Classification of the Late Cambrian (Steptoean) trilobite genera *Cheilocephalus* Berkey, 1898 and *Oligometopus* Resser, 1936 from Laurentia

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Abstract: All recent work has assigned the genera *Cheilocephalus* Berkey, 1898 and *Oligometopus* Resser, 1936 to the family Cheilocephalidae Shaw, 1956, a small group of largely Laurentian trilobites from the Late Cambrian Steptoean Stage. New data from Nevada and Newfoundland indicate that the Cheilocephalidae is polyphyletic and that *Cheilocephalus* and *Oligometopus* are allied with different superfamilies. The Cheilocephalidae, which includes *Cheilocephalus* and *Pseudokingstonia* Palmer, 1965, is assigned to the Dameselloidea Kobayashi, 1935, and a pygidium from the Cow Head Group of Newfoundland indicates that *Cheilocephalus* first appears in the late Marjuman. The Dameselloidea disappeared on other continents at an extinction interval at the end of the Marjuman, but *Cheilocephalus* survived and underwent modest diversification in Laurentia in the succeeding Steptoean Stage. *Oligometopus* is transferred to the leiostegioidean family Leiostegiidae Bradley, 1925. The genus shows closest affinities with such Gondwanan genera as *Idamea* Whitehouse, 1939, and its appearance in mid-Steptoean strata records immigration of the Leiostegoidea into shelf-margin environments of Laurentia.

Résumé : Tous les travaux récents affectent les genres *Cheilocephalus* Berkey, 1898 et *Oligometopus* Resser, 1936 à la famille des Cheilocéphalidés Shaw, 1956, un petit groupe de trilobites principalement laurentiens de l'étage steptoéen du Cambrien tardif. De nouvelles données issues du Nevada et de Terre-Neuve indiquent que les Cheilocéphalidés sont polyphylétiques et que *Cheilocephalus* et *Oligometopus* sont alliés à différentes super-familles. Les Cheilocéphalidés, qui comprennend *Cheilocephalus* et *Pseudokingstonia* Palmer, 1965, sont affectés aux Dameselloïdés Kobayashi, 1935, et un pygidium provenant du groupe de Cow Head de Terre-Neuve indique que *Cheilocephalus* est apparu pour la première fois durant le Marjumien tardif. Les Dameselloïdés ont disparu d'autres continents durant un intervalle d'extinction à la fin du Marjumien, mais *Cheilocephalus* a survécu et n'a subi qu'une diversification limitée en Laurentie durant l'étage suivant du Steptoéen. *Oligometopus* est transféré à la famille léiostegioïdienne Léiostegiidés Bradley, 1925. C'est avec des genres gondwaniens tels qu'*Idamea* Whitehouse, 1939 que ce genre présente les plus étroites affinités, et son apparition dans des strates du Steptoéen moyen témoigne de l'immigration des Léiostegiidés dans des milieux de marges de plate-forme de la Laurentie.

[Traduit par la Rédaction]

Introduction

Cheilocephalus Berkey, 1898, is an uncommon but widespread component of Upper Cambrian (Steptoean) trilobite assemblages of Laurentian North America, with occurrences in the Upper Mississippi Valley (Berkey 1898), Oklahoma, Texas, and Pennsylvania (Resser 1942), Quebec and Newfoundland (Rasetti 1944, this paper), Wyoming (Shaw 1956), Nevada and Utah (Palmer 1960, 1965), Montana (Lochman and Hu 1962*b*), Alaska (Palmer 1968), Missouri (Kurtz 1975), New York (Theokritoff 1984), the Canadian Rocky Mountains (Westrop 1986), Arkansas (Hohensee and Stitt 1989), the Mackenzie Mountains of northern Canada (Pratt 1992), and South Dakota (Stitt and Perfetta 2000). Along with the even less common genera *Oligometopus* Resser, 1936, and *Pseudokingstonia* Palmer, 1965, it has been assigned to the leiostegioidiean Family Cheilocephalidae Shaw, 1956.

New collections from Nevada provide information on poorly known or previously unknown sclerites of *Cheilocephalus* and *Oligometopus* that allow both genera to be evaluated more completely. We present evidence to suggest that the Cheilocephalidae is polyphyletic and that *Cheilocephalus* is allied with the Dameselloidea rather than the Leiostegoidea (e.g., see Westrop 1986). We also document species of *Cheilocephalus* from Newfoundland, including a pygidium that demonstrates that the stratigraphic range of the genus extends down into the upper Marjuman Stage.

Despite some general similarities in glabellar outline and in the absence of a preglabellar field, detailed comparisons

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suggest that *Oligometopus* is not related to *Cheilocephalus*. Rather, it shows strong affinities with coeval genera from Australia, such as *Idamea* Öpik, 1967, and likely belongs to the leiostegioidean family Leiostegiidae Bradley, 1925.

Biostratigraphically, *Cheilocephalus* first appears in the uppermost Marjuman and ranges throughout the Steptoean Stage in Laurentia. Data on the distribution of *Oligometopus* are limited, but all occurrences are in the upper Steptoean Stage (*Dunderbergia* to lower *Elvinia* zones).

Sample localities

Extended discussion of the stratigraphy and sedimentary facies of the study sites is beyond the scope of this paper. The material from the Corset Spring Shale was collected from two bioclastic grainstone to rudstone beds located 18.25 and 18.6 m above the base of the formation at Shingle Pass, Lincoln County, Nevada. Palmer (1965, p. 95) and Westrop et al. (2007) provide summaries of the stratigraphy and faunas. Sclerites from the Emigrant Springs Formation were obtained from a collection that was made 1 m below the top of Member B (Kellogg 1963) at Patterson Pass, Lincoln County, Nevada (see Westrop et al. 2007, fig. 2B for locality information).

Trilobites described from the Cow Head region, western Newfoundland, are part of extensive collections made by C.H. Kindle from boulders in debris flows of the Shallow Bay Formation (Cow Head Group). Kindle (1982) provided an overview of the locality and faunas, and James and Stevens (1986) presented comprehensive documentation of the stratigraphy and sedimentary facies of the Cow Head Group. On the Cow Head Peninsula, samples are from the Downes Point Member at Beachy Cove (boulder CH 20 from bed 5 in the measured section of James and Stevens 1986, fig. 12) and at Point of Head (boulder CH 57 from bed 5 at the base of the measured section of James and Stevens 1986, fig. 12). Boulder HC 202 is from a debris flow exposed on the coast to the west of Hickey Cove (Kindle 1982, fig. 1.2).

Biogeographic and biostratigraphic significance

Over most of Laurentia, species of *Cheilocephalus* enter the succession with other immigrants (e.g., *Aphelaspis* Resser, 1935) at the base of the Steptoean Stage. New data presented here demonstrate that this genus was in fact present as a rare component of Late Marjuman faunas in shallow-water carbonate environments in shelf-margin settings. *Cheilocephalus* was the only dameselloidean trilobite to survive the extinction event at the base of the Steptoean and correlatives in other biogeographic regions. Dameselloideans were eliminated in biogeographic regions that had been major centers of diversity for this clade, including South China, North China, and Gondwana (e.g., Öpik 1967; Peng et al. 2004). Although never numerically abundant in any facies, the genus undergoes a modest diversification in Laurentia during the Steptoean, only to be extinguished in the extinction at the base of the Sunwaptan Stage.

Oligometopus records immigration of the Leiostegioidea from Gondwana and first appears in Laurentia in mid-Steptoean strata (*Dunderbergia* Zone; Palmer 1965, 1968). Like *Cheilocephalus*, the oldest known occurrences of the genus are in shelf-margin carbonate facies (Hillard Limestone of Alaska, Palmer 1968; Shallow Bay Formation, Newfoundland, Kindle 1982).

Systematic paleontology

Figured material is housed in the following repositories: Geological Survey of Canada, Ottawa, Ontario, Canada (GSC); National Museum of Natural History, Washington, D.C., USA (USNM); Oklahoma Museum of Natural History, University of Oklahoma, Norman, Oklahoma, USA (OU); Paleontology Repository, University of Iowa, Iowa City, Iowa, USA (SUI); Yale Peabody Museum of Natural History, New Haven, Connecticut, USA (YPM). Localities are indicated by the following abbreviations: SHP, Shingle Pass, Lincoln County, Nevada; PP, Patterson Pass, Lincoln County, Nevada; CH, Cow Head Penninsula, western Newfoundland; HC, Hickey Cove, western Newfoundland. Collections numbers for locality SHP indicate metres above the base of the Corset Spring Shale; numbers for western Newfoundland refer to individual boulders collected from debris flows and are not indicative of stratigraphic level. 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 Photoshop.

Superfamily Dameselloidea Kobayashi, 1935
Family Cheilocephalidae Shaw, 1956

DIAGNOSIS: Dameselloidea with lateral glabellar furrows barely perceptible to obsolete. Small palpebral lobe located well in front of glabellar mid-length. Thoracic segments with narrow (transverse (tr.)), bluntly rounded spines. Pleural field weakly furrowed or effaced apart from prominent, convex pleural band at anterior; abaxially, posterior margin of band curved forward.

ASSIGNED GENERA: *Cheilocephalus* Berkey, 1898; *Pseudokingstonia* Palmer, 1965

DISCUSSION: Recent assessments of the Cheilocephalidae have proposed an assignment to the Leiostegoidea (e.g., Westrop 1986; Fortey 1997), although Pratt (1992) argued for a relationship with the Kingstoniidae. New information, particularly on the articulation of *Cheilocephalus*, allows a better evaluation of the affinities and content of the family to be made. Both cranidia and pygidia show details of the articulation that have previously unrecognized phylogenetic significance. Palmer (1954, p. 758; see also Palmer 1968, p. 57) described the posterior cranidial margin of *Cheilocephalus* as having a "distinct 'elbow'…. between one-third and two-thirds the total length of the limb from the dorsal furrow" (described in other papers (e.g., Palmer 1965, p. 29) as a "shoulder"), which, as recognized by Taylor et al. (1999, p. 334), is part of the articulation with the anterior end of the thorax. In detail (Figs. 1*a*, 1*d*, 2*a*, 3*i*, 3*j*, 5*f*), there is a narrow flange at the rear of the posterior border that extends from the axial furrow to the fulcrum (the "shoulder" or "elbow"). It expands (exsagittal (exsag.)) distally to form a distinct projection at the fulcrum that is probably the upper surface of a fulcral socket. A similar flange (probably a fulcral process; see also Taylor et al. 1999, p. 334) is

Fig. 1. *Cheilocephalus* cf. *C. brachyops* Palmer, 1965 from the Corset Spring Shale, section SHP, Shingle Pass, south Egan Range, Nevada; all from collection SHP 18.25. (***a, b***) cranidium, OU 12366, (*a*) dorsal and (*b*) anterior views, × 5; flange at arrow in (*a*). (*c*) cranidium, OU 12367, dorsal view, × 9. (***d–f***) cranidium, OU 12368, (*d*) dorsal, (*e*) anterior, and (*f*) lateral views, × 12; flange at arrow in (*d*). (***g–i***) cranidium, OU 12369, (*g*) lateral, (*h*) dorsal, and (*i*) anterior views, × 9. (***j–l***) hypostome, OU 12370, (*j*) posterior, (*k*) lateral, and (*l*) ventral views, × 6.

