

The Late Cambrian (Steptoean; Furongian) trilobite *Pseudokingstonia* Palmer, 1965 in North America

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Abstract: The poorly known Late Cambrian (Steptoean; Furongian) genus *Pseudokingstonia* Palmer is revised using new material from the type area in west-central Utah. Previously undocumented features of pygidial morphology, including patterns of segmentation of the axis and pleural fields, and articulating flanges on the anterior margin, confirm that the genus is closely related to the dameselloidean *Cheilocephalus* Berkey and that together they constitute the family Cheilocephalidae Shaw. *Pseudokingstonia* is diagnosed by a high degree of cranidial and, especially, pygidial effacement, an exceedingly short anterior border on the cranidium, and steeply sloping pygidial borders. In addition to the Great Basin of Nevada and Utah, the genus is also known from Alberta, Arkansas, and Pennsylvania, and all occurrences are confined to the lower half of the late Steptoean *Elvinia* Zone.

Résumé : *Pseudokingstonia* Palmer, un genre méconnu du Cambrien tardif (Steptoéen ; Furongien), est revu à la lumière de nouveau matériel provenant de la région type, dans le centre-ouest de l'Utah. Des caractères de la morphologie pygidiale qui n'avaient pas encore été documentés, dont les motifs de segmentation de l'axis et des champs pleuraux et des rebords articulaires sur la marge antérieure, confirment qu'un lien étroit existe entre le dameselloïdéen *Cheilocephalus* Berkey et *Pseudokingstonia* Palmer, et que ces deux genres constituent la famille Cheilocephalidae Shaw. Le diagnostic de *Pseudokingstonia* repose sur un degré élevé d'effacement cranidial et, en particulier, pygidial, une bordure antérieure excessivement courte sur le cranidium et des bordures pygidiales fortement inclinées. Outre dans le Grand bassin du Nevada et de l'Utah, ce genre a également été recensé en Alberta, en Arkansas et en Pennsylvanie, et tous les cas sont confinés à la moitié inférieure de la zone à *Elvinia* du Steptoéen tardif.

[Traduit par la Rédaction]

Introduction

We recently published a revision of two genera, *Cheilocephalus* Berkey, 1898, and *Oligometopus* Resser, 1936, that were assigned to Cheilocephalidae Shaw, 1956 (Westrop et al. 2008). We concluded that these genera were not closely related and that the latter was allied with an entirely different family and superfamily (Leiostegidae Bradley, 1925 and Leiostegioidea Bradley). We also presented evidence that supported a relationship between *Cheilocephalus* and Superfamily Dameselloidea Kobayashi, 1935. In Gondwana, Dameselloidea disappeared in an extinction at the base of the Furongian Series, and the occurrence of *Cheilocephalus* in the younger Steptoean stage of Laurentia records survival of the superfamily in that continent.

One other Laurentian genus, *Pseudokingstonia* Palmer, 1965, has been included in the Cheilocephalidae by previous authors (e.g., Palmer 1965; Westrop 1986; Hohensee and Stitt

1989). *Pseudokingstonia* is poorly known. Palmer's (1965, p. 32, pl. 1, figs. 16, 18, 19) original description was based on two cranidia and one pygidium from Utah and, since then, subsequent records in other regions have added only five additional figured sclerites (Westrop 1986, pl. 9, fig. 1; Hohensee and Stitt 1989, fig. 5.4–5.6; Westrop et al. 2007, figs. 8B, 8E–8F). Consequently, we were unable to produce a definitive evaluation of the genus in our previous paper, although we tentatively accepted it as a member of the Cheilocephalidae. In June 2008, one of us (SRW) resampled a section through the Corset Spring Shale Member of the Orr Formation at Orr Ridge, Utah (see Westrop and Adrain 2007 for locality information), in the type area of *P. exotica* in the northern House Range. *Pseudokingstonia* proved to be relatively common, and our new material (Figs. 1, 2) allows us to revise the genus and demonstrate that it is indeed closely related to *Cheilocephalus*. We also provide an evaluation of the biostratigraphic significance of the genus.

