpleural furrows well defined and extend onto inner edge border; anterior pleural band slightly longer than posterior band. Remaining furrows indistinct to obsolete. External surface of axis and pleural field with fine tubercles and coarse granules; border with coarse granules that are not expressed on internal mould.

Discussion. Cranidia of the stratigraphically oldest species of *Burnetiella* in the Honey Creek Formation resemble the holotype of *B. urania* (Walcott) (Fig. 21E–G) in possessing an evenly sloping anterior border. However, the presence of a distinct, relatively long preglabellar field differentiates them from the latter. They also differ from *B.* sp. nov. 1 (Fig. 25A–F) in this respect, whereas *B. exilis* has a longer anterior border than *B.* cf. *B. urania*. The pygidium of *B.* cf. *B. urania* (Fig. 21H, I) is less strongly furrowed than that of *B.* sp. nov. 1 (Fig. 25K–O) and the border is relatively wider (tr.).

Burnetiella sp. nov. 1

(Figs 25A-F, K-M, 25G-J, ?25N-O ?22L-N, ?28F, G)

- 1949 *Burnetia urania*; Frederickson: 348, pl. 70, figs 12–13. 1949 *Burnetia exilis* Frederickson; Frederickson: 348, pl.
- 70, figs 10, 11 only [fig. 9 = *Burnetiella* sp. indet.]. 1951 *Burnetia urania* Frederickson; Wilson: 625, pl. 89,
- figs 13–18. ?1971 Burnetiella ectypa (Frederickson); Stitt: 18, pl 1, fig.
- ?1975 *Burnetiella exilis* (Frederickson); Kurtz: 1022, pl. 2, fig. 21, pl. 4, fig. 30.

Material. Figured sclerites from Pennsylvania include two cranidia, a librigena and two pygidia; three figured cranidia from Oklahoma are assigned questionably.

Occurrence. Ore Hill Member, Gatesburg Formation, Pennsylvania. ?Honey Creek Formation, southern Oklahoma.

Description. Cranidium subpentagonal outline, in rounded anteriorly, and strongly arched in anterior and lateral views. Glabella occupies 67% (64-68) of cranidial length and stands well above fixigenae; tapers forward, particularly in front of S1, and is rounded anteriorly. Axial and preglabellar furrows expressed as shallow grooves on external surface and internal mould. SO well incised and nearly transverse medially but curves forward near axial furrow. LO occupies 17% (16-18) of glabellar length and inflated abaxially to produce convex lateral lobes. S1 oblique, firmly impressed on external surface and internal mould, centred within band of smooth exoskeleton; L1 slightly longer than LO. S2 expressed on external surface as faint, gently curved furrow and area of exoskeleton that lacks sculpture; slightly deeper on internal mould. S3 obsolete on external surface and internal mould.



Frontal area accounts for 34% (33-36) of cranidial length. Preglabellar field short, equal to 7% (6-9) of frontal area length, and slopes steeply downward. Anterior border furrow bowed forward, shallow on external surface but more firmly impressed on internal mould. Anterior border moderately long, length equal to 47% (42-51) of glabellar length. In lateral view, border unevenly sloping; steeply sloping at border furrow, but flattening anteriorly. Anterior cranidial margin moderately curved forward. Palpebral area of fixigena wide, equal to about 40% of glabellar width at SO, and gently upsloping from axial furrow. Palpebral lobe incompletely preserved but apparently long, equal to about 35% of glabellar length and centred just posterior of S1. Palpebral furrow finely etched, arcuate groove on external surface but more firmly impressed on internal mould. Palpebral ridge oblique, extending forward and inward to reach axial furrow in front of S2. Anterior branches of facial sutures diverge strongly forward, so that cranidial width at anterior tip of palpebral lobe is about 75% of width at anterior border furrow; posterior branches diverge abruptly backward in faintly sigmoid curve. Posterior border furrow is well-incised groove on external surface and internal mould; becomes slightly longer (exsag.) distally. Posterior border is short ridge and curves gently backward. External surface of glabella (excluding areas around furrows) and postocular and palpebral fixigenae with fine tubercles and closely spaced fine granules; on preglabellar and preocular fields, tubercles are located on caecal ridges. Only tubercles are expressed on internal mould. Anterior border carries fine to coarse granules that are not expressed on internal mould.

Librigena with long genal spine curved outward and backward; lateral border gently inflated at base of spine. Librigenal field broad, convex, width equal to about 60% of maximum librigenal width. Lateral and posterior borders shallow but well-defined grooves, confluent and extend as single furrow along inner edge of genal spine. Lateral border wide, flexed downward from border furrow but flattens to narrow rim at lateral margin; lateral doublure broad, extening inward as far as border furrow. Posterior border is gently convex. On internal mould, librigenal field with caecal markings that carry fine tubercles; remainder of librigena is smooth.

Pygidium subelliptical in outline with anterior margin curved backward at well defined articulating facet; length about 45% of maximum width. Axial furrows shallow and defined largely by abrupt change in slope between axis and pleural field. Axis strongly convex, occupies about 70% of pygidial length and 25% of pygidial width; extended into narrow (tr.) post-axial ridge in small specimen (Fig. 25K, M) but absent in larger specimen assigned tentatively to the species (Fig. 25N, O). Axis composed of five segments, two of which are incorporated into terminal piece. Articulating half-ring semielliptical in outline, separated from rest of axis by finely etched, transverse articulating furrow; accounts for about 10% of axis length. Three transverse axial ring furrows that reach axial furrows define three axial rings; terminal piece comprises slightly more than 35% of axis length, with segmentation recognizable from incomplete ring furrow that is obsolete across crest of axis. Pleural field nearly flat adjacent to axis but is flexed downward distally. Five pairs of pleural and interpleural furrows are firmly impressed on small specimen (Fig. 25K-M) and extend to pygidial margin; shallower on larger specimen, particularly towards rear (Fig. 25M). Anterior and posterior pleural bands subequal in length; straight and oblique over most of pleural field but curved backward behind articulating facet. Border ill-defined, flattened on small specimen (Fig. 25K-M) but broader and distinctly concave on larger specimen (Fig. 25N, O); border furrow obsolete. External surface exclusive of furrows covered with granulose sculpture.