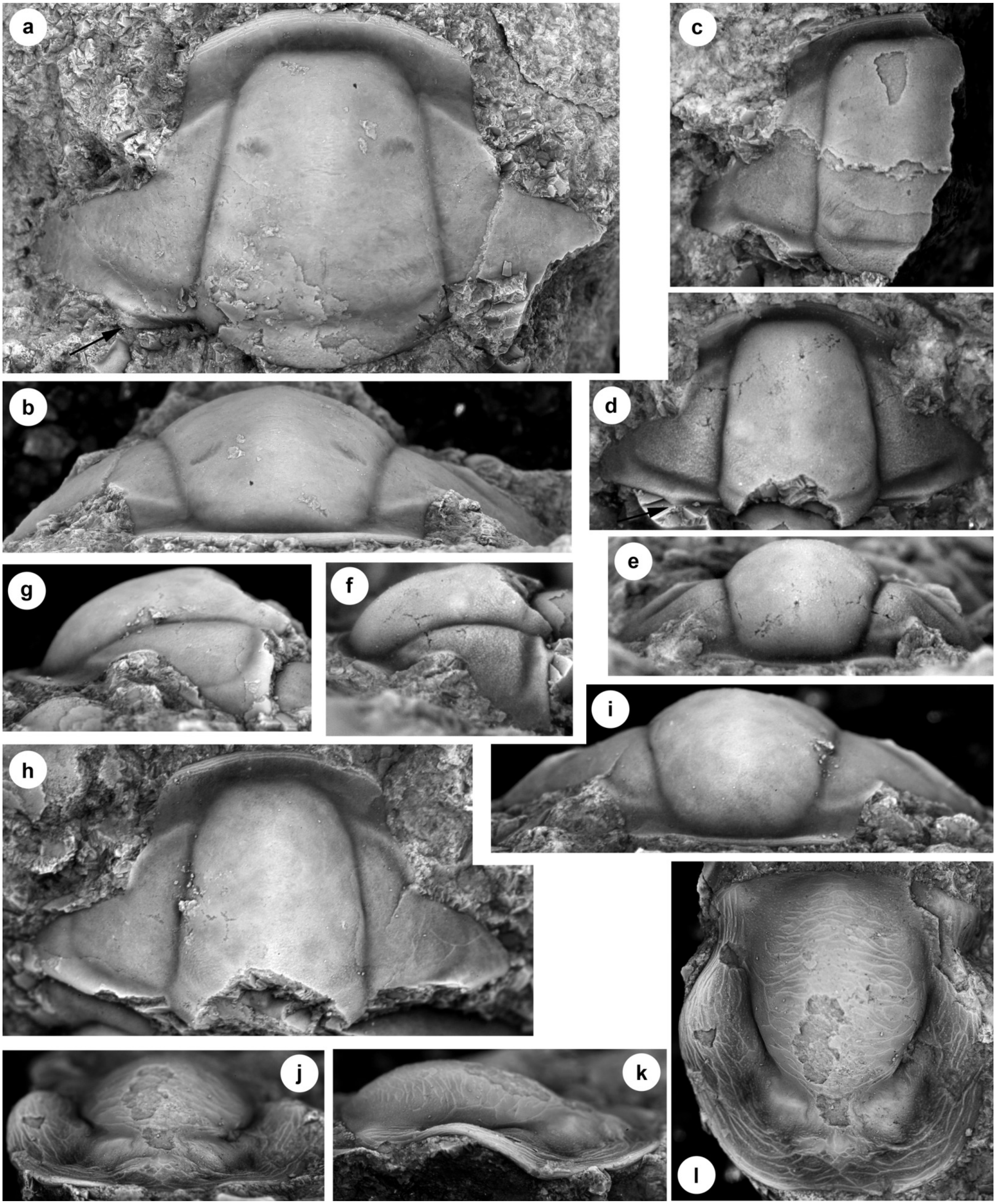
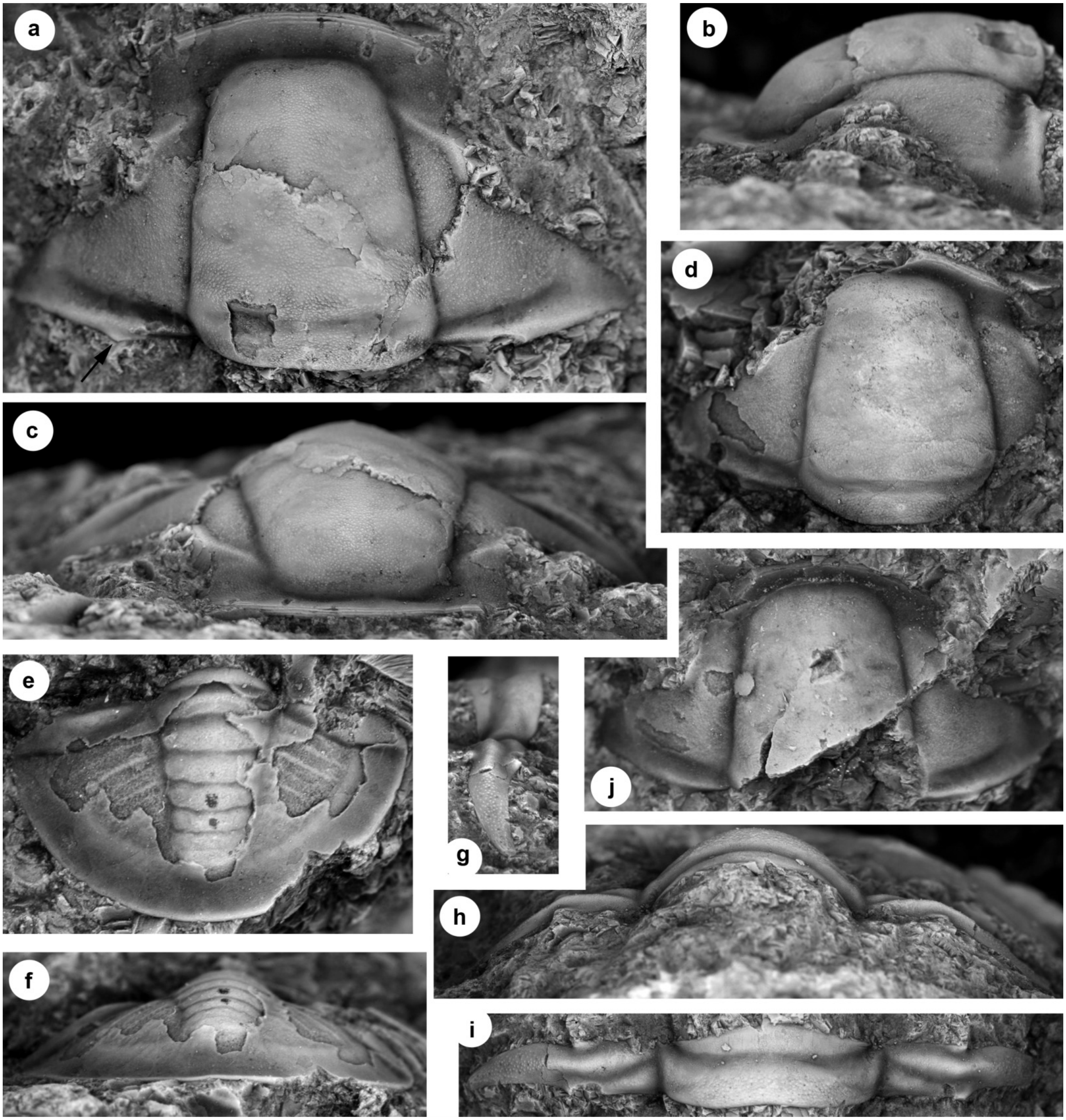


Fig. 2. *Cheilocephalus* cf. *C. brachyops* Palmer, 1965 from the Corset Spring Shale, section SHP, Shingle Pass, south Egan Range, Nevada; all from collection SHP 18.25, except (*b*) and (*c*) (SHP 18.6). (***a–c***) cranidium, OU 12371, (*a*) dorsal, (*b*) anterior, and (*c*) lateral views, × 6; flange at arrow in (*a*). (***d***) cranidium, OU 12372, dorsal view, × 8. (***e, f***) pygidium, OU 12373, (*e*) dorsal and (*f*) posterior views, × 8. (***g–i***) thoracic segment, OU 12374, (*g*) lateral, (*h*) posterior, and (*i*) dorsal views, × 6. (*j*) cranidium, OU 12375, dorsal view, × 9.



present on the anterior margin of the pygidium, and also widens distally to terminate at the fulcrum (Figs. 3*a*, 4*a*, 4*d*, 4*i*, 5*e*). An incomplete exoskeleton (Fig. 5*a*–5*d*) of *C. brevilobus* (Walcott, 1916), from the Nolichucky Formation of Tennessee, displays limited details of the articulation, although a fulcral process is evident on the anterior edge of some segments (Fig. 5*b*). However, an isolated thoracic segment from the Corset Spring Shale (Fig. 2*g*–2*i*) also has a flange and fulcral process on the anterior side and what is presumably the upper surface of a fulcral socket at the posterior side. These various articulating structures are not present in cranidia or pygidia of *Oligometopus* (e.g., Figs. 8*e*, 8*i*, 9*m*, 9*w*, 10*a*, 10*i*, 10*l*, 10*n*), nor do they occur in leiostegiids (e.g., Hintze 1953, pl. 8, figs. 9, 10; Berg and Ross 1959, pl. 21, figs. 1, 3, 4, 6, 10–13; Shergold 1975, pl. 36, figs. 4, 6, 7, pl. 37, figs. 1, 4, 6; Shergold 1982, pl. 13, figs. 6, 7; Wittke 1984, pls. 8, 9; Peng et al. 2004, pl. 25, figs. 3, 7, 9, 13–15, 18). However, similar, pygidial flanges are evident in the Cambrian (Wulingian) genus *Protaitzehoia* Yang, 1978 in Yin and Li 1978 (e.g., Peng et al. 2004, pl. 32, fig. 6; pl. 34, fig. 3), some species of which, like *Cheilocephalus*, have non-spinose lateral and posterior pygidial margins. There has been some debate on the affinities of *Protaitzehoia* in recent years. Yuan and Yin (2001) compared *Protaitzehoia* with *Cheilocephalus* and, following criticism of their classification of the former in the family Ordosiidae Lu 1954 by Peng et al. (2003), they suggested an assignment to the Cheilocephalidae (Yuan and Yin 2003). Peng et al. (2003, 2004) have considered the relationships of *Protaitzehoia* at length, and here we follow them in assigning the genus to the Damesellidae Kobayashi, 1935. Other damesellids with pygidial flanges include *Palaeadotes* Öpik, 1967 (e.g., Zhang and Jell 1987, pl. 105, figs. 1, 2; Peng et al. 2004, pl. 39, fig. 9, pl. 40, fig. 5); and *Paradamesella* Yang, in Zhou et al. 1977 (e.g., Peng et al. 2004, pl. 44, fig. 12). There are also weak cranidial flanges on species of *Palaeadotes* (e.g., Peng et al. 2004, pl. 41, fig. 4), and a small process at the fulcrum is present along the posterior cranidial margin of some species of *Protaitzehoia* (e.g., Peng 2004, pl. 33, fig. 9).