Biostratigraphy of *Pseudokingstonia*

Palmer's types (1965, pl. 1, figs. 16, 18, 19) of *Pseudokingstonia exotica* are from a single collection (United States Geological Survey (USGS) 2977-CO) at "Granite Canyon" in the northern House Range, Utah. No information was provided on the associated fauna, if any, although Palmer indicated that the specimens were from the *Elvinia* Zone. Other occurrences mentioned by Palmer (1965, p. 32) are in his Cherry Creek section in the Cherry Creek Range

Received 4 February 2009. Accepted 4 June 2009. Published on the NRC Research Press Web site at cjes.nrc.ca on 9 July 2009.

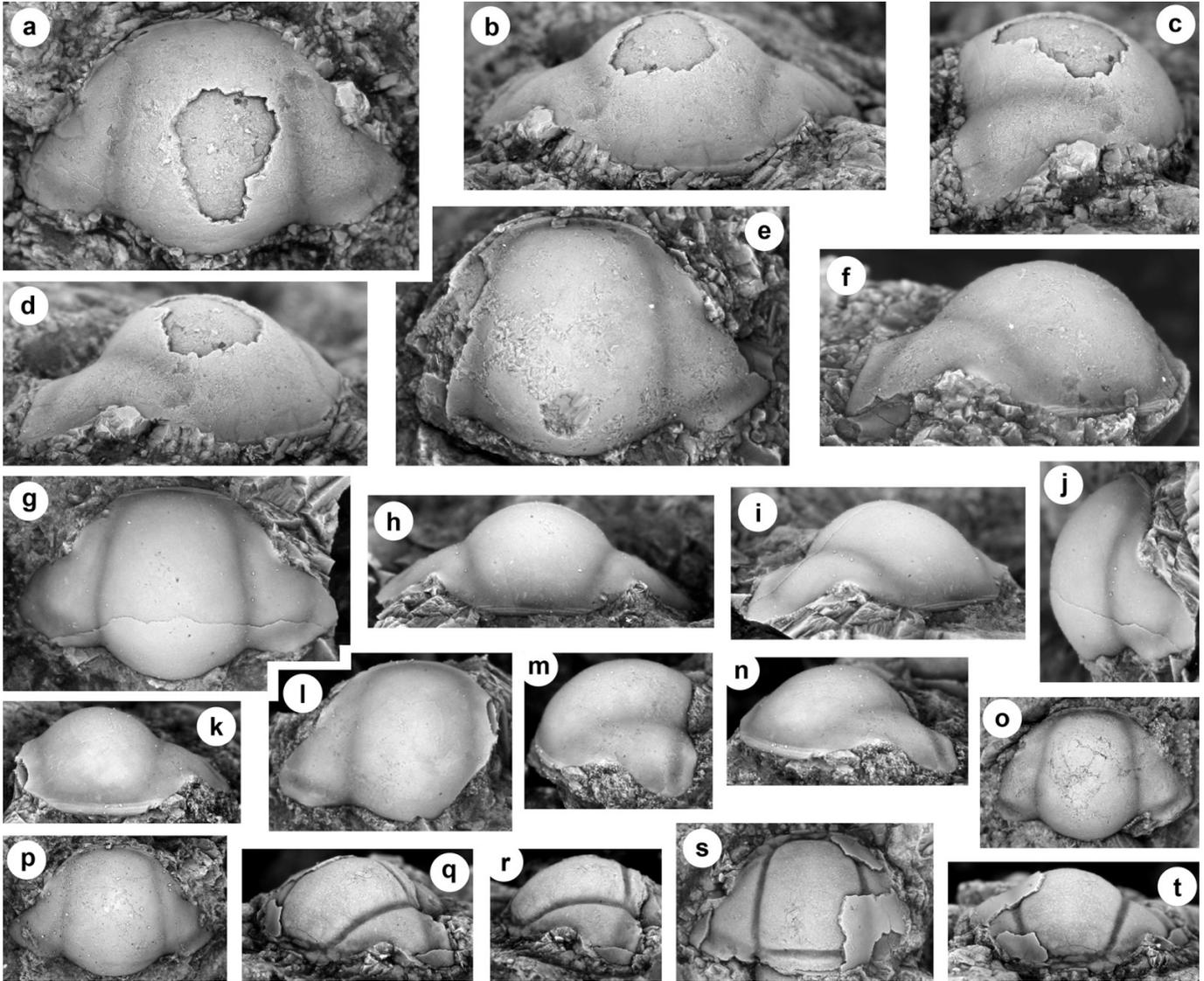
Paper handled by Associate Editor J. Jin.