Remarks. Material from the Gatesburg Formation of Pennsylvania that was identified as Burnetiella urania (Walcott) by Wilson (1951) represents a new species characterized by a moderately long anterior border equal to 47% (42–51) of glabellar length. In lateral view, the border is unevenly sloping, steeply sloping at the border furrow, but flattening anteriorly. The anterior cranidial margin moderately curved forward. Because of limited material and uncertainty over the correct association of some sclerites, it will not be named formally. Only specimens from the Potter Creek locality (Wilson 1951) are assigned confidently to the species (Fig. 25A-F, K-M). A librigena (Fig. 22L-N) and an external mould of a pygidium (Fig. 25N, O) are from other localites and, although Wilson regarded them as conspecific with the sclerites from Potter Creek, they are assigned questionably to B. sp. nov. 1. Cranidia from Oklahoma (Figs 25G–J, 28F, G) are indistinguishable from

Figure 25. A–F, K–M, *Burnetiella* sp. nov. 1, Ore Hill Member, Gatesburg Formation, Pennsylvania. A–C, partly exfoliated cranidium (YPM 18572), Potter Creek, Wilson (1951) collection 47–5w.8a, × 4: A, dorsal view; B, lateral view; C, anterior view. D–F, mostly exfoliated cranidium (YPM 18540), Potter Creek, Wilson (1951) collection 47–5w.8a, × 4: D, lateral view; E, anterior view; F, dorsal view. K–M, testate pygidium (YPM 18570), ridge south of Potter Creek, Wilson (1951) collection 47.6w.5, × 6: K, posterior view; L, lateral view; M, dorsal view. N, O, *?Burnetiella* sp. nov. 1, Ore Hill Member, Gatesburg Formation, Pennsylvania; pygidium (YPM 18538), cast from external mould, Snowberger Quarry, Wilson (1951) collection 47.8w.6, × 4: N, posterior view; O, dorsal view. G–J, *?Burnetiella* sp. nov. 1, Honey Creek Formation, Arbuckle Mountains, Oklahoma: G, exfoliated cranidium (OU 4293), Frederickson (1949) locality 11, dorsal view, × 4: H–J, mostly exfoliated cranidium (OU 4294), Frederickson (1949) locality 12; H, dorsal view; I, lateral view; J, anterior view.

the Pennsylvanian cranidia and likely represent the same species. However, more material is required for an unqualified identification.

Burnetiella exilis (Resser, 1942) (Figs 22A–I, 23A–D, G–I) is most similar to *B*. sp. nov. 1, but differs in possessing a longer anterior border that is equal to 61% (57–66) of glabellar length. Both *B. alta* (Resser, 1942) (Fig. 28J, K) and *B. pennsylvanica* (Resser, 1942) (Fig. 24A–D) have relatively short anterior borders.

Genus Edithiella Kurtz, 1975

Type species. *Edithiella missouriensis* Kurtz, 1975, from the Davis Formation, Missouri, by original designation.

Diagnosis. Long frontal area in which both pregleballar field and anterior border slope steeply forward. Lateral glabellar furrows barely perceptible to obsolete. External surface of the cranidium smooth.

Remarks. The librigena of *Edithiella* sp. indet. 2 (Fig. 26K) has a long, stout genal spine that follows the curvature of the lateral margin. This contrasts with the orientation in *Dokimocephalus, Iddingsia, Plataspella, Burnetiella* and *Stittella*, in which the spine is curved outward and backward. Although *Edithiella* lacks this synapomorphy, a relationship with other members of Dokimocephalidae *s.s.* is supported by the long anterior border (character state 13 (1)) and a posteriorly positioned palpebral lobe (character state 8 (2)).

At Cleve Creek, Nevada, *Edithiella* occurs with *Dellea* and *Kindbladia*, and the genus occurs towards the top of the range of the latter in Missouri (Kurtz 1975). All occurrences appear to be broadly coeval within the lower division of the *Elvinia* Zone as defined by Westrop *et al.* (2007).

Edithiella missouriensis Kurtz, 1975 (Fig. 26A–H)

1975 Edithiella missouriensis Kurtz: 1038, pl. 2, figs 9-11.

Types. The holotype (OU 3528a; Fig. 26A–C) and paratypes (OU 3513b, 3513c; Fig. D–H) are cranidia from the upper Member B, Davis Formation, St. Francois County, Missouri (section 9, collection 977.67–3; Kurtz 1975, fig. 3).

Diagnosis. Very long LO equal to 28% (24–32; higher values in smaller cranidia) of glabellar length. Anterior border long, equal to 38% (36–41) of glabellar length.