Other features of *Cheilocephalus* are consistent with a relationship with the Dameselloidea. The short, flat to gently upsloping anterior border is matched in such genera as *Protaitzehoia* (e.g., Peng et al. 2004, pl. 33, fig. 8), *Prodamesella* Zhang, 1959 (e.g., Zhang and Jell 1987, pl. 100, fig. 5), and *Parablackwelderia* Kobayashi, 1942 (Peng et al. 2004, text fig. 12*c*). Hypostomal morphology (Figs. 1*j*–1*l*; see also Palmer 1968, pl. 9, fig. 5; Westrop 1986, pl. 29, fig. 9), including the broad borders, is similar to *Parablackwelderia* (e.g., Öpik 1967, pl. 44, fig. 9) and *Palaeadotes* (e.g., Öpik 1967, pl. 50, fig. 3). Although the pleural field is weakly furrowed to effaced on large pygida of *Chelliocephalus*, small individuals (e.g., Fig. 4*g*) have oblique, well-incised pleural furrows that separate broad anterior pleural bands from shorter and narrower posterior pleural bands; the anterior pleural band expands distally. The same configuration occurs in *Protaitzehouia* (e.g., Peng et al. 2006, pl. 32, figs. 5–7, pl. 34, figs. 1–7), which differs only in the course of the distal portion of the anterior pleural band. The distal third of the anterior pleural band tapers abaxially in *Cheilocephalus* to become roughly ogival in outline (Figs. 2e, 3a, 3d, 3f, 4a, 4d, 4g, 4i). In contrast, the pleural band in *Protaitzehouia* is curved back sharply distally, a difference that must reflect the presence of longer thoracic pleural spines (cf. *Palaeadotes*; Peng et al. 2004, pl. 40, figs. 1–4).

With the removal of *Oligometopus*, the only other genus assigned to the Cheilocephalidae is *Pseudokingstonia* Palmer (1965, pl. 1, figs. 16, 18, 19). This genus is strongly effaced and, therefore, difficult to evaluate. Articulating flanges are not evident on the cranidial and pygidial margins. However, the distal portion of an expanded pleural band similar to those of *Cheilocephalus* pygidia is evident on the otherwise effaced pleural field of the paratype pygidium of *P. exotica* Palmer (1965, p. 29, pl. 1, fig. 19). The short, flat anterior border of the cranidium (Palmer 1965, pl. 1, fig. 18) also resembles those of *Cheilocephalus*. Thus, although effacement has reduced the amount of morphologic information available, a case can be made for a relationship between *Pseudokingstonia* and *Cheilocephalus*. However, there is little other than glabellar and pygidial effacement, and, possibly, the small, anteriorly positioned palpebral lobes and the morphology of the thoracic pleural spines, to act as synapomorphies for the Cheilocephalidae, and the family is used here with some reservation. Clarification of the status of the family must await a phylogenetic analysis of the Dameselloidea, a task that is well beyond the scope of this paper.

All previously described dameselloidean trilobites are from strata that are correlative with the Marjuman stage of Laurentia (e.g., Öpik 1967; Peng et al. 2004), whereas *Cheilocephalus* has been documented only from the younger Steptoean Stage (e.g., Palmer 1965). However, a previously undescribed pygidium from a boulder in the Cow Head Group of Newfoundland (Figs. 4*i*, 4*j*) demonstrates that *Cheilocephalus* makes its first appearance in the Late Marjuman. This pygidium is part of a collection that includes *Catillicephala fowleri* Shaw, 1952 and *Kingstonia walcotti* Resser, 1938 (Dengler 2005). With the assignment of the Cheilocephalidae to the Dameselloidea, the superfamily persists into the Furongian Series in Laurentia.

Genus *Cheilocephalus* Berkey, 1898

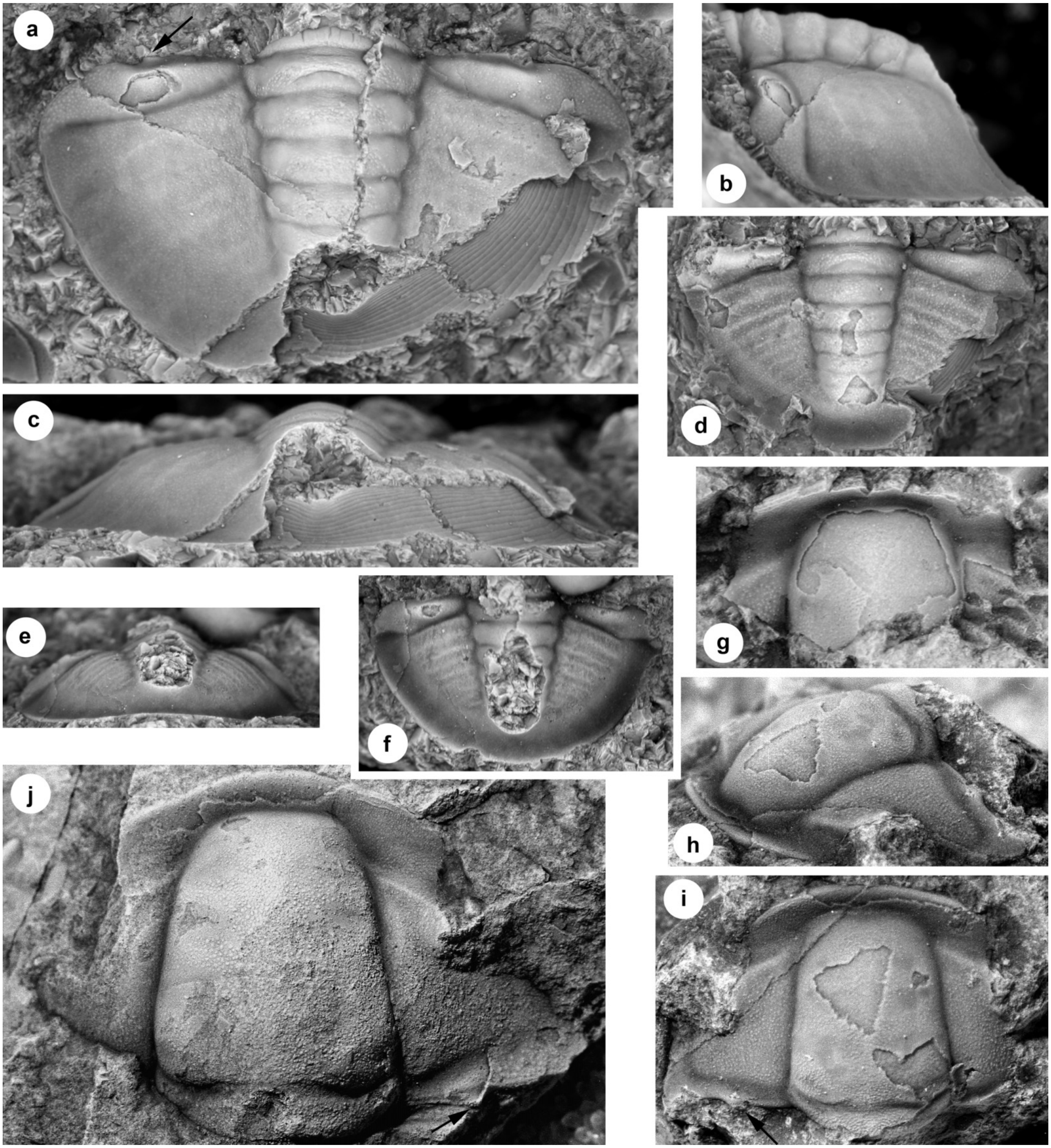
TYPE SPECIES: *Cheilocephalus st.croixensis* Berkey, 1898, from the Upper Cambrian rocks of Minnesota (by original designation).

DIAGNOSIS: Cheilocephalidae with conspicuous articulating flanges at fulcrum on posterior margin of cranidium and anterior margin of pygidium. Glabella weakly arched and trapezoidal in outline; glabellar furrows weakly impressed to barely perceptible. Palpebral lobe short, centered opposite S2 lateral furrow (where latter is expressed; e.g., Fig. 1*a*). Pygidium with prominent, convex pleural band at anterior; remainder of pleural field weakly furrowed to effaced on larger specimens. Pygidial border broad, concave.

ASSIGNED SPECIES: Species from Laurentia: *Cheilocephalus st.croixensis*; *C. hisingeri* (Billings, 1865); *C. brevilobus* (Walcott, 1916); *C. buttsi* Resser, 1942; *C. wichitaensis* Resser, 1942; *C. minutus* Palmer, 1954; *C. delandi* Shaw, 1956; *C. omega* (Lochman and Hu, 1962*b*); *C. brachyops* Palmer, 1965; *C. granulosus* Palmer, 1965; *C. expansus* Palmer, 1968; *C. vermontanus* (Clark and Shaw, 1968); *C. quadratus* Taylor, Loch, and Perfetta, 1999. *Cheilocephalus*? sp. Stitt, 1998, from the lower Deadwood Formation of South Dakota is of uncertain status (see later in the text). The poorly known *Cheilocephalus triquetrus* Lazarenko, 1968, is a likely occurrence of the genus in Siberia; *C. fragmentus* (Walcott, 1911) from North China is another probable extra-Laurentian representative.

DISCUSSION: Species of *Cheilocephalus* are persistent but generally rare elements in Steptoean trilobite faunas of Laurentia. The genus is represented by at least 13 Laurentian species, but most are known from only a few figured specimens. With limited knowledge of variability and, in most

Fig. 3. *Cheilocephalus* from Nevada, Newfoundland and Quebec. (***a–f***) *Cheilocephalus* cf. *C. brachyops* Palmer, 1965 from the Corset Spring Shale, section SHP, Shingle Pass, south Egan Range, Nevada; all from collection SHP 18.25, except (*d*) (SHP 18.6). (***a–c***) pygidium, OU 12376, (*a*) dorsal, (*b*) lateral, and (*c*) posterior views, × 8; flange at arrow in (*a*). (***d***) pygidium, OU 12377, dorsal view, × 9. (***e–f***) pygidium, OU 12378, (*e*) dorsal and (*f*) posterior views, × 9. (***g–i***) *Cheilocephalus* cf. *C. hisingeri* (Billings, 1865), from the Shallow Bay Formation, western Newfoundland, boulder HC 180. (*g*) incomplete cranidium, GSC 127683, dorsal view, × 9. (*h*, *i*) cranidium, GSC 68550, anterior-oblique and dorsal views, × 9; flange at arrow in (*i*). (***j***) *Cheilocephalus hisingeri* (Billings, 1865), from the Lévis Formation, Lévis, Quebec. (***j***) cranidium, holotype, GSC 868a, dorsal view, × 8; flange at arrow in (*j*).