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Fig. 1. *Pseudokingstonia exotica* Palmer, 1965. All from the Corset Spring Shale Member, Orr Formation, Orr Ridge, northern House Range, Millard County, Utah, except *a–d* (Dunderberg Formation, McGill, White Pine County, Nevada). All sclerites are cranidia and are testate, except where indicated. All $\times 9$. (*a–d*) OU 12468 (partly exfoliated), dorsal, anterior, lateral and anterior-oblique views, collection MG2 69–70.5. (*e, f*) OU 12469, dorsal and anterior-oblique views, collection ORR 7.5T. (*g–j*) OU 12470, dorsal, anterior, anterior-oblique and lateral views, collection ORR 14.8–15. (*k–n*) OU 12471, anterior, dorsal, lateral, and anterior-oblique views, collection ORR 14.8–15. (*o*) OU 12472, dorsal view, collection ORR 7.5T. (*p*) OU 12473, dorsal view, collection ORR 7.5T. (*q–t*) OU 12474 (mostly exfoliated), anterior-oblique, lateral, dorsal and anterior views.

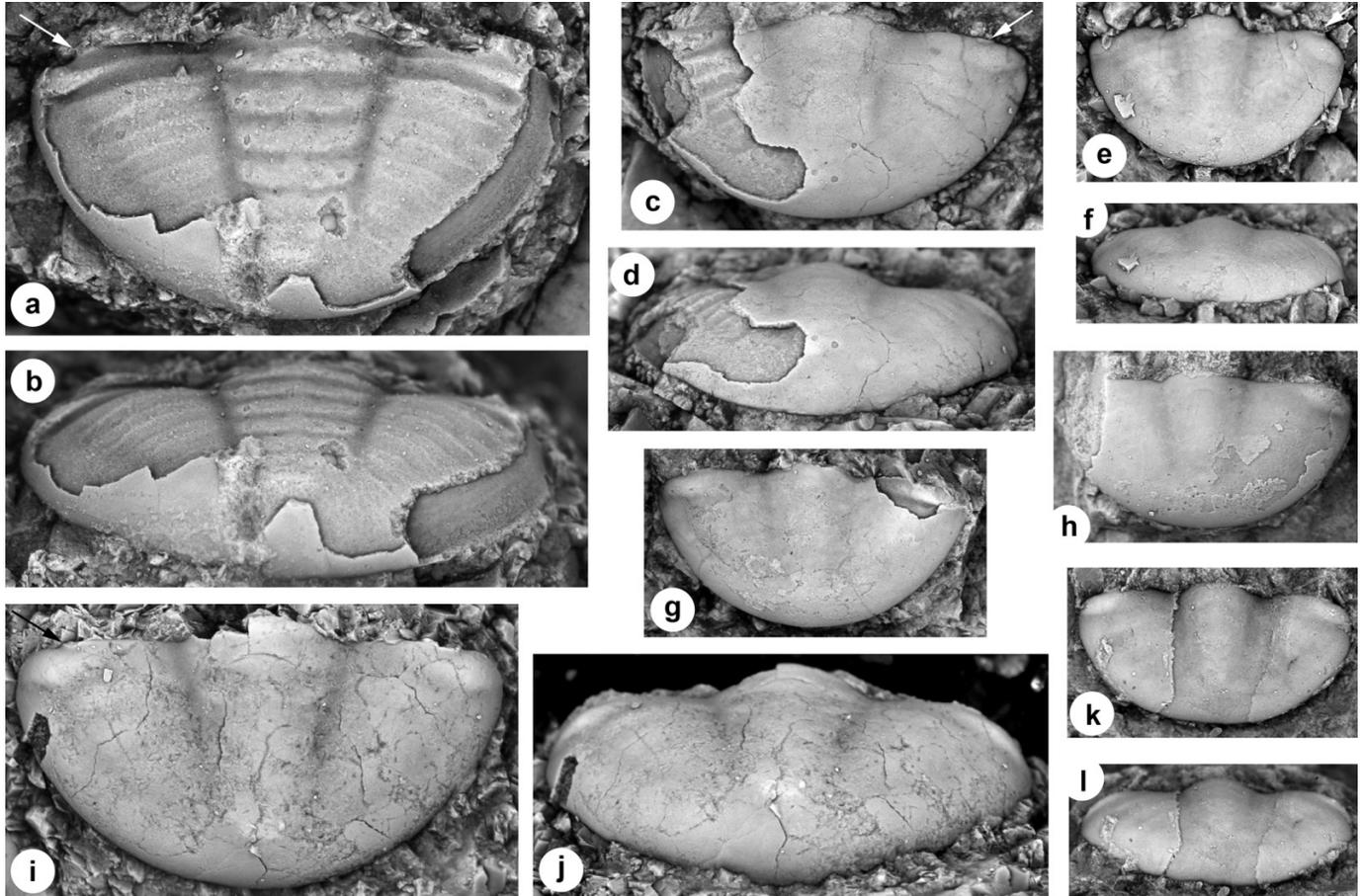


and in the Schell Creek Range of Nevada, and both involve unfigured material. The latter locality is undocumented, and *Pseudokingstonia* is not indicated as occurring at Bastian Peak, the only site in the Schell Creek Range for which Palmer (1965, pl. 22) provided collection and stratigraphic range data. At Cherry Creek, *P. exotica* is reported from the base of the Barton Canyon Limestone (collection 2557-CO), where it occurs with *Kindbladia* Frederickson, 1949, *Bynumina* Resser, 1942, *Dellea* Wilson, 1949, and *Cheilocephalus*. This assemblage is correlative with the informal lower division of the *Elvinia* Zone (Westrop et al. 2007), which is characterized by *Kindbladia*, among other genera.