Occurrence. Upper Member B, Davis Formation, St. Francois County, Missouri. Description. Cranidium strongly arched in anterior and lateral views, particularly in larger individuals, and subpentagonal in outline with rounded anterior margin; width across palpebral lobes approximately 85% of length. Glabella convex, tapers evenly forward from SO and anteriorly rounded; glabellar width at SO equal to 58% (55-62; higher values in smaller cranidia) of glabellar length; accounts for 66% (65-68) of cranidial length and about 45% of cranidial width across the palpebral lobes. SO is well defined on internal mould, nearly transverse; LO very long, particularly in smaller individuals (e.g. Fig. 26G, H) and occupies 28% (24-32; higher values in smaller cranidia) of glabellar length; slopes upward and backwards from SO. Three pairs of oblique lateral furrows barely expressed on some small individuals (e.g. Fig. 26D-F). Frontal area is long, occupying 34% (32-35) of cranidial length, and slopes steeply forward. Preglabellar field short, comprising 26% (25-27) of frontal area length. Anterior border furrow shallow, and expressed partly by a 'step' in slope of frontal area at border. Anterior border raised somewhat above preglabellar field, but slopes forward at similar angle; long, equal to 38% (36-41) of glabellar length. Palpebral area of fixigena wide, equal to 44% (37-48) of glabellar width at SO, and gently upsloping. Palpebral lobe is nearly flat, gently curved band, with length equal to 27% (24-29) of glabellar length and centred at glabellar mid-length. Palpebral furrow is well defined groove on internal mould. Palpebral ridge oblique, extending forward and inward from palpebral lobe to intersect axial furrow opposite S3; well defined on small internal moulds (e.g. Fig. 26F), but less convex on larger individuals (e.g. Fig. 26A). Anterior branches of facial sutures diverge forward and reach maximum separation in front of anterior border furrow; then converge forward along anterior cranidial margin. Posterior branches not preserved. Posterior border furrow well defined along posterior area of fixigena; posterior border short (exsag.), gently convex and curved gently backwards. Internal mould is smooth except for median node on LO; patches of exoskeleton preserved on glabella also smooth.

Remarks. *Edithiella missouriensis* is the best-known member of the genus but is represented by only the three type specimens in the collections of the Oklahoma Museum of Natural History. The location of the six other specimens mentioned by Kurtz (1975, p. 1038) is unknown. A handful of sclerites collected during the course of this study document the presence of *Edithiella* in the Great Basin (Fig. 26I–N). In frontal area proportions, *E. missouriensis* is similar to *E.* sp. 1 from the Corset Spring Shale (Fig. 26I, J) but has a relatively longer occipital ring. *Edithiella* sp. 2 (Fig. 26K–N) is also from the Corset Spring Shale and has a long occipital ring comparable to that of *E. missouriensis*, but is characterized by a relatively shorter anterior border that is equal to about 25, rather than about 38% (36–41) of glabellar length.

Occurrence. Corset Spring Shale, Patterson Pass, Lincoln County, Nevada, collection PP 302.

Remarks. A single cranidium from Patterson Pass occurs with *Elvina* cf. *E. roemeri* (Shumard, 1861) and *Sigmacheilus flabellifer* (Hall & Whitfield, 1877); in collections from Shingle Pass, about 20 km to the west of Patterson Pass, the latter species is part of a lower *Elvinia* Zone fauna that includes *Kindbladia* (Westrop *et al.* 2007, p. 360). *Edithiella* sp. 1 retains a considerable part of the exoskeleton and demonstrates that the external surface is smooth. It differs from both *E. missouriensis* and *E.* sp. 2 in possessing a relatively short LO.

Edithiella sp. 2 (Fig. 26K–N)

Material. One cranidium and one librigena.

Occurrence. Corset Spring Shale, Cleve Creek, Schell Creek Range, White Pine County, Nevada (Float sample).

Remarks. The short anterior border that is equal to only 25% of glabellar length separates *Edithiella* sp. 2 from both *E. missouriensis* and *E.* sp. 1.

Stittella gen. nov.

Type species. *Stittella beeae* from the Honey Creek Formation, northern Comanche County, Oklahoma.

Diagnosis. Very short frontal area that occupies less than 20% of cranidial length. Librigena with long, stout genal spine directed backward steeply upward. Pygidium relatively narrow, with length equal to half of width; anterior margin curved sharply backward abaxially; articulating facet long.

Etymology. Named for James H. Stitt.

Remarks. Cranidia of two new species from the Honey Creek Formation resemble *Burnetiella* in possessing coarsely granulose to tuberculate sculpture that is well expressed on both the external surface and internal mould. Both are characterized by unusually short frontal areas that occupy less than 20% of cranidial length, whereas species of *Burnetiella* have frontal areas that are in the range of 30–40% of cranidial length. The distinction is somewhat arbitrary, and it could be argued that future discoveries might bridge the gap, but at present the species assigned herein to *Stittella* represent outliers in frontal area proportions.

In the most completely known species, Stittella beeae sp. nov., additional apomorphic states of the librigenal and pygidia morphology are present. They were not coded in the phylogenetic analysis because they are known only from this species and would therefore be uninformative. The librigena is characterized by a genal spine that is directed sharply upward (Fig. 28A-C), whereas genal spines of all other dokimocephalid s.s. genera and the outgroup are nearly horizontal to gently inclined (e.g. Figs 7Q, R, 14E, F, 20A, 22K, M). The pygidium of S. beeae (Fig. 28D, E) is relatively narrow with an anterior margin that is curved sharply backward abaxially. Where known, pygidia of other dokimocephalid s.s. genera are relatively wider with roughly transverse anterior margins that are gently curved backward near the anterior corner at a relatively small articulating facet (e.g. Figs 12K, L, 15E, 21H). Stit*tella* sp. nov. 1 is assigned tentatively to the genus on the basis of the short frontal area but sclerites other than the cranidium are currently unknown.

> *Stittella beeae* sp. nov. (Figs 27, 28A–E)

Types. The holotype is a cranidium (OU 12459; Fig. 27A–C); paratypes include three cranidia (OU, 124060, 12461, 12462) one librigena (OU 12463) and a pygidium (OU 12464). All sclerites are from the Honey Creek Formation, Ring Top Mountain, Kimbell Ranch, northern Comanche County, Oklahoma.

Diagnosis. Very short frontal area that comprises about 10% of cranidial length.