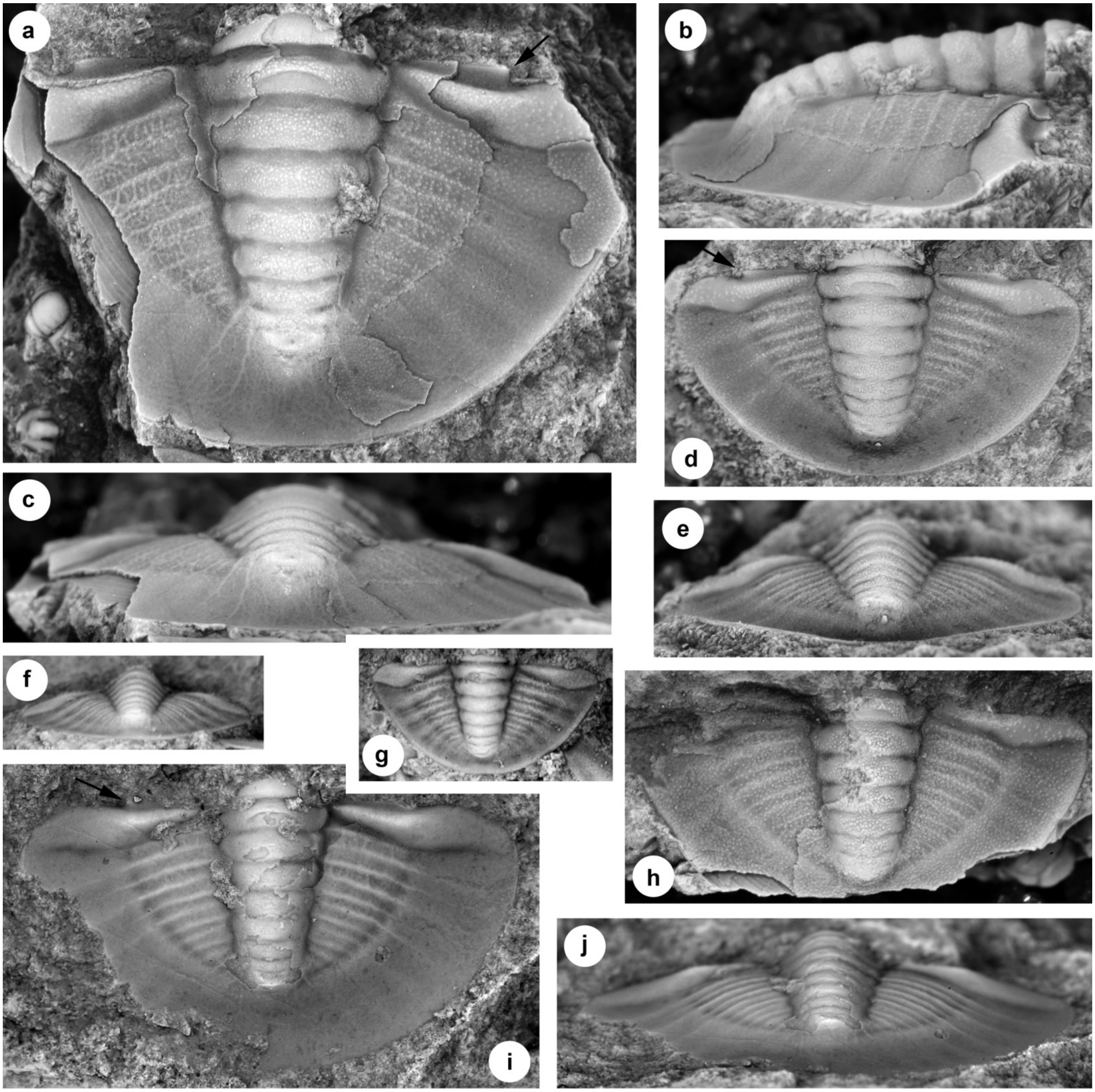


Fig. 4. *Cheilocephalus* from the Shallow Bay Formation, western Newfoundland. **(*a–h*)** *Cheilocephalus hisingeri* (Billings, 1865). (*a–c*) pygidium, GSC 127684, (*a*) dorsal, (*b*) lateral, and (*c*) posterior views, boulder CH 57, × 7; flange at arrow in (*a*). (*d*, *e*) pygidium, GSC 127685, (*d*) dorsal and (*e*) posterior views, boulder HC 202, × 9; flange at arrow in (*d*). (*f*, *g*) pygidium, GSC 127686, (*f*) posterior and (*g*) dorsal views, boulder CH 57, × 12. (*h*) pygidium, GSC 127687, dorsal view, boulder HC 202, × 9. **(*i, j*)** *Cheilocephalus* sp. indet., from the Shallow Bay Formation, western Newfoundland. (*i*, *j*) pygidium, GSC 127688, (*i*) dorsal and (*j*) posterior views, boulder CH 20, × 8; flange at arrow in (*i*).

cases, sclerite associations, critical evaluation of these species is difficult. Possible occurrences of the genus outside Laurentia are based on even sparser material (e.g., Rozova, in Zhuravleva 1977, pl. 9, figs. 16–17; Zhang and Jell 1987, pl. 119, fig. 9).

Cranidia from the lower Deadwood Formation of South Dakota that were assigned questionably to *Cheilocephalus* by Stitt (1998, figs. 7.22–7.24) are significantly older (Marjuman) than any other occurrences of the genus, including those reported in this paper. However, these sclerites are poorly preserved sandstone internal molds and their identity is far from certain. There are some similarities between Stitt's specimens and Steptoean species of *Cheilocephalus* in, for example, the short frontal area that includes a very

Fig. 5. *Cheilocephalus brevilobus* (Walcott, 1916), Nolichucky Formation (Steptoean), 1.5 miles (1 mile = 1.609 km) south of Greeneville, Greene County, Tennessee. (***a–d***) cranidium and thorax, USNM 62852 (holotype), (*a*, *b*) dorsal views, (*c*) anterior, and (*d*) lateral views, × 3; arrows in (*b*) point to fulcral processes. (***e***) pygidium, USNM 62854 (paratype) dorsal view, × 8. (***f*, *g***) cranidium, USNM 536935 (previously unfigured specimen from type lot), (*f*) dorsal and (*g*) anterior-oblique views, × 8; flange at arrow in (*f*). (***h*, *i***) cranidium, USNM 62853 (paratype) (*h*) dorsal and (*i*) anterior-oblique views, × 8.

short preglabellar field and glabellar outline, but comparable features are also present in such Marjuman kingstoniids as *Blountia* Walcott, 1916 (e.g., Stitt and Perfetta 2000, figs. 11.8, 11.9, 8.19) and *"Ankoura" orbiculata* Lochman (Lochman and Hu, 1962*a*, pl. 4, figs. 35, 41, 42, 47, 48, 51, 52). We agree with Stitt (1998, p. 1042) that the status of these sclerites cannot be resolved without additional information.

Pseudokingstonia Palmer (1965, pl. 1, figs. 16, 18, 19; Westrop 1986, pl. 29, fig. 1; Hohensee and Stitt 1989, figs. 5.4–5.6 is poorly known and differs from *Cheliocephalus* in the extent of pygidial effacement, with only the distal tip of the anteriormost pleural band expressed on the pleural field. The steeply down-sloping flanks of the pygidium, which lack any trace of a border, contrast with the wider, concave pygidial border of *Cheilocephalus*. Cranidia of *Pseudokingstonia* are also effaced relative to those of *Cheilocephalus* and have an abbreviated anterior border.

Cheilocephalus hisingeri (Billings, 1865) Figs. 3*h*–3*j*, 4*a*–4*h*

Dikelocephalus hisingeri Billings, 1865, p. 196, fig. 182.
Pseudolisania hisingeri (Billings); Rasetti, 1944, p. 252, pls. 37, 26, 27.

HOLOTYPE: A cranidium (GSC 868a) from the Lévis Formation, Quebec (Fig. 3*j*).

DIAGNOSIS: *Cheilocephalus* with granulose exoskeleton. Posterior branches of the facial sutures abruptly divergent. Pygidium with border wider (tr.) than pleural field.

DESCRIPTION: Cranidium subtrapezoidal in outline, with width at anterior border furrow about 55% of cranidial width at posterior; posterior cranidial margin with subtriangular flange at fulcrum. Axial and preglabellar furrows narrow, shallow to moderately incised grooves. Gently convex glabella is truncate anteriorly, occupies 90% (89%–91%) of cranidial length (sagittal (sag.)) and 40% of cranidial width at posterior; tapers anteriorly with glabellar width opposite anterior ends of palpebral ridges 77% (75%–79%) of width at SO. SO gently impressed; nearly transverse medially but shallows and narrows distally. LO occupies 14% (13%–15%) of glabellar length. Three pairs of very faint glabellar furrows. Anterior border flat and separated from preoccular and preglabellar fields largely by change in slope. Palpebral lobe situated anterior to glabellar midpoint, length equal to 18% (16%–20%) of glabellar length; separated from fixigena by change in slope. Palpebral ridge extends obliquely forward and inward to terminate near anterior end of glabella. Palpebral area of fixigena nearly flat and equal to 24% (20%–29%; lower values in larger specimens) of glabellar width at SO. Anterior branches of facial sutures subparallel before curving inward along anterior cranidial margin. Posterior branches of facial sutures diverge abruptly along nearly transverse course before curving almost straight back. Posterior border furrow, shallow and nearly transverse near glabella but curves forward along posterolateral projection. Posterior border expands distally, markedly so near posterior corner of cranidium. Entire surface of cranidium with sculpture of low, closely-spaced granules; terrace lines present along outer edge of border.

Pygidium subsemicircular in outline; pygidial length 54% (52%–56%) of maximum pygidial width at anterior corners. Axial furrows are shallow grooves. Convex axis accounts for 28% (28%–29%) of pygidial width at anterior and occupies 84% (79%–87%; lowest value in largest specimen, Fig. 4*a*); tapers posteriorly, so that width at anterior end of terminal piece is 52% (51%–53%) of width at anteriormost ring; pygidial border. Six well-defined axial rings separated by roughly transverse axial ring furrows; two additional segments incorporated into terminal piece, identifiable by barely perceptible transverse furrow. Pleural field downsloping to wider, weakly concave border. Anterior pleural furrow well-defined through available size range of pygidia (compare Figs. 4*a* and 4*g*). Furrow curves obliquely backward near axis, separating long, laterally expanding (exsag.) anterior pleural band from shorter posterior band; opposite distal tip of articulating flange, furrow curves forward so that anterior band narrows distally. Posterior pleural band bounded posteriorly by shallow, but clearly defined, oblique interpleural furrow that is inclined at about 15° to transverse plane. Smallest specimen (Fig. 4*g*) shows pleural and interpleural furrow configuration with prominent anterior pleural bands over remainder of pleural field. On larger specimens (e.g., Figs. 4*a*, 4*d*) morphology of pleural bands (apart from anteriormost band) is modified by partial effacement. Near axis, anterior bands are reduced to narrow (exsag.) ridges that resemble posterior pleural bands, but expressed as indistinct, broader, weakly inflated areas on border. Pleural and interpleural furrows are closely comparable in depth, length (exsag.) and oblique course across pleural field. Pygidial border weakly concave, of constant width in larger specimens but narrowing toward axis in smaller specimens. Sculpture of closely spaced granules on axis, pleural field, and border; internal mold with caecal markings extending from pleural bands and tip of axis.

DISCUSSION: The holotype of *Cheilocephalus hisingeri* from the Lévis Formation of Quebec (Fig. 3*j*) has abruptly divergent posterior branches of the facial sutures that are matched in cranidia from the Shallow Bay Formation in Newfoundland (Figs. 3*h*–3*i*). All cranidia assigned to this species also share coarsely granulose sculpture. There are no data on the age of the holotype (Rasetti 1944, p. 252), but material from Newfoundland occurs in boulders that are correlative with the mid-Steptoean *Dunderbergia* Zone (Eoff 2002).