One of our new collections (MG 69–70.5) was made in the upper Dunderberg Formation at Palmer's (1965, p. 94)

McGill section in White Pine County, Nevada, 1.5 m below the base of the Barton Canyon Limestone. The associated fauna includes *Irvingella* cf. *I. angustilimbatus* Kobayashi, 1938, *Housia* cf. *H. ovata* Palmer, 1960, *Pseudosaratogia* Wilson, 1951, *Pulchricapitus* Kurtz, 1975, *Cliffia* Wilson, 1949, *Dellea* and *Kindbladia*, and also falls into the lower division of the *Elvinia* Zone. Two other collections are from the Corset Spring Shale Member of the Orr Formation at Orr Ridge, northern House Range, Utah, a locality that is very close to "Granite Canyon" (see later in the text). The lower of these collections (ORR 7.5T) was made from loose blocks of bioclastic limestone 7.5 m above the base of the member. In addition to *P. exotica*, this collection has yielded *Bynumina globosa* (Walcott, 1884), *Dellea*, *Kindbladia*,

Fig. 2. *Pseudokingstonia exotica* Palmer, 1965. All from the Corset Spring Shale Member, Orr Formation, Orr Ridge, northern House Range, Millard County, Utah. All sclerites are pygidia and are testate, except where indicated. Arrows show articulating flanges. All $\times 9$. (a, b) OU 12475 (mostly exfoliated), anterior and posterior views, collection ORR 7.5T. (c, d) OU 12476 (partly exfoliated), anterior and posterior views, collection ORR 7.5T. (e, f) OU 12477, anterior and posterior views, collection ORR 7.5T. (g) OU 12478, dorsal view, collection ORR 7.5T. (h) OU 12479, dorsal view, collection ORR 14.8–15. (i, j) OU 12480, dorsal and posterior views, collection ORR 7.5T. (k, l) OU 12481, dorsal and posterior views, collection ORR 14.8–15.