Etymology. Named for Samantha Bee.

Occurrence. Honey Creek Formation, Ring Top Mountain, Kimbell Ranch, northern Comanche County, Oklahoma, collection KR1 19.

Description. Cranidium subquadrate in outline, length equal to about 90% of width across palpebral lobes, and strongly arched in anterior and lateral views. Axial furrows are firmly impressed grooves; preglabellar furrow shallows medially. Glabella strongly convex and long, occupying 90% of cranidial length and 50% of cranidial width



across palpebral lobes; tapers anteriorly in front of L1 and gently rounded anteriorly. SO shallow medially, particularly on external surface, and nearly transverse; deepens and curves gently forward near axial furrow. LO comprises 16% (14-19) of glabella and is inflated abaxially to form convex lateral lobes. S1 lightly impressed on external surface and internal mould, although better defined on smallest available specimen (Fig. 27I, J), curved gently backward and located within band of exoskeleton that lacks sculpture. L1 slightly longer than LO. S2 shallower than S1 and recognizable partly by absence of sculpture; curved very gently backward. L2 equal in length to L1. S3 expressed only as patch of smooth exoskeleton. Frontal area short, accounting for only 10% of cranidial length. Preglabellar field very short, length equal to 3% (2-3) of glabellar length, and slopes nearly vertically downward. Anterior border furrow shallow, defined in part by change in slope between preglabellar field and border, and bowed gently forward; forward curvature increases in front of glabella in some specimens (e.g. Fig. 27G, H). Anterior border short, length equal to slightly less than 10% of glabellar length, and flexed gently upward from border furrow. Palpebral area of fixigena wide, equal to 35% (34-37) of glabellar width at SO, and gently upsloping. Palpebral lobe is weakly upturned, arcuate band; length is equal to 28% (26-33) of glabellar length and centred just behind S1. Palpebral furrow is shallow groove on testate surfaces and more firmly impressed on internal mould. Palpebral ridge gently convex, better expressed on internal mould, extends obliquely inward to reach axial furrow near S3. Anterior branches of facial sutures diverge forward, reaching maximum separation just behind border furrow, then converge inward along cranidial margin. Posterior branches diverge sharply backward in weakly sigmoid curve. Posterior border convex, widening (exsag.) abaxially and curved gently backward. Posterior border furrow is firmly impressed groove. External surface of glabella, except for smooth bands associated with furrows, covered with fine tubercles that grade into coarse granules in front of S3. Papebral area and posterior area of fixigena also with fine turbercles; palpebral lobe with scattered coarse granules; preglabellar and preocular fields with fine tubercles mounted on caecal ridges; anterior border with scattered coarse granules.

Librigena with long, stout genal spine directed backward and upward at about 40° from horizontal. Librigenal field slopes steeply downward from eye socle, width (tr.) equal to about 65% of maximum librigenal width. Lateral border furrow shallow. Lateral border narrow (tr.) and gently upturned anteriorly but inflated posteriorly at intersection with genal spine; posterior border not preserved. Librigenal field with fine tubercles that are also expressed on exfoliated areas; base of spine and border with fine granules that are not expressed on exfoliated surfaces; outer edge of border with terrace ridges that continue onto doublure.

Pygidium convex and relatively narrow, with length equal to half of width; anterior margin curved sharply backward abaxially; articulating facet long. Axis subquadrate in outline, with length approximately equal to width; occupies about 70% of pygidial length and about one-third of axis width. Two transverse axial ring furrows are firmly impressed on internal mould and divide axis into two rings and terminal piece. Terminal piece occupies about 40% of axis length and, although unfurrowed, probably composed of two segments. Pleural field flat adaxially but flexed downward distally. Two pairs of firmly impressed pleural furrows present; anterior pair curved backward and separates subequal, strongly convex anterior and posterior pleural bands. Interpleural furrows well incised. Border recognizable only as downsloping area that lacks pleural and interpleural furrow; border furrow obsolete. External surface with coarse to fine granules that are not expressed on external mould.

Remarks. The very short anterior border and, consequently, frontal area of *Stittella beeae* are unique among dokimocephalid *s.s.* species. The pygidium is also unusual, but both its large size and granulose sculpture support the association.

Stittella sp. nov. 1 (Figs 29, 30)

Material. Three figured cranidia.

Occurrence. Honey Creek Formation, Royer Ranch section, Arbuckle Mountains (Stitt 1971), collection RR140 (float); Ring Top Mountain, Kimbell Ranch, northern Comanche County, Oklahoma, collection KR1 20.5

Figure 26. A–H, *Edithiella missouriensis* Kurtz, 1975, upper Member B, Davis Formation, St Francois County, Missouri, section 9, collection 977.67–3 (Kurtz 1975, fig. 3). A–C, holotype cranidium, exfoliated (OU 3528a), \times 5; note that part of the right side of specimen was reconstructed by Kurtz with a plaster cast from the counterpart mould: A, dorsal view; B, anterior view; C, lateral view. D–F, paratype cranidium, exfoliated (OU 3513b), \times 8: D, anterior view; E, lateral view; F, dorsal view. G, H, paratype cranidium, exfoliated (OU 3513c), \times 8: G, anterior-oblique view; H, dorsal view. I, J, *Edithiella* sp. 1, Corset Spring Shale, Patterson Pass, Lincoln County, Nevada, collection PP 302; partly exfoliated cranidium (OU 12458), \times 5: I, dorsal view; J, anterior oblique view. K–N, *Edithiella* sp. 2, Lincoln Peak Formation, Cleve Creek, Schell Creek Range, White Pine County, Nevada: K, silicified librigena (SUI 111497), \times 15, dorsal view; K–N, silicified cranidium (SUI 111498), \times 7.5: L–N anterior view, dorsal view, lateral view.