Cheilocephalus hisingeri is most similar to *C. expansus* Palmer (1968, pl. 9, figs. 1–7) from the Jones Ridge Limestone of Alaska. The two species share a pygidial border that is wider than the pleural field, a condition that Palmer (1968, p. 58) considered to be a diagnostic of *C. expansus*,

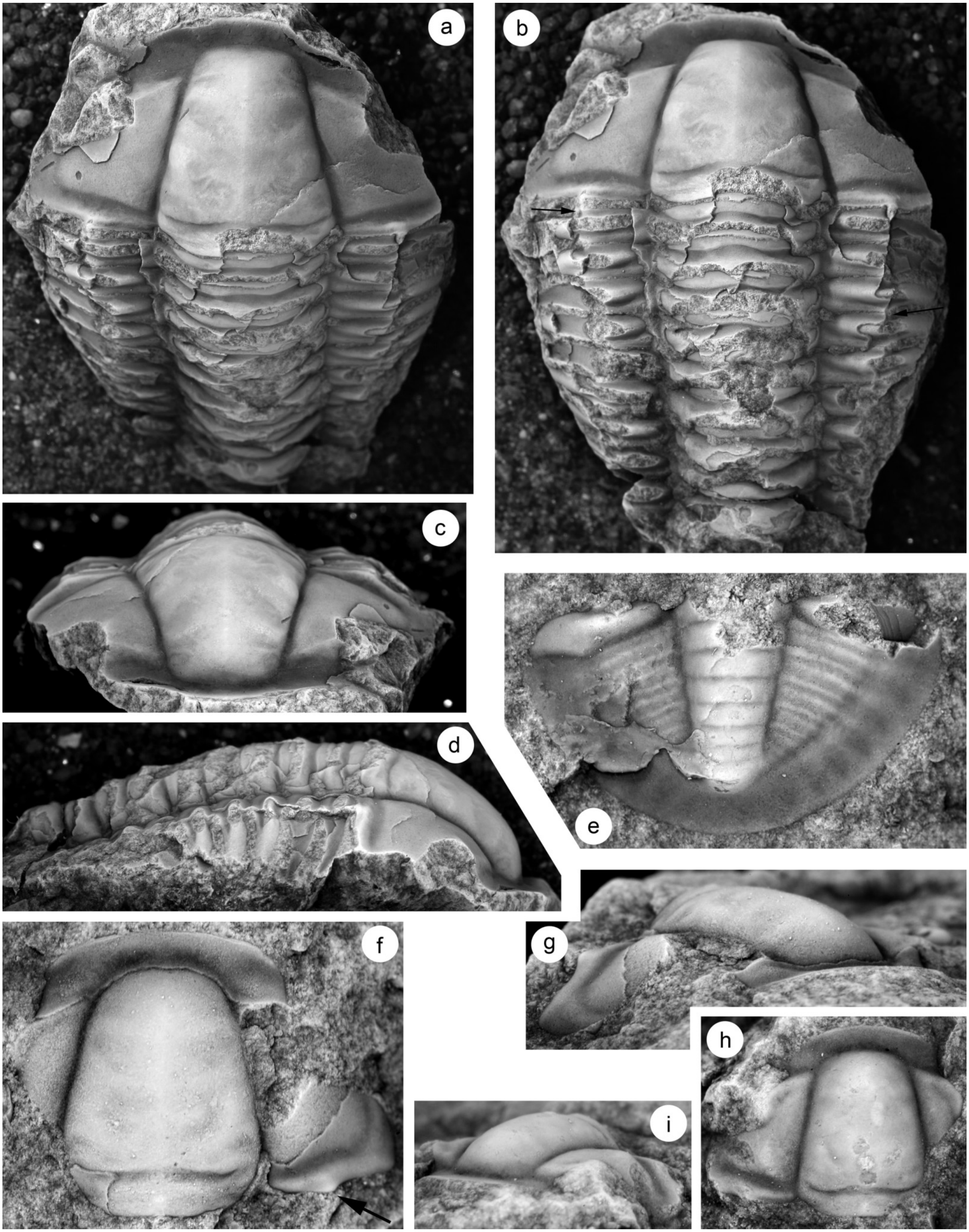

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Fig. 6. *Cheilocephalus* cf. *C. granulosus* Palmer, 1965, from Member B of the Emigrant Springs Formation, Patterson Pass, Schell Creek Range, Nevada. All from collection PP 96.95. (***a–c***) cranidium. SUI 108311, (*a*) dorsal, (*b*) lateral, (*c*) and anterior views, × 3. (***d–f***) cranidium, SUI 108312, (*d*) anterior-oblique, (*e*) dorsal, and (*f*) anterior views, × 3. (***g–i***) cranidium, SUI 108315, (*g*) dorsal, (*h*) anterior, and (*i*) lateral views, × 5. (***j***) cranidium, SUI 108313, dorsal view, × 3. (***k***) cranidium, SUI 108314, dorsal view, × 5.

and granulose sculpture. However, cranidia of *C. expansus* appear to lack the very abrupt divergence of the posterior sutures that characterizes *C. hisingeri*. The poorly known *C. buttsi* Resser (1942, pl. 11, fig. 6), from the Ore Hill Member of the Gatesburg Formation, is another granulose member of the genus. The holotype cranidium is incomplete, but an apparently conspecific cranidium, figured by Wilson (1951, pl. 91, fig. 19), shows that this species is characterized by a short anterior border and a narrow palpebral area of the fixigenae, so that the palpebral lobe is much closer to the glabella than in *C. hisingeri*. The cranidium attributed to *C. wichitaensis* Resser, 1942 by Stitt (1977, pl. 1, fig. 4) also differs from *C. hisingeri* in the latter respect, but has a relatively long anterior border; an associated pygidium (Stitt 1977, pl.1, fig. 5) is exfoliated and poorly preserved, but has a pygidial border that is clearly narrower (tr.) than the pleural field. *Cheilocephalus granulosus* Palmer (1965, pl. 1, figs. 6–8) is known from a single, incomplete, granulose cranidium and two pygidia, one of which was assigned questionably to the species. Cranidial comparisons are difficult because information is limited, but *C. granulosus* appears to have a longer anterior border than *C. hisingeri*. Pygidia of *C. granulosus* from Nevada are characterized by very narrow borders, although Palmer (1965) also assigned specimens from Montana (Lochman and Hu 1962*b*, pl. 69, figs. 16, 17, 20–24) to this species that are closer to *C. hisingeri* in border length.

Several species differ from *C. hisingeri* in having smooth, rather than granulose, cranidia, including *C. brevilobus* (Walcott 1916; Figs. 5*f*–5*h*), and *C. delandi* Shaw (1956, p. 50, pl. 10, pl. 11) and its possible synonym, *C. omega* (Lochman and Hu, 1962*b*, pl. 70, figs. 1–21). All three species possess relatively long anterior cranidial borders. In addition, pygidia of *C. delandi* and *C. omega* are effaced even at small sizes (e.g., Lochman and Hu 1962*b*, pl. 70, fig. 5). Cranidia of *Cheilocephalus vermontensis* (Clark, in Clark and Shaw 1968, pl. 56, figs. 1–4) are also characterized by smooth external surfaces (Clark and Shaw 1968, p. 393). This species is differentiated from *C. hisingeri* by a very short anterior border that wraps around the anterior end of the glabella.

Cheilocephalus brevilobus Walcott, 1916 Figs. 5*a*–5*i*

Lisania? breviloba Walcott, 1916, p. 404, pl. 66, figs. 3–3c.

Cheilocephalus brevilobus (Walcott); Palmer, 1954, p. 759, pl. 88, figs. 1–4 (see for synonymy).

Cheilocephalus brevilobus (Walcott); Rasetti, 1965, p. 103, pl. 17, figs. 1–5.

Cheilocephalus brevilobus (Walcott); Pratt, 1992, p. 69, pl. 24, figs. 18–28 (see for synonymy).

Cheilocephalus brevilobus (Walcott); Stitt and Perfetta, 2000, p. 218, figs. 12.5, 12.9, 12.10.

HOLOTYPE: A nearly complete exoskeleton (USNM 62852) from the Nolichucky Formation, Greene County, Tennessee (Figs. 5*a*–5*d*).

DIAGNOSIS: *Cheilocephalus* with smooth external surface. Cranidium with long anterior border that occupies at least 12% of cranidial length.

DISCUSSION: *Cheilocephalus brevilobus* (Walcott) has been reported widely from early Steptoean strata of Laurentia (Palmer 1954, 1965; Rasetti 1965; Pratt 1992; Stitt and Perfetta 2000). Sclerites illustrated here include the holotype (Figs. 5*a*–5*d*), paratypes (Figs. 5e, 5h, 5i) and a previously unfigured cranidium from the type lot (Figs. 5*f*–5*g*). The cranidia possess relatively long anterior borders, and patches of exoskeleton preserved on the mostly exfoliated specimens are smooth. Other cranidia from the type area illustrated by Rasetti (1965, pl. 17, figs. 1–5) share the smooth surface and long anterior border with the types, and the smaller of his pygidia (Rasetti 1965, pl. 17, fig. 5) is closely comparable to Walcott's specimen (see Fig. 5*e*). The larger pygidium figured by Rasetti (1965, pl. 17, fig. 1) has a relatively shorter axis and longer border than other pygidia from Tennessee. This difference between large and small specimens resembles the ontogenetic variation in pygidia of *C. hisingeri* (Figs. 4*a*–4*h*).

Cranidia from Texas (Palmer 1954, pl. fig.) and the Mackenzie Mountains (Pratt 1992, pl. fig.) have anterior borders that are slightly longer than Walcott's types, but are similar to specimens figured by Rasetti (1965, pl. 17, figs. 2, 3).

The holotype (Figs. 5*a*–5*d*) is the only know specimen of *Cheilocephalus* with thoracic segments articulated with the cranidium. The nine segments are poorly preserved but are closely comparable in discernable details to the single segment (Figs. 2*g*–2*i*) of *C.* cf. *C. brachyops* Palmer 1965, that is described in detail in the following description. Similarities include broad axes with long articulating half-rings, relatively narrow (tr.) pleurae that end in short, bluntly pointed spines, firmly impressed, oblique pleural furrows and anterior pleural bands that expand distally, and conspicuous fulcral processes on anterior margins.

Cheilocephalus cf. *C. brachyops* Palmer, 1965 Figs. 1*a*–1*l*, 2*a*–2*i*, 3*a*–3*f*