Pseudosaratogia, and *Deckera* Frederickson, 1949. A little less than 8 m higher in the section, collection ORR 14.8–15 contains *P. exotica* in association with *Housia* cf. *H. ovata*, *Bynumina globosa*, and species of *Dellea*, *Kindbladia*, and *Pseudosaratogia*. These assemblages indicate that the interval that yields *P. exotica* at Orr Ridge overlaps with occurrences in Nevada, and all lie within the lower division of the *Elvinia* Zone.

In addition to Nevada and Utah, *Pseudokingstonia* has also been recorded from Alberta, Arkansas, and Pennsylvania. In Alberta, the genus is represented by a single pygidium in the upper Lyell Formation at Chaba Creek, Jasper National Park. It was assigned to *P. exotica* by Westrop (1986, pl. 29, fig. 1), but this identification is questionable in the absence of other sclerites. This specimen occurs at a sparsely fossiliferous horizon that also yields *Camaraspis* Ulrich and Resser (in Ulrich, 1924), *Drabia* Wilson, 1951, *Housia*, and *Pulchricapitus*. The assemblage is assignable to the *Elvinia* Zone and, as it occurs about 20 m below the first appearance of *Kindbladia*, it may represent the oldest known occurrence of the genus. Hohensee and Stitt (1989) reported the presence of *Pseudokingstonia* in the Collier Shale of Arkansas as part of diverse lower *Elvinia* faunas that also in-

cluded *Bynumina*, *Cliffia*, *Dellea*, *Drabia*, *Elvinia*, *Housia*, *Kindbladia*, *Pseudosaratogia*, and *Pulchricapitus*, among others. Finally, a single pygidium that was assigned to *Bynumina terrenda* by Wilson (1951) is the only record of *Pseudokingstonia* in eastern North America (Westrop et al. 2007, p. 362, figs. 8B, 8E, 8F). It occurs in strata of the Gatesburg Formation that belong to the lower division of the *Elvinia* Zone (Westrop et al. 2007) at Wilson's Drab section, south-central Pennsylvania (Wilson 1951, p. 619; collection 47-3w.22).

Although *Pseudokingstonia* is a rare taxon in the Steptoean succession of North America, our new data show that it is locally common in the Great Basin. Here, all occurrences are confined to the lower division of the *Elvinia* Zone, and all records in other regions are of equivalent ages. Thus, the genus has biostratigraphic significance and will likely contribute to a refined zonal scheme for the upper Steptoean.

Systematic paleontology

Figured material is housed at the Oklahoma Museum of Natural History, University of Oklahoma (OU). Localities are indicated by the abbreviations: MG, McGill, White Pine

County, Nevada (Palmer 1965, p. 94); ORR, Orr Ridge, Millard County, Utah. Proportions expressed in percentages in descriptions and diagnoses are means, with numbers in parentheses indicating the range of values (% symbols not shown). All measurements were made on digital images to the nearest tenth of a millimetre using the Measure Tool of Adobe Photoshop™.

Superfamily Dameselloidea Kobayashi, 1935
Family Cheilocephalidae Shaw, 1956

DIAGNOSIS: See Westrop et al. (2008, p. 726).

DISCUSSION: Previously undocumented features of the pygidial anatomy demonstrate that *Pseudokingstonia* is related to *Cheilocephalus*. The anterior margin possesses small articulating flanges (Figs. 2a, 2c, 2e, 2i), although compared with the same features on *Cheilocephalus* (Westrop et al. 2008, figs. 3a, 4a, 4d, 4i, 7b), they are mere vestiges on the more strongly effaced dorsal surface. The pygidial segmentation is visible only on internal molds (Figs. 2a, 2b). Although the axis is less convex than in *Cheilocephalus*, the number and relative sizes of the axial rings are closely comparable, and the pattern of segmentation of the pleural field is identical (e.g., compare Fig. 2a with Westrop et al. 2008, fig. 2e). One obvious difference between *Pseudokingstonia* and *Cheilocephalus* lies in the expression of the articulating flange on the posterior margin of the cranidium. Uniquely among dameselloideans, this feature is well defined and broad (transverse (tr.)) in *Cheilocephalus* but is completely effaced in *Pseudokingstonia*. In both genera, the posterior margin is curved abruptly forward and downward at the fulcrum.