Figure 28. A–E, *Stittella beeae* sp. nov., Honey Creek Formation, Ring Top Mountain, Kimbell Ranch, northern Comanche County, Oklahoma, collection KR1 19.0. A–C, paratype librigena, partly exfoliated (OU 12463), × 4: A, dorsal view; B, lateral view; C, anterior view. D, E, paratype pygidium, partly exfoliated (OU 12464), × 4L: D, posterior view; E, dorsal view. F–I, *?Burnetiella* sp. nov. 1, Honey Creek Formation, Kimbell Ranch, northern Comanche County, Oklahoma, collection KR1 19.0; testate cranidium (OU 12465), × 8: F, dorsal view; G, anterior-oblique view; H, anterior view; I, lateral view. J, K, *Burnetiella alta* (Resser, 1942), Davis Formation, Flat River, St. Francois County, Missouri; holotype cranidium, mostly testate (USNM 108806), × 3: J, dorsal view; K, anterior-oblique view. L, *Burnetiella alta* (Resser, 1942), Davis Formation, Washington County, Missouri (Kurtz 1975 collection 977.35.6); exfoliated cranidium (OU 3496), dorsal view; × ??.

Figure 27. *Stittella beeae* gen. et sp. nov., Honey Creek Formation, Ring Top Mountain, Kimbell Ranch, northern Comanche County, Oklahoma, collection KR1 19.0. A–C, holotype cranidium, partly exfoliated (OU 12459), \times 3: A, dorsal view; B, lateral view; C, anterior view. D–F, paratype cranidium, partly exfoliated (OU 12460), \times 3: D, dorsal view; E, anterior view; F, lateral view. G, H, paratype cranidium, mostly testate (OU 12461), \times 4: G, dorsal view; H, anterior-oblique view. I, J, paratype cranidium, partly exfoliated (OU 12462), \times 4: I, dorsal view; J, anterior-oblique view.



Figure 29. *Stittella* sp. nov. 1, Honey Creek Formation, Oklahoma. All from Royer Ranch section, Arbuckle Mountains (Stitt, 1971), collection RR140 (float), except G–I from Ring Top Mountain, Kimbell Ranch, northern Comanche County, Oklahoma, collection KR1 20.5. A–C, testate cranidium (OU 12225), \times 4: A, anterior view; B, dorsal view; C, lateral view. D–F, mostly exfoliated cranidium (OU 12267), \times 4: D, dorsal view; E, lateral view; F, anterior view. G–I, testate cranidium (OU 12466), \times 6: G, dorsal view; H, lateral view; I, anterior-oblique view.

Description. Strongly arched cranidium subquadrate in outline, length equal to 90% (89–91) of cranidial width across palpebral lobes. Axial furrows shallow but clearly defined, particularly on internal mould; preglabellar furrow shallows medially. Glabella tapered forward, particularly beyond S1, and rounded anteriorly; convex, standing well above fixigena; occupies 83% (81–85) of cranidial length and 49% (49–50) of cranidial width across palpebral

lobes. SO well incised, nearly transverse medially but curved forward and deeper abaxially. LO comprises 18% (17–19) of glabellar length and is inflated near axial furrows to produce lateral lobes. S1 curved backward, gently impressed on external surface and internal mould, and centred within band of exoskeleton that lacks sculpture. L1 slighly longer than LO. S2 expressed only as smooth, oblique band on external surface and as faint furrow on



Figure 30. External surface of right preocular field of *Stittella* sp. nov. 1 (OU 12225; Fig. 29B), showing sculpture of coarse granules arrayed along caecal markings, \times 13.

internal mould. S3 is narrow (exsag.), nearly transverse, smooth area on exoskeleton. Frontal area short, equal to 17% (15-19) of cranidial length. Preglabellar field very short, constituting only 14% (13-15) of frontal area length, and slopes steeply forward. Anterior border furrow shallow and expressed in part by abrupt change in slope between preglabellar field and border. Anterior border short, equal to 17% (15–19) of glabellar length, and nearly flat. Palpebral area of fixigena wide, equal to 36% (35-38) of glabellar width at SO, and gently upsloping. Palpebral lobe long, arcuate band, length equal to 34% (32-36) of glabellar length, centred just behind S1. Palpebral furrow is welldefined groove on external surface and internal mould. Palpebral ridge weakly convex, oblique, extending forward to reach axial furrow opposite S3. Anterior branches of facial suture diverge forward, reaching maximum separation near anterior border furrow, so that cranidial width at anterior tip of palpebral lobe is 80% (80-84) of width at border furrow; sutures then converge forward along anterior cranidial margin. Posterior branches of sutures diverge abruptly backwards in faintly sigmoid curve. Posterior border furrow shallow near axial furrow but deepens and widens (exsag.) abaxially. Posterior border short and convex adaxially but widens and becomes curved gently backward along posterolateral projection. Glabella with finely tuberculate sculpture that grades forward into fine granules beyond S3; posterior and palpebral areas also with fine tubercles, and fine granules on palpebral lobe. Preocular and preglabellar fields with coarse tubercles arrayed along caecal markings (Fig. 30); weakly expressed on internal mould, which is punctate (Fig. 29D). External surface of anterior border with granules that become finer anteriorly; internal mould is smooth.

Remarks. Cranidia from the Honey Creek Fomation at two localities represent a new species but it will not be

named herein because other sclerite types are unknown. In the absence of librigena and pygidia, assignment to *Stitella* is provisional. It differs from *S. beeae* in the longer anterior border.