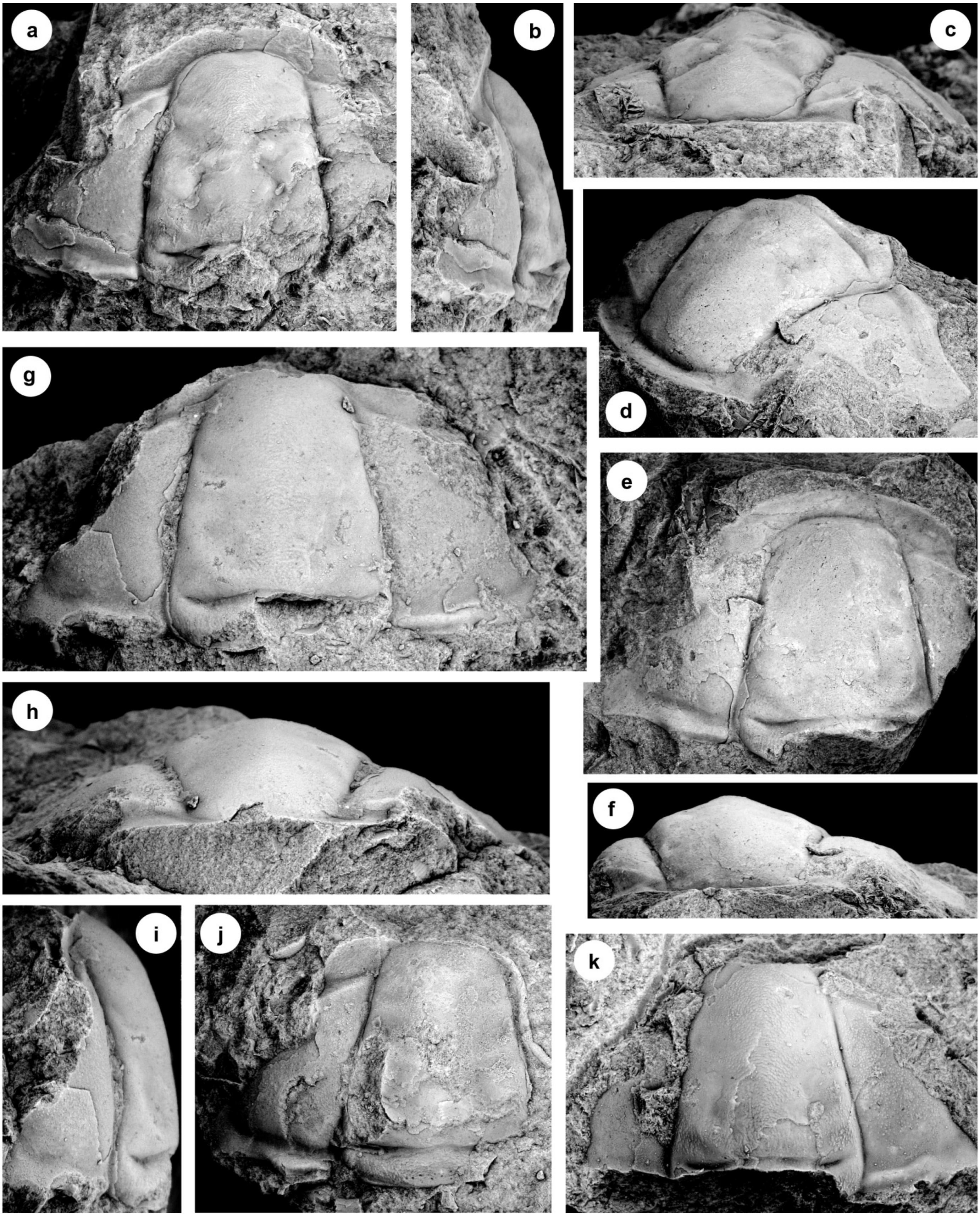
cf. *Cheilocephalus brachyops* Palmer, 1965, p. 30, pl. 1, figs. 12–15, 17.

cf. *Cheilocephalus brachyops* Palmer; Rasetti, 1965, p. 104, pl. 17, figs. 6–11

? cf. *Cheilocephaus brachyops* Palmer; Hohensee and Stitt, 1989, p. 864, figs. 5.–5.3.

? cf. *Cheilocephaus brachyops* Palmer; Pratt, p. 69, pl. 25, figs. 26–29.

DISCUSSION: Sclerites of *Cheilocephalus* from the Corset Spring Shale at Shingle Pass were collected from two closely spaced horizons (35 cm apart) in an interval of bioclastic grainstone and rudstone. Cranidia show variation in sculpture, glabellar outline and length of frontal area. Varia-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bility in the latter is size-related, with the largest specimens (Figs. 1*a*, 2*a*) possessing proportionately longer frontal areas than smaller individuals (e.g., Figs. 1*d*, 1*h*). Most cranidia have granulose sculpture (Figs. 1*d*, 2*a*, 2*d*, 2*j*), but some are smooth (Figs. 1*a*, 1*h*); this variation is not a function of size. The majority of specimens have anteriorly tapered glabellae, although the degree of taper varies (e.g., compare Figs. 1*a* and 1*h*). In a few specimens (e.g., Fig. 1*c*), the glabella is nearly parallel-sided.

Among pygidia, variation is size-related. Smaller individuals display well-defined pleural and interpleural furrows (Figs. 3*d*, 3*f*), but these become effaced in larger specimens (Fig. 3*a*). Sculpture is generally in the form of fine granules (Figs. 3*a*, 3*d*), but some specimens are smooth (Fig. 2*e*).

A single thoracic segment (Figs. 2*g*–2*i*) is assigned confidently because of similarities both with the anterior pleural bands on the associated pygidia (Figs. 2*e*, 3*a*, 3*d*, 3*f*), and with segments of a nearly complete articulated specimen of *C. brevilobus* (Figs. 5*a*–5*d*). The segment has a strongly arched axis that occupies about 40% of segment width and accounts for about half of segment height in anterior view. Axial furrows are shallow grooves. The axis is divided into a long axial ring and a shorter articulating half-ring by a well-defined furrow that is nearly transverse medially but curves forward and downward near axial furrows. The inner portion of pleura is nearly flat and with flanges on the anterior and posterior margins that expand distally into fulcral processes; posterior process is presumably underlain by fulcral socket. An oblique pleural furrow extends posteriorly and abaxially from the anterior end of axial furrow to terminate at the outer edge of the posterior fulcral process. The anterior pleural band expands distally, with concomitant taper of the posterior band. The outer portion of the pleura is flexed steeply downward; its anterior edge is curved strongly backward, but the posterior edge is weakly curved; distal termination is in form of bluntly rounded spine. Sculpture of fine granules is present on outer portion of pleura and the central portion of axial ring; the remainder of segment smooth.

Cheilocephalus brachyops Palmer, 1965 (pl. 1, figs. 12–15, 17) is based on only two small cranidia and two pygidia from Shingle Pass that, judging from Palmer's (1965, pl. 22) lithologic column, were likely collected about 10 m stratigraphically below the specimens illustrated herein. One of the two cranidia illustrated by Palmer (1965, pl. 1, fig. 12) is similar to one of our specimens (Fig. 1*c*) in glabellar outline, but the absence of additional, larger individuals in the type lot makes further comparison impossible. Pygidia (Palmer 1965, pl. 1, figs., 13, 15, 17) of *C. brachyops* have relatively short borders comparable to those of the pygidia illustrated here (Figs. 2e, 3a, 3d, 3f) but appear to have more firmly impressed pleural and interpleural furrows. It is possible that our material will prove to be conspecific with *C. brachyops*, but until more specimens are available of the latter, we prefer to use open nomenclature.

Pratt (1992, pl. 25, figs. 26–29) assigned a cranidium and pygidium from the Rabbitkettle Formation of northern Canada to *C. brachyops*. The pygidium is relatively longer and narrower than any in our collections, and the axis (incomplete posteriorly) appears to have terminated closer to the posterior margin. The cranidium falls within the range of variation of specimens from the Corset Spring Shale. The sclerites attributed to *C. brachyops* by Hohensee and Stitt (1989, figs. 5.1–5.2) are very small (2–3 mm in sagittal length) and, in our opinion, they are inadequate for a confident species-level identification.

Cheilocephalus cf. *C. granulosus* Palmer, 1965 Figs. 6*a*–6*k*, 7*a*–7*g*

cf. *Cheilocephalus granulosus* Palmer, 1965, p. 31, pl. 1, figs. 9–11 (see for synonymy).

? cf. *Cheilocephalus granulosus* Palmer; Pratt, 1992, p. 69, pl. 24, fig. 17.

DISCUSSION: Sclerites from basal Steptoean (*"Coosella" perplexa* subzone of the *Aphelaspis* Zone; Palmer 1979) shallow-water carbonate facies of the Emigrant Springs Formation at Patterson Pass, Nevada, record one of the earliest occurrences of *Cheilocephalus* inboard of the Laurentian shelf margin. Testate surfaces of cranidia (Fig. 6*k*) are coarsely granulose, with granules arranged in a bertillon pattern on the glabella. Among other granulose species, cranidia from Montana (Lochman and Hu 1962*b*, pl. 69, figs. 1–7, 19) that were transferred to *C. granulosus* by Palmer (1965) are closely comparable to those illustrated here, differing in having a somewhat longer anterior border (e.g., pl. 69, fig. 19). Pygidia of *C. granulosus* from Montana (Lochman and Hu 1962*b*, pl. 69, figs. 16, 17, 20–24) possess relatively broader borders and more strongly furrowed pleural fields; furrows extend onto the border. The pygidium from the Mackenzie Mountains that was attributed to this species by Pratt (1992, pl. 24, fig. 17) is too poorly preserved for a confident identification. *Cheilocephalus hisingeri* (Billings; Figs. 3*h*–3*j*) is characterized by more sharply divergent posterior sutures than *C.* cf. *C. granulosus*. In addition, pygidia of the former have relatively longer borders and, consequently, narrower (tr.) pleural fields than the latter. The material from Patterson Pass may well represent a new species, but it will not be named until additional, more completely preserved material becomes available.

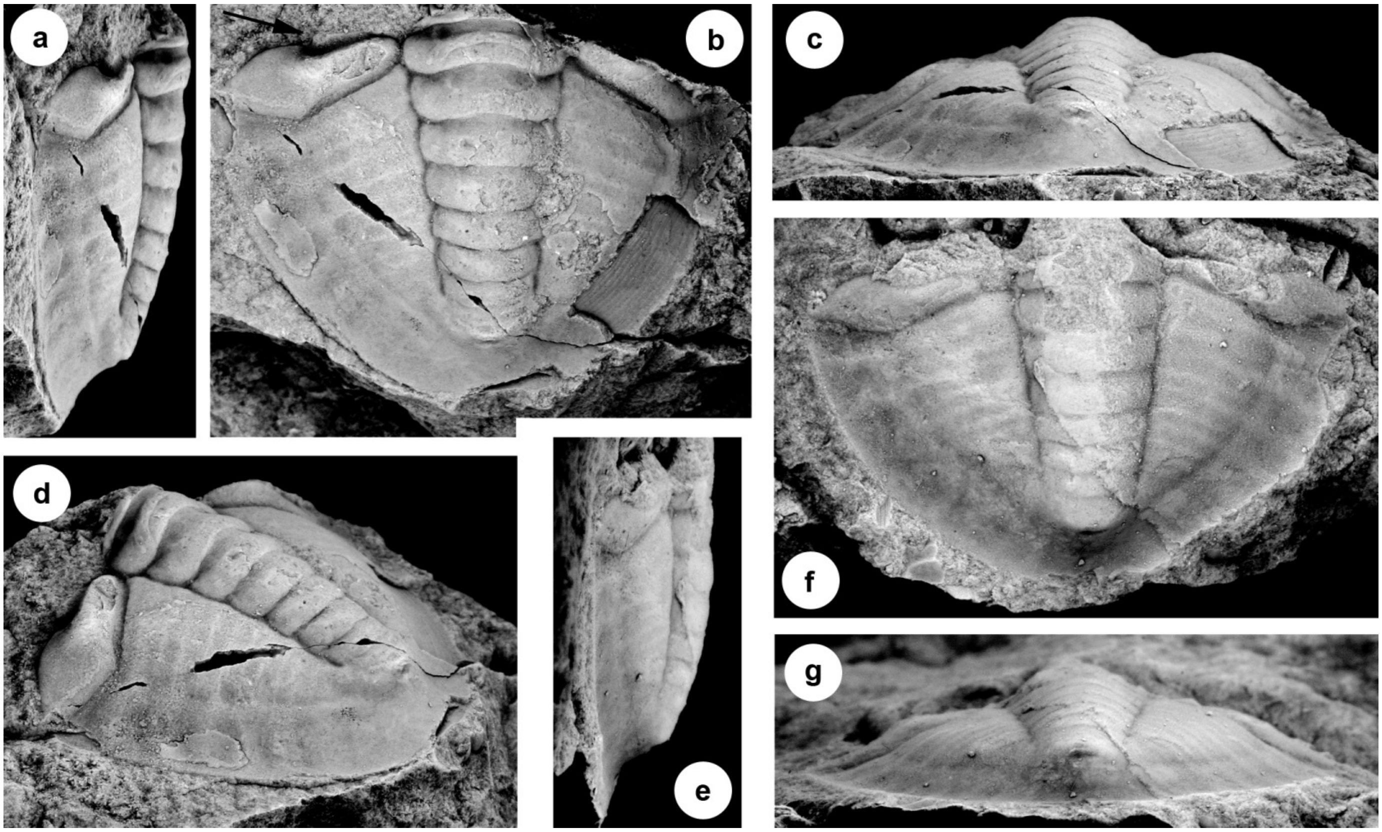
Cheilocephalus sp. indet. Figs. 4*i*, 4*j*

DISCUSSION: A single large pygidium from a late Marjuman boulder in the Shallow Bay Formation, Cow Head Group, Newfoundland, demonstrates that *Cheilocephalus* was established in Laurentian shelf margin environments prior to the Steptoean. The narrow pleural field and broad (sag., tr.) border are most like those of similarly sized specimens of *C. brevilobus* (Walcott, 1916) from the slightly younger (early Steptoean; *Aphelaspis* Zone) of the Nolichucky Formation, Tennessee (e.g., Rasetti 1965, pl. 17, fig. 1).