The new material also confirms the diagnosis of the Cheilocephalidae provided by Westrop et al. (2008, p. 726). Effacement of glabellar furrows is shared by both *Cheilocephalus* and *Pseudokingstonia* (Fig. 1) and stands in contrast to the furrowed glabellae in other dameselloideans (e.g., Peng et al. 2004, pl. 27, figs. 1–5, pl. 31, figs. 1, 4, 5, 8, 11, pl. 32, figs. 1–4, pl. 35, figs. 1–12; pl. 38, figs. 7–10). Similarly, the small, anteriorly positioned palpebral lobes of *Cheilocephalus* and *Pseudokingstonia* also depart from the relatively large-eyed condition typical of dameselloideans. The closest similarities lie in species of *Parablackwelderia* Kobayashi, 1942. However, in this genus the palpebral lobes and eyes are on stalks, some of which are remarkably long and elevated far above the glabella (Peng et al. 2008). Finally, the pygidia figured here (Fig. 2) demonstrate that the morphology of the anterior pleural band is identical in *Cheilocephalus* and *Pseudokingstonia*, with the latter differing only in the greater degree of effacement.

Genus *Pseudokingstonia* Palmer, 1965

TYPE SPECIES: *Pseudokingstonia exotica* Palmer, 1965, from the Corset Spring Shale Member of the Orr Formation, northern House Range, Millard County, Utah (by original designation).

DIAGNOSIS: Strongly effaced with glabellar furrows unexpressed on external surface and only SO present on internal mold. Anterior border reduced to very short, wire-like rim. Pygidium with lightly impressed axial furrows but axis and pleural field unfurrowed, except for weak pleural furrow at anterior that shallows adaxially. Internal mold with well-

defined axial ring furrows and shallow pleural and interpleural furrows; border expressed as narrow, unfurrowed region that curves steeply downward. Small articulating flange present on anterior pygidial margin.

DISCUSSION: Comparisons of *Pseudokingstonia* with *Cheilocephalus* (e.g., Westrop et al. 2008) and potential outgroup taxa among the Dameselloidea (e.g., Peng et al. 2004) indicate that the genus can be diagnosed by several apomorphic character states. The extent of effacement of the glabellar and, particularly, pygidial furrows is unique. The anterior border of the cranidium is reduced to an extremely short, wire-like rim. There are a variety of border morphologies among dameselloideans but where reduced in length (e.g., Öpik 1967, pl. 48, figs. 1, 5, 6; Peng et al. 2004, pl. 30, fig. 6, pl. 41, fig. 4, pl. 44, figs. 5, 6), they are upturned, ridge-like and separated from the glabella by a well-incised furrow. The pygidial border of *Pseudokingstonia* slopes steeply downward (Fig. 2b) and contrasts with the concave borders of *Cheilocephalus* (e.g., Westrop et al. 2008, figs. 4b, 4c, 4e, 4f, 4j, figs. 7a, 7c, 7e, 7g). Other dameselloideans are also characterized by concave to flat borders, regardless of whether the pygidial margin is spinose (e.g., Peng et al. 2004, pl. 29, figs. 12, 13, pl. 31, figs. 1–6, pl. 43, figs. 3–6) or entire (e.g., Peng et al. 2004, pl. 32, fig. 7, pl. 33, fig. 6), indicating that the condition in *Cheilocephalus* is the plesiomorphic state.