Acknowledgements

This study was supported by NSF grant EAR 0308685 to Adrain and Westrop. Ken Dotson and the Kimbell Family generously provided access to their properties in the Arbuckle and Wichita mountains, respectively. Roger Burkhalter, Jennifer Eoff and Colt Nickel assisted in fieldwork in Oklahoma, and Neo McAdams in Wyoming; Burkhalter also provided invaluable help in the field in the Great Basin and in various aspects of laboratory work. Jad Bean and David Schultz collected some of the specimens of Iddingsia similis from Patterson Pass, Nevada. The systematics could not have been completed without restudy of numerous type specimens, and we thank Conrad Labandiera, Jan Thompson and Daniel Levin at the National Museum of Natural History and Susan Butts and Copeland MacClintock at the Yale Peabody Museum of Natural History for facilitating various loans. Reviewers Nigel Hughes and Adrian Rushton, and editor Greg Edgecombe contributed a number of comments that improved the final version of this paper.

References

- Bell, W. C., Feniak, O. W. & Kurtz, V. E. 1952. Trilobites of the Franconia Formation, southeast Minnesota. *Journal of Paleontology*, 26, 175–198.
- Chatterton, B. D. E. & Ludvigsen, R. 1998. Upper Steptoean (Upper Cambrian) trilobites from the McKay Group of southeastern British Columbia, Canada. *Paleontological Society Memoir*, 49, 1–43.
- Deland, C. R. & Shaw, A. B. 1956. Upper Cambrian trilobites from western Wyoming. *Journal of Paleontology*, 30, 542–562.
- Evitt, W. 1951. Some Middle Ordovician trilobites of the families Cheiruridae, Harpidae and Lichidae. *Journal of Paleontology*, 25, 587–616.
- Frederickson, E. A. 1948. Upper Cambrian trilobites from Oklahoma. *Journal of Paleontology*, 22, 798–803.
- Frederickson, E. A. 1949. Trilobite fauna of the Upper Cambrian Honey Creek Formation. *Journal of Paleontology*, 23, 341–663.
- Goloboff, P., Farris, J. & Nixon, K. 2008. TNT: a free program for phylogenetic analysis. *Cladistics*, 24, 774–786.
- Grant, R. E. 1965. Faunas and stratigraphy of the Snowy Range Formation (Upper Cambrian) in southwestern Montana and northwestern Wyoming. *Geological Society of America Memoir*, 96, 1–171.
- Hall, J. & Whitfield, R. P. 1877. Palaeontology. *Geological Exploration of the Fortieth Parallel*, 4(2), 198–302.
- Hintze, L. F. & Palmer, A. R. 1976. Upper Cambrian Orr Formation: Its subdivisions and correlatives in western Utah. United States Geological Survey Bulletin, 1405-G, 1–25.

- Hohensee, S. R. & Stitt, J. H. 1989. Redeposited *Elvinia* Zone (Upper Cambrian) trilobites from the Collier Shale, Ouachita Mountains, west-central Arkansas. *Journal of Paleontology*, 63, 857–879.
- Hu, C. H. 1971. Ontogeny and sexual dimorphism of Lower Paleozoic Trilobita. *Palaeontographica Americana*, 7, 1–155.
- Hughes, N. C. & Labandeira, C. C. 1995. The stability of species in taxonomy. *Paleobiology*, 21, 401–403.
- Kobayashi, T. 1935. The Cambro-Ordovician formations and faunas of South Chosen. Palaeontology, part III. Cambrian faunas of South Chosen with special study on the Cambrian trilobite genera and families. *Journal of the Faculty of Science, Imperial University of Tokyo, Section II*, 4(2), 49–344.
- Kurtz, V. E. 1975. Franconian (Upper Cambrian) trilobite faunas from the Elvins Group of southeast Missouri. *Journal of Paleontology*, **49**, 1009–1043.
- Lochman, C. 1953. Notes on Cambrian trilobites: homonyms and synonyms. *Journal of Paleontology*, 27, 886– 889.
- Lochman, C. 1958. Sulcocephalus Wilson, 1948, to replace Berkeia Resser, 1937, and Burnetiella to replace Burnetia Walcott, 1924. Journal of Paleontology, 32, 247.
- Lochman, C. 1964. Upper Cambrian faunas from the subsurface Deadwood Formation, Williston Basin, Montana. *Journal of Paleontology*, 38, 33–60.
- Longacre, S. A. 1970. Trilobites of the Upper Cambrian Ptychaspid Biomere, Wilberns Formation, central Texas. *Paleontological Society Memoir*, 4, 1–70.
- Nixon, K. C. 2002. *WinClada ver. 1.00.08*. Published by the author, Ithaca, NY, USA.
- Palmer, A. R. 1960. Trilobites of the Upper Cambrian Dunderberg Shale, Eureka District, Nevada. United States Geological Survey Professional Paper, 334-C, 53–108.
- Palmer, A. R. 1965. Trilobites of the Late Cambrian Pterocephaliid Biomere in the Great Basin, United States. United States Geological Survey Professional Paper, 493, 1– 105.
- Palmer, A. R. 1968. Cambrian trilobites of east-central Alaska. United States Geological Survey Professional Paper, 559-B, 1–115.
- Paterson, J. R. 2005. Systematics of the Cambrian trilobite family Nepeidae, with revision of Australian species. *Palaeontology*, 48, 479–517.
- Peng, S. C. 1992. Upper Cambrian biostratigraphy and trilobite faunas of the Cili-Taoyuan area, northwestern Hunan, China. *Memoirs of the Association of Australasian Palaeontologists*, 13, 1–119.
- Phleger, F. 1936. Lichadian Trilobites. Journal of Paleontology, 10, 593–615.
- Resser, C. E. 1942. New Upper Cambrian trilobites. Smithsonian Miscellaneous Collections, 103(5), 1–136.
- Saltzman, M. R. 1999. Upper Cambrian carbonate platform evolution, *Elvinia* and *Taenicephalus* zones (Pterocephaliid–Ptychaspid biomere boundary), northwestern Wyoming. *Journal of Sedimentary Research*, 69, 926–938.
- Shergold, J. H. 1980. Late Cambrian trilobites from the Chatsworth Limestone, western Queensland. Australian Bureau of Mineral Resources, Geology and Geophysics Bulletin, 186, 1–109.
- Shimer, H. W. & Shrock, R. R. 1944. Index Fossils of North America. Technology Press, Massachusetts Institute of Technology, Boston.
- Shumard, B. F. 1861. The primordial zone of Texas, with descriptions of new fossils. *American Journal of Science, Second Series*, 32, 213–221.