Superfamily Leiostegioidea Bradley, 1925
Family Leostegiidae Bradley, 1925

DISCUSSION: *Oligometopus* is most similar to a group of genera, including *Pagodia* Walcott, 1905, *Chuangia* Walcott, 1911, *Prochuangia* Kobayashi, 1935, *Idamea* Whitehouse, 1939, and *Lotosoides* Shergold, 1975, that have been considered by many workers to represent a separate subfamily within the Leiostegidae, the Pagodiinae Kobayashi, 1935 (e.g., see Öpik 1967; Shergold 1975; Wittke 1984; Ludvigsen et al. 1989; Peng 1990). However, the Leiostegiidae

Fig. 7. *Cheilocephalus* cf. *C. granulosus* Palmer, 1965, from Member B of the Emigrant Springs Formation, Patterson Pass, Schell Creek Range, Nevada. All from collection PP 96.95. (***a–d***) pygidium, SUI 108316, (*a*) lateral, (*b*) dorsal, (*c*) posterior, and (*d*) posterior-oblique views, × 3; flange at arrow in (*b*). (***e–g***) pygidium, SUI 108317, (*e*) lateral, (*f*) dorsal, and (*g*) posterior views, × 5.



have not been revised in modern terms, and it remains to be seen if the taxa currently assigned to the Pagodiinae are a distinct monophyletic group. Many, including *Pagodia* itself, are based on limited material (e.g., see Zhang and Jell 1987) and their relationship with such superficially similar Laurentian genera as *Ptychopleurites* Kobayashi, 1936 and *Phoreotropis* Raymond, 1924 (see Ludvigsen et al. 1989, p. 33), needs to be re-evaluated. All of this work is well beyond the scope of this paper, and we will follow Zhang and Jell (1987) in leaving the Leiostegiidae undivided at the subfamilial level.

Genus *Oligometopus* Resser, 1936

TYPE SPECIES: *Ptychoparia* (*Solenopleura*?) *breviceps* Walcott, 1884, from the Dunderberg Formation, Eureka District, Nevada (by original designation).

DIAGNOSIS: Leiostegiidae with tapered glabella that is well rounded anteriorly in at least larger cranidia. Palpebral lobe small, equal to about 25%–33% of cranidial length and centered opposite L2 glabellar lobe; consequently, posterior area of fixgena long (exsag.). Pygidium with entire margin; pleural furrows firmly impressed on dorsal surface and terminating close to margin. Axis relatively short with three or four segments.

ASSIGNED SPECIES: *Oligometopus breviceps* (Walcott, 1884); *O. minutus* (Frederickson, 1949); *O. contractus* Palmer, 1965.

DISCUSSION: As argued earlier in the text, several characters, including details of the articulation, ally *Cheilocephalus* with the Dameselloidea. The articulation devices of the cranidial and pygidial margin of *Cheilocephalus* are absent in *Oligometopus* and, despite such cranidial similarities as an abbreviated frontal area and an anteriorly tapered glabella, a relationship between these genera seems unlikely. There are, however, a number of comparisons that may be made between *Oligometopus* and such leiostegioidean genera as *Chuangia* Walcott, 1911 and *Idamea* Whitehouse, 1939.

The anterior border of *Oligometopus* is a conspicuous, nearly vertical feature that is plastered onto the front of the cranidium and is defined posteriorly by a firmly impressed border furrow that merges medially with the preglabellar furrow (e.g., Figs. 8*a*–8*r*). This contrasts with the shorter, nearly flat border of *Cheilocephalus* (e.g., Figs. 1*a*–1*h*, 2*a*–2*d*, 5*a*–5*d*) but is identical to the configuration in *Idamea* (e.g., Öpik 1967, pl. 17, fig. 1; Shergold 1982, pl. 13, figs. 1–4) and also compares favorably with the morphology of some species of *Prochuangia* Kobayashi, 1935 (e.g., Wittke 1984, pl. 9, fig. 4), *Meropallia* Öpik, 1967 (pl. 18, fig. 7, p1. 19, fig. 4), and *Paraszechuanella* Liu, 1977 (Peng 1990, pl. 4, figs. 1–6). Cranidia of *Oligometopus* also resemble these genera in possessing wide palpebral areas of the fixigenae. Although the posterior border of *Oligometopus* is relatively long (exsag.) on testate surfaces (Fig. 8*e*), it is expressed as a short ridge on internal molds (Fig. 8*r*), much like the posterior border on molds of *Idamea* (e.g., Öpik 1967, pl. 17, fig. 1).

Fig. 8. *Oligometopus breviceps* (Walcott, 1884), from the Corset Spring Shale, section SHP, Shingle Pass, south Egan Range, Nevada. All from collection SHP 18.25. (***a–c***) cranidium, OU 12379, (*a*) dorsal, (*b*) anterior, and (*c*) lateral views, × 9. (***d–f***) cranidium, OU 12380, (*d*) lateral, (**e**) dorsal, and (**f**) anterior views, × 9. (***g–i***) cranidium, OU 12381, (*g*) dorsal, (*h*) lateral, and (*i*) anterior views, × 12. (***j***) cranidum, OU 12382, dorsal view, × 12. (***k–l***) cranidium, OU 12383, (*k*) anterior and (*l*) dorsal views, × 10. (***m–o***) cranidium, OU 12384, (*m*) dorsal, (*n*) lateral, and (*o*) anterior views, × 12. (***p***) cranidium, OU 12385, dorsal view, × 12. (***q–r***) cranidium, OU 12386, (*q*) anterior and (*r*) dorsal views, × 10.

The pygidia of at least two species of *Oligometopus* are identified here for the first time (Fig. 10). They are semielliptical in outline and lack borders. Well-defined pleural and interpleural furrows extend from the axis almost to the pygidial margin; pleural bands are subequal in length and convex. In these respect, the pygidia are comparable to those of *Idamea* (e.g., Öpik 1967, pl. 17, figs. 5–7, pl. 18, fig. 5), although the pleural fields of the latter are relatively effaced, with furrows and pleural bands expressed clearly only on internal molds. The axis of *Idamea* consists of five segments, whereas that of *Oligometopus* consists of no more than four segments (Fig. 10*g*).

Several morphologic similarities between *Oligometopus* and *Idamea* suggest that the former is allied with the Leiostegidae. In this context, glabellar outline is a potential apomorphy of *Oligometopus*. Although glabellae of some leiostegiids narrow forward (e.g., Öpik 1967, pl. 18, figs. 6, 7; Zhang and Jell 1987, pl. 90, fig. 5, pl. 91, fig. 8, none approaches the conspicuous anterior taper of *Oligometopus* (e.g., Figs. 8*a*, 8*e*, 8*n*), which increases with size (Fig. 11*a*). Moreover, glabellae of at least large cranidia of *Oligometopus* are bluntly rounded anteriorly, whereas those other leiostegiids have roughly transverse anterior terminations. *Oligometopus* has strikingly shorter (exsag.) palpebral lobes than otherwise similar genera such as *Idamea* (Öpik 1967, pl. 17, fig. 2) and *Paraszechuanella* Liu, in Zhou et al. 1977 (Peng 1990, pl. 4, figs. 1–6), but some other leiostegiids, including *Pagodia*, are closely comparable to the former in this respect (e.g., Zhang and Jell 1987, pl. 95, figs. 2–5). As such, palpebral lobe size is equivocal as a potential apomorphy of *Oligometopus*.

Oligometopus breviceps (Walcott, 1884) Figs. 8*a*–8*r*, 9*a*–9*c*, 9*k*–9*x*, 10*a*–10*j*

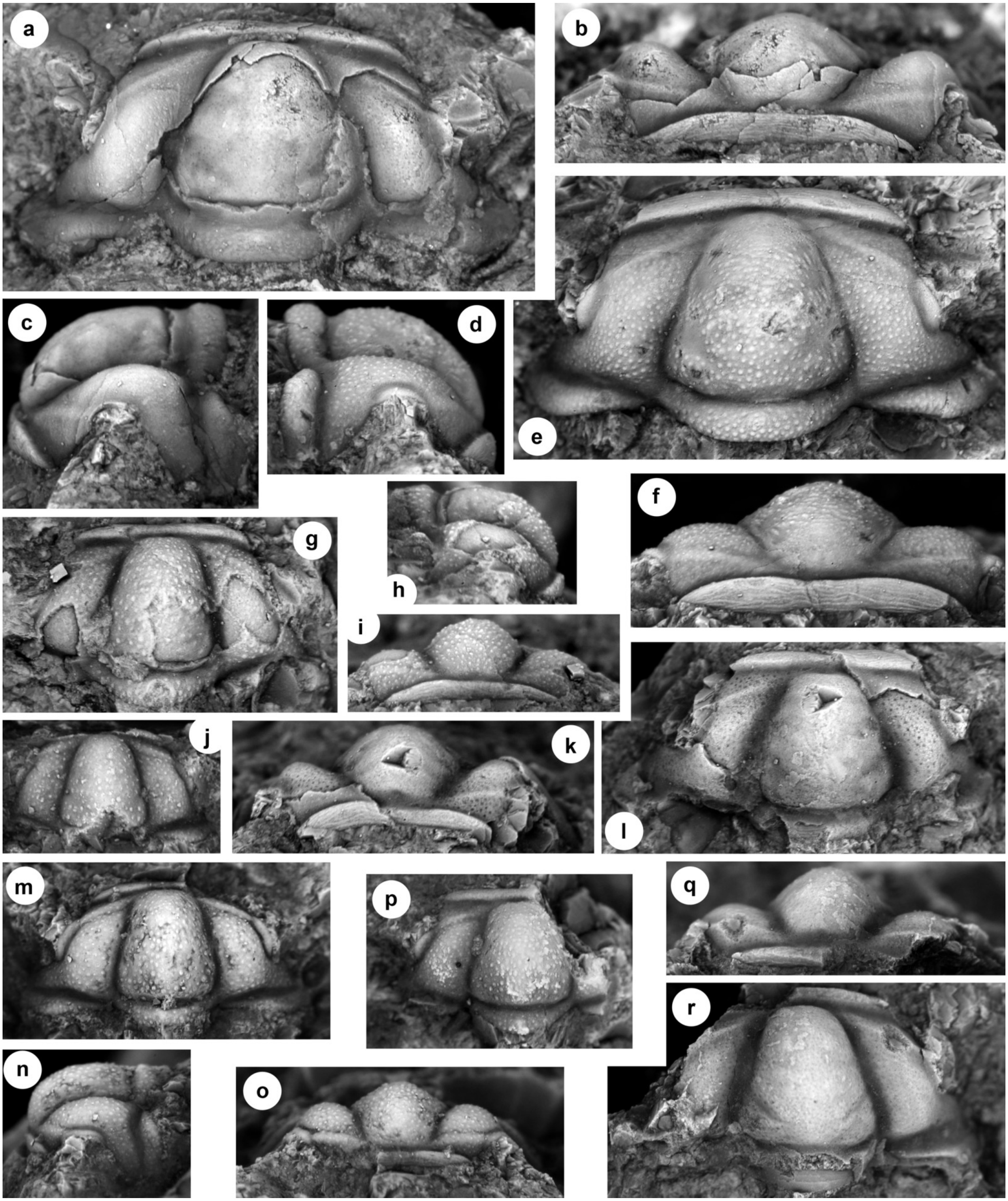
Ptychoparia (*Solenopleura*?) *breviceps* Walcott, 1884, p. 49, pl. 10, fig. 9.
Oligometopus breviceps (Walcott); Resser, 1936, p. 29.
Stenelymus breviceps (Walcott); Raymond, 1937, p. 1101.
Oligometopus breviceps (Walcott); Palmer, 1960, p. 100, pl. 10, figs. 19, 20.
Oligometopus breviceps (Walcott); Palmer, 1965, p. 32, pl. 1, fig. 3
? *Oligometopus breviceps*? (Walcott); Palmer, 1968, p. 58, pl. 7, figs. 30, 31.
? *Oligometopus* sp. Kindle, 1982, pl. 1.4, fig. 7

HOLOTYPE: A cranidium (USNM 24577) from the Dunderberg Formation, Eureka Mining District, Eureka County, Nevada (Figs. 9*a*–9*c*).