Pseudokingstonia has been reported from the Cambrian (Mindyallan; Guzhangian) Spurs Formation, northern Victoria Land, Antarctica (Cooper et al. 1990, 1996). The figured cranidia (Cooper et al. 1990, figs. 7c, 7e, 7i) are somewhat deformed, but it is still evident that they are misidentified. Similarities between these cranidia and *Pseudokingstonia* are limited to the short rim-like anterior border. The glabella of the former is subcircular in outline, with maximum width at S1 furrow. The occipital furrow is shallow but clearly defined and bifurcates abaxially, and this contrasts with the nearly transverse furrow of *Pseudokingstonia*, which is expressed only on the internal mold (e.g., Fig. 1s). In addition, the palpebral lobes are larger, more posteriorly positioned so that the posterior area of the fixigena is relatively short (exsagittal (exsag.)). Finally, the posterior border furrow is nearly transverse, whereas this furrow is curved forward abaxially in *Pseudokingstonia* (e.g., Fig. 1g). The identity of the Antarctic material is uncertain, although affinity with Family Catillicephalidae Raymond, 1938 is possible, as suggested by Cooper et al. (1990).

Finally, the new material confirms Westrop et al.'s (2007, p. 362) suggestion that the paratype pygidium of *Bynumina terrenda* Wilson, 1951 (Westrop et al. 2007, figs. 8B, 8E, 8F) is better assigned to *Pseudokingstonia*. This specimen is closely comparable to the pygidia illustrated here (Fig. 2), differing only in displaying a very faint border furrow on the dorsal surface.

Pseudokingstonia exotica Palmer, 1965

Figs. 1, 2

Pseudokingstonia exotica Palmer, 1965, p. 32, pl. 1, figs. 16, 18, 19.

?*Pseudokingstonia exotica* Palmer; Westrop, 1986, p. 68, pl. 29, fig. 1.

?*Pseudokingstonia exotica* Palmer; Hart et al. 1987, fig. 3F.

?*Pseudokingstonia exotica* Palmer; Hohensee and Stitt, 1989, p. 864, figs. 5.4–5.6.

HOLOTYPE: A cranidium (USNM 141519) from the Corset Spring Shale, northern House Range, Millard County, Utah, illustrated by Palmer (1965, pl. 1, fig. 16).

DISGNOSIS: As for genus.

DESCRIPTION: Cranidium subtrapezoidal in outline with gently rounded anterior margin, length 61% (58–64) of maximum width across posterior area of fixigena; strongly convex in anterior and lateral views. Axial and preglabellar furrows shallow but clearly defined on external surface; expressed as more firmly impressed grooves on internal molds (Figs. 1*q–1t*). Glabella very long, accounting for almost all (97%; 95–99) of cranial length, and wide, with width at posterior end of axial furrows equal to 47% (44–50) of maximum cranial width; tapers gently forward, with gently rounded anterior margin (Fig. 1*s*) and posterior margin curved backward; strongly arched, with lateral profile convex, reaching maximum elevation at mid-length and descending steeply anteriorly. External surface of glabella unfurrowed apart from barely perceptible SO furrow on some smaller individuals (Fig. 1*p*). SO well-incised and nearly transverse on internal molds (Fig. 1*s*); LO occupies about 16% of glabellar length. Anterior border is exceedingly short rim. Palpebral area narrow, equal to 26% (23–30) of maximum glabellar width, and flexed downward. Palpebral lobe small, length equal to 14% (11–18) of cranial length, and anteriorly positioned, centered opposite point 69% (67–73) of glabellar length from posterior margin of glabellar margin; palpebral furrow obsolete so palpebral lobe differentiated from fixigena only by flattening of slope. Palpebral ridge not expressed on external surface but present on internal mold; weakly convex and trends obliquely forward and inward to reach axial furrow near anterior end of glabella (Figs. 1*q–1t*). Anterior branches of facial suture converge forward before swinging abruptly inward along anterior cranial margin; posterior branches initially strongly divergent backward but become nearly parallel at posterior border furrow. Posterior area of fixigena broad (tr.) with maximum width 220% (198–238) of width of palpebral area; maximum length (exsag.) of posterolateral projection immediately behind palpebral lobe is equal to 46% (45–50) of cranial length (sagittal (sag.)). Posterior margin of posterior area of fixigena transverse near axial furrow but curves forward sharply and is flexed more steeply downward at fulcrum. Posterior border and border furrow roughly parallel margin of posterior area; border furrow is lightly impressed on external surface and somewhat deeper on internal mold; border is gently convex. External surface of cranidium is smooth apart from sculpture of terrace ridges on anterior border; internal mold is entirely smooth.