- Stitt, J. H. 1971. Late Cambrian and earliest Ordovician trilobites, Timbered Hills and lower Arbuckle Groups, western Arbuckle Mountains, Murray County, Oklahoma. Oklahoma Geologic Survey Bulletin, 110, 1–83.
- Stitt, J. H. 1977. Late Cambrian and Earliest Ordovician trilobites, Wichita Mountains area, Oklahoma. Oklahoma Geological Survey Bulletin, 124, 1–79.
- Strong, E. E. & Lipscomb, D. 1999. Character coding and inapplicable characters. *Cladistics*, 15, 363–371.
- Swofford, D. 2000. PAUP*: Phylogenetic Analysis Using Parsimony (* and Other Methods), Version 4. Sinauer Associates, Sunderland, Massachusetts.
- Ulrich, E. O. 1924. Notes on new names in table of formations and on physical evidence of breaks between Paleozoic systems in Wisconsin. *Transactions of the Wisconsin Academy* of Sciences, Arts and Letters, 21, 71–107.
- Walcott, C. D. 1884. The paleontology of the Eureka District, Nevada. United States Geological Survey Monograph, 8, 1–298.
- Walcott, C. D. 1890. Description of new forms of Upper Cambrian fossils. *Proceedings of the United States National Museum*, 13, 267–279.
- Walcott, C. D. 1924. Cambrian geology and paleontology V, no. 2, Cambrian and lower Ozarkian trilobites. *Smithsonian Miscellaneous Collections*, 75(2), 53–60.
- Walcott, C. D. 1925. Cambrian geology and paleontology V, no. 3, Cambrian and lower Ozarkian trilobites. *Smithsonian Miscellaneous Collections*, 75(3), 61–146.
- Westrop, S. R. 1986. Trilobites of the Upper Cambrian Sunwaptan Stage, southern Canadian Rocky Mountains, Alberta. *Palaeontographica Canadiana*, 3, 1–179.
- Westrop, S. R. & Adrain, J. M. 2007. Bartonaspis new genus, a trilobite species complex from the base of the Upper Cambrian Sunwaptan Stage in North America. Canadian Journal of Earth Science, 44, 987–1003.
- Westrop, S. R., Waskiewicz, R. A. & Adrain, J. M. 2007. The Late Cambrian (Steptoean) trilobite genus Bynumina Resser, 1942, in North America. Memoirs of the Association of Australasian Palaeontologists, 34, 357– 376.
- Wilkinson, M. 1995. Coping with abundant missing entries in phylogenetic inference using parsimony. *Systematic Biology*, 44, 501–514.
- Wilson, J. L. 1948. Two Upper Cambrian Elvinia Zone trilobite genera. Journal of Paleontology, 22, 30–34.
- Wilson, J. L. 1949. The trilobite fauna of the *Elvinia* Zone in the basal Wilberns Formation of Texas. *Journal of Paleontology*, 23, 25–44.
- Wilson, J. L. 1951. Franconian trilobites of the central Appalachians. Journal of Paleontology, 25, 617–654.
- Wilson, J. L. & Frederickson, E. A. 1950. The Irvingella major ("Ptychopleurites") faunizone of the Upper Cambrian. American Journal of Science, 248, 891–902.

Appendix: character states

Cranidia

 Glabellar furrows: expressed weakly on external surface and mould (0) (e.g. Palmer 1965, pl. 4, fig. 8; unpublished specimens from the Orr Formation, Utah); deep S1 on external surface and mould (1) (e.g. Fig. 14K); furrows effaced on external surface and mould (2) (e.g. Fig. 19A–L).