Pygidium convex with steeply sloping flanks, subsemicircular in outline, length equal to 55% (53–57) of maximum pygidial width. Small articulating flange evident on anterior pygidial margin (Figs. 2*c*, 2*e*, 2*i*) and is somewhat better defined on internal mold (Fig. 2*a*). Axis weakly arched, barely raised above pleural field; outlined by shallow axial furrows that are expressed more clearly on internal

mold. It occupies 82% (80–86) of pygidial length and 31% (28–35) of pygidial width at anterior; tapers backward so that width at posterior is 56% (55–57) of width at anterior. Axial rings and ring furrows obsolete on dorsal surface but are expressed on internal mold (Figs. 2*a*, 2*b*). Axis is composed of seven segments, with posteriormost pair combined into terminal piece that is crossed medially by barely perceptible furrow. Five transverse axial ring furrows, posteriormost expressed as finely etched groove but others more firmly impressed, define five transverse axial rings that are subequal in length; each ring accounts for slightly less than 15% of axis length. Articulating half-ring is narrow, arcuate band bounded posteriorly by well-defined articulating furrow. Pleural field gently inflated, with only single pleural band evident on external surface at anterior corner of pygidium; abaxially, posterior margin of band curves forward to produce bluntly pointed outline (e.g., Fig. 2*c*). Pleural and interpleural furrows are expressed on internal mold, as is very shallow border furrow that defines inner edge of down-sloping, unfurrowed border that maintains an even width along the lateral and posterior margins. Behind well-defined anterior pleural band, pleural and interpleural furrows are straight and oblique and lightly impressed on surface of mold; pleural furrows are roughly twice length (exsag.) of interpleural furrows. External surface of entire pygidium is smooth; internal mold is smooth aside from very faint pitting on pleural field.

DISCUSSION: Palmer's (1965) types came from USGS collection 2977-CO, which he collected on the south side of "Granite Canyon" in the northern House Range in 1959. Unfortunately, this name has been abandoned and does not appear on any topographic map. According to Palmer (personal communication, 2009) Granite Canyon is "the next major canyon south of Little Horse Canyon". This places the type locality somewhere on the same spur ascending from Orr Ridge as our ORR section (Westrop and Adrain 2007, fig. 1*a*). Our specimens were likely collected no more than a few hundred metres along strike from Palmer's types. There are no discernible differences between our material (Figs. 1, 2) and the latter (Palmer 1965, pl. 1, figs. 16, 18, 19).

Hohensee and Stitt (1989) assigned two cranidia and a pygidium from the Collier Shale of Arkansas to *P. exotica*. Detailed comparisons with our material and Palmer's types are hindered by the small sizes of these sclerites. However, the preocular fields of both cranidia (Hohensee and Stitt 1989, figs. 5.4, 5.5) are wider than those of any of our specimens, and the smaller of the two (fig. 5.5) has a well-defined occipital ring. The pygidium (Hohensee and Stitt 1989, fig. 5.6) is less rounded in outline than any of ours (Fig. 2) or Palmer's (1965, pl. 1, fig. 19) and, judging from the stereo image, it is less convex. The significance of these various differences is beyond evaluation in a sample of only three figured sclerites, and Stitt and Hohensee's identification is, therefore, questionable. Similarly, the species identities of single pygidia from Alberta (Westrop 1986, pl. 29, fig. 1) and Pennsylvania (Westrop et al. 2007, figs. 8*b*, 8*e*, 8*f*) are uncertain.

Acknowledgements

This research was supported by National Science Foundation Grant EAR 0308685 to Adrain and Westrop. Roger

Burkhalter assisted in fieldwork in Utah and in processing of samples in the laboratory. Pete Palmer and Mark Webster helped identify the location of the Granite Canyon site. We thank reviewers Bruce Lieberman and Brian Pratt, and Associate Editor Jisuo Jin for helpful comments on an earlier draft of the manuscript.

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