- Occipital ring: aspinose (0) (e.g. Figs 4J; 15A; 29B; 19F; Hu 1971, pl. 15, figs 18–20); long occipital spine (1) (Figs 6A–C; 19J–L).
- 3. Occipital ring length: short (0) (e.g. Figs 4A, N; 23A); extended (1) (Fig. 26A, F, H, M)
- Fixigena: flat to weakly inflated (0) (Figs 4A–C; 8A–C; 19E, G, L; 29A–I); strongly upsloping in larger holaspid (1) (Figs 15B, N; 16B, F).
- 5. Bacculae in large holaspids: absent (0) (e.g. Palmer 1965, pl. 4, fig. 8); present (1) (e.g. Fig. 19C–E, J, L). A reviewer raised the possibility that the presence of bacculae in trilobites might be linked with cranidial effacement. However, in such groups as Nepeidae, bacculae are associated with wellfurrowed cranidia (e.g. see Paterson 2005), so character linkage is unlikely.
- Palpebral lobe size: short, < 33% of preoccipital glabellar length (0) (e.g. Palmer 1965, pl. 4, fig. 8); > 33%, < 50% of preoccipital glabellar length (1) (e.g. Figs 14A, G; 19C, I, J; 27A; 29A–I); very long, equal to almost 60% of preoccipital glabellar length (2) (e.g. Wilson 1951, pl. 94, figs 14, 18, 20, 21).
- Palpebral lobe position: anterior, centred slightly behind intersection of S2 furrow and lateral glabellar margin (0) (e.g. Palmer 1965, pl. 4, fig. 8; unpublished specimens from the Orr Formation, Utah); intermediate, centred slightly in front of intersection of S1 furrow and lateral glabellar margin (1) (e.g. Kurtz 1975, pl. 3, figs 7–12); posterior, centred behind intersection of S1 furrow and lateral glabellar margin (2) (e.g. Figs 14A, G; F; 19I, J; 23A; 29B).
- Palpebral lobe shape: simple flap, upturned (0) (e.g. Palmer 1965, pl. 4, fig. 8); arcuate, nearly flat band (1) (e.g. Figs 14A–C, G; 15L, N; 19C, E, J, L; 27A–C; 29A–I)
- Palpebral furrow: shallow, nearly straight groove (0) (e.g. Palmer 1965, pl. 4, fig. 8); firmly impressed furrow on both external surface and internal mould (1) (e.g. Fig. 12C, D).
- Frontal area length: long, occupying about 30% or more of cranidial length (0) (e.g. Palmer 1965, pl. 4, fig. 8; Figs 6A–C, 14A, 16A, 19A, 23E, 26A); short, less than 20% of cranidial length (1) (e.g. Figs 27A, 29B).
- Preglabellar field length: long, exceeds length of occipital ring (0) (e.g. Palmer, 1965 pl. 4, fig. 8; Figs 16A, 16D, 19A); short, less than length of occipital ring, but more than half of length (1) (e.g. Fig. 4A–C); very short, less than one-third of length of occipital ring (2) (Figs 8A–C, 14A, 23A, 29B). In all cases, measurement of the length of

the occipital ring excludes the occipital spine, where present.

- Anterior border length: short, about 20% of preoccipital glabellar length (0) (e.g. Palmer 1965, pl. 4, fig. 8; Kurtz 1975, pl. 3, figs 7–12); long, about 30–40% of preoccipital glabellar length (1) (Figs 15P, 16A, D); very long, at least 50% of preoccipital glabellar length (2) (Figs 6A–C, 14A, L, K).
- 13. Anterior border lateral profile: nearly flat or gently sloping (0) (e.g. Palmer 1965, pl. 4, fig. 8; Fig. 16C, E, K); concave slope that flattens anterorly (1) (e.g. Figs 22A–C, 25D); slopes upward anteriorly to reach a level opposite or above anterior end of glabella (2) (e.g. Fig. 14C, J, M); flexed downward anteriorly (3) (e.g. Fig. 4A–C); slopes steeply and evenly forward, with no change in slope between border and preglabellar field (4) (e.g. Fig. 26C). Lateral profile is in part a function of length, but the 'very long border' state [12 (2)] encompases species with the four profile states, i.e. [13(1); 13(2); 13(3), 13(4)].
- 14. Spatulate to spinose projection of anterior border: absent (0); present (1) (e.g. Figs 4A, H, 14A, L).
- 15. Shape of border projection: evenly tapered forward (1) (e.g. Fig. 4A); subparallel sides to slightly expanded anteriorly (2) (Figs 11F–H, 14A, L).
- Dorsal surface of anterior border projection: flat (1) (Fig. 11F–H); concave (2) (e.g. Fig. 14A, L).
- 17. Minimum width (tr.) of projection of anterior border behind point at which sutures begin to converge sharply forward along anterior cranidial margin: subequal to glabellar width (1) (e.g. Fig. 10A–F); appreciably narrower than glabellar width (2) (e.g. Figs 11A–G, 14A, L).
- Exoskeleton curved under anterior border to form 'pocket': absent (0); present (1) (e.g. Figs 8A–C, K, L, 9G)
- Course of anterior branches of facial suture: divergent between palpebral lobe and anterior border furrow, so that pre-ocular area of fixigena expands forward (0) (e.g. Palmer 1965, pl. 4, fig. 8; Fig. 23A, E); bowed gently outward between palpebral lobe and anterior border furrow, so that there is no net increase in the width of pre-palpebral area (1) (e.g. Figs 4A–C, 7A–C, 14A, L, K). Note that state 1 does not covary with eye size and position.
- 20. Sculpture: granules, and tubercles, if present, poorly defined or not expressed on internal mould (0) (Palmer 1965, pl. 4, fig. 8; Fig. 8A–K); granules and tubercles, tubercles well defined on the internal mould (1) (e.g. Fig. 29A–F); smooth external surface and mould (2) (e.g. Fig. 19C–E, J–L).

Librigena

- 21. Genal spine: curved gently backwards and extends curvature of lateral margin of librigena without interruption (0) (e.g. Palmer 1965, pl. 4, fig. 15); initially curves outward and backward, with interruption of the curvature of lateral margin of librigena (1) (e.g. Figs 14D–F, 16L, 20A, B).
- 22. Inflation of lateral border at intersection of genal spine: absent (0); present (1) (e.g. Fig. 14D–F).
- 23. Accessory rim along lateral border of librigena: absent (0); present (1) (Fig. 14D–F).

Pygidia

- Segments in pygidial axis: 0, four, including two in terminal piece (0) (e.g. Palmer 1965, pl. 4, fig. 10; Figs 12K, L, 15E, 20C); five (1) (e.g. Fig. 21H)
- 25. Axis width: relatively short and wide (0) (e.g. Palmer 1965, pl. 4, fig. 10; Figs 12K, L, 15E, 20C); relatively long and narrow (1) (e.g. Figs 21H, I, 25K–O).
- Pygidial border: flat to downsloping (0) (e.g. Palmer 1965, pl. 4, fig. 10; Figs 12K, L, 15E, 20C); concave (1) (e.g. Figs 21H, I, 25K–O).