DIAGNOSIS: *Oligometopus* with strongly tapered, anteriorly rounded glabella, particularly in larger cranidia (Fig. 11*a*). Palpebral area broad, equal to 47% (40%–52%) of glabellar width at SO. Palpebral lobe short, equal to 27% (22%–23%) of glabellar length and centered opposite L2 glabellar lobe. Pygidium with distal portions of pleural field flexed strongly downward; pleural and interpleural furrows well defined at anterior but become shallower posteriorly.

DESCRIPTION: Cranidium subtrapezoidal in outline, with width at anterior border furrow equal to 55% (53%–61%) of maximum cranidial width at posterior; strongly arched transversely and sagittally. Convex glabella long, occupying 92% (88%–95%) of cranidial length, and width at SO equal to 38% (35%–40%) of maximum cranidial width at posterior. It tapers strongly forward in larger cranidia (e.g., Figs. 8*a*, 8*b*, 9*m*) with width opposite anterior tips of palpebral ridges 53% (44%–59%) of width at SO; taper reduced in smaller cranidia (e.g., Figs. 8*i*, 8*l*, 9*p*), so that width opposite anterior tips of palpebral ridges 62% (56%–67%) of width at SO; rounded anteriorly. Axial and preglabellar furrow shallow but clearly defined grooves. LO accounts for 20% of glabellar length (15%–23%). SO well incised and of uniform depth; nearly transverse medially but curved forward abaxially. S1 furrows shallow and oblique; best defined on specimens with well-developed tubercles as areas that lack sculpture (e.g., Figs. 8*e*, 9*m*). Oblique to subtransverse S2 and S3 furrows may also be expressed similarly on strongly granulose cranidia. Anterior border dips nearly vertically forward and forms short rim. Anterior border furrow well defined and curved gently forward; merges medially with preglabellar furrow. Palpebral lobe equal to 27% (22%–23%) of glabellar length and separated from fixigena by shallow palpebral furrow; centered opposite L2 glabellar lobe. Palpebral ridge extends obliquely forward from palpebral lobe to reach axial furrow near anterior tip of glabella. Anterior branches of facial sutures converge gently forward before swinging inward along anterior cranidial margin; posterior branches abruptly divergent near palpebral lobe before becoming subparallel near posterior border furrow. Fixigena weakly (e.g., Figs. 8*f*, 8*i*, 8*q*) to more strongly inflated (e.g., Figs. 8*b*, 8*k*, 9*b*, 7*g*). Palpebral area broad, equal to 47% (40%–52%) of glabellar width at SO. Posterior area long (exsag.), equal to 34% (31%–40%) of cranidial length. Posterior border convex, short (exsag.) near axial furrow but expands distally; posterior border furrow well incised and directed slightly forward from axial furrow. Posterior border much shorter and border furrow longer on internal mold (Fig. 8*r*). Posterior cranidial margin nearly transverse along postocular area of fixigena but curves forward along posterior projection. Sculpture strongly tuberculate in many specimens (Figs. 8*e*–8*j*, 9*m*–9*o*, 9*v*–9*x*) but tubercles subdued to varying degrees in others (Figs. 8*a*–8*c*, 8*h*, 9*a*–9*c*, 9*k*–9*l*, 9*p*–9*r*); larger, median tubercle expressed on occipital ring of most specimens (e.g., Figs. 8*a*, 8*e*, 9*m*, 9*u*, 9*w*), and anterior border with terrace ridges (e.g., Fig. 8*f*). Internal molds with faint (Fig. 8*a*) to strong (Fig. 8*r*) punctae on fixigena.

Gently arched pygidium semielliptical in outline, length



equal to 53% (46%–58%; lower values in smaller, relatively wider specimens). Axis convex, occupies 76% (74%–77%) of axis length and tapers backward, with width at second axial ring furrow 71% (66%–74%) width at first axial ring; axial furrows very shallow grooves. Small pygidia (Figs. 10*f*, 10*g*) with four rings, but only three evident on larger specimens (e.g., Figs. 10*a*, 10*i*); articulating half-ring semielliptical in outline, length slightly more than half of first axial

Fig. 9. *Oligometopus* and *Cheliocephalus* from Nevada and Oklahoma. (***a–c, k–x***) *Oligometopus breviceps* (Walcott, 1884), from the Corset Spring Shale, section SHP, Shingle Pass, south Egan Range, Nevada, collection SHP 12.6, except (*a*)–(*c*) (Dunderberg Formation, Eureka District, Nevada). (***a–c***) Cranidium, holotype, USNM 24577, (*a*) dorsal, (*b*) anterior, (*c*) and lateral views, × 10. (***k, l***). Cranidium, OU 12387, (*k*) anterior-oblique and (*l*) anterior views, × 10. (***m–o***) cranidium, OU 12388, (*m*) dorsal, (*n*) anterior, and (*o*) lateral views, × 10. (***p–r***) cranidium, OU 12389, (*p*) dorsal, (*q*) anterior, and (*r*) lateral views, × 12. (***s–u***) cranidium, OU 12390, (*s*) lateral, (*t*) anterior, and (*u*) dorsal views, × 12. (***v–x***) cranidium, OU 12391, (*v*) lateral, (*w*) dorsal, and (*x*) anterior views, × 12. (***d–f***) *Oligometopus contractus* Palmer, 1965, from the Corset Spring Shale, section SHP, Shingle Pass, south Egan Range, Nevada, collection 2563—CO. (***d–f***) cranidium, holotype, USNM 141507, (*d*) dorsal, (*e*) lateral, and (*f*) anterior views, × 12. (***g–i***) *Oligometopus minutus* (Frederickson, 1949), from the Honey Creek Formation, Blue Creek Canyon, Wichita Mountains, Oklahoma. (***g–i***) cranidium, holotype, OU 4203a, (*g*) dorsal, (*h*) anterior, and (*i*) lateral views, × 12. (***j***) *Cheilocephalus* sp. indet., from the Honey Creek Formation, Blue Creek Canyon, Wichita Mountains, Oklahoma. (***j***) Cranidium, OU 4203b (designated as a paratype of *O. minutus* by Frederickson, 1949), dorsal view, × 12.

ring. Articulating furrow and axial ring furrows well defined and transverse. Pleural field gently inflated near axis, but flexed steeply downward abaxially; border and border furrow absent. Two pairs of firmly impressed, backwardly curved pleural furrows, and shallower third pair (latter defined more clearly on small specimens; e.g., Fig. 10*f*); interpleural furrows are finely etched grooves. Anteriormost pleural bands strongly convex and subequal in length anteriorly but become less convex posteriorly. Sculpture of fine tubercles covers entire surface, except for furrows and articulating half-rings; as with cranidia, sculpture relatively subdued on some specimens (e.g., Figs. 10*d*, 10*g*).

DISCUSSION: *Oligometopus breviceps* is characterized by a glabella that tapers evenly forward, with the extent of taper increasing with cranidial size (Fig. 11*a*). The only known specimen of *O. minutus* (Frederickson, 1949; Figs. 9*g*–9*i*) also has a conspicuously tapered glabella (Fig. 11*a*), but comparisons with other species are difficult because of incomplete preservation. It appears to differ from *O. breviceps* in having fixigenae that are flexed downward, a somewhat smaller palpebral lobe, and tuberculate sculpture that is restricted to distal portions of the fixigenae and the crest of the glabella.

Material of *O. breviceps* from the Corset Spring Shale show variation in sculpture and in the degree of inflation of the fixigenae, although these traits do not covary. Morphs with weakly (e.g., Figs. 8*f*, 8*i*, 8*q*) and more strongly inflated fixigenae (Figs. 8*b*, 8*k*, 9*b*, 7*g*) include both specimens with well-defined tubercles and those in which tuberculate sculpture is subdued. Pygidia show size-related variation in the expression of the pleural and interpleural furrows. In smaller pygidia, three firmly impressed furrows are present (Figs. 10*e*, 10*f*). The anterior pair of furrows continues to be well defined in larger individuals, but the remainder of the pleural field becomes more weakly furrowed towards the rear (e.g., Figs. 10*a*, 10*i*). In larger specimens, third and fourth axial segments are fused into the terminal piece (compare Figs. 10*a* and 10*g*).

Two cranidia from the Hilliard Creek Limestone of Alaska, assigned questionably to *O. breviceps* by Palmer (1968), are inadequate for a confident identification. The larger of the two specimens (Palmer 1968, pl. 7, fig. 30) is incomplete and exfoliated, but shows deeply incised S1 and S2 furrows that are quite different from the shallow to barely perceptible furrows evident on internal molds of *O. breviceps* from Nevada (e.g., Figs. 8*a*, 8*l*, 8*r*). The other cranidium (Palmer 1968, pl. 7, fig. 30) is very small but has larger palpebral lobes than similarly sized specimens from our collections (Figs. 9*p*–9*r*). We doubt that either specimen is conspecific with *O. breviceps*, but they are significant because they represent an early occurrence of the genus in correlatives of the lower *Dunderbergia* Zone of the Great Basin. The single specimen of *Oligometopus* from the Cow Head Group of western Newfoundland (Kindle 1982, pl. 1.4, fig. 7) also appears to represent a mid-Steptoean record of the genus. It is similar to cranidia of *O. breviceps* but is not complete enough for a firm identification.

Oligometopus minutus (Frederickson, 1949) Figs. 9*g*–9*i*

Bernicella minuta Frederickson, 1949, p. 348, pl. 68, figs. 14, 15 (only; pl. 68, fig. 17 = *Cheilocephalus* sp. indet.; see Palmer 1965, p. 31)

HOLOTYPE: An incomplete cranidium (OU 4203a) from the Honey Creek Formation, Wichita Mountains, Oklahoma (Figs. 9*g*–9*i*).

DIAGNOSIS: *Oligometopus* with fixigenae flexed downward from axial furrow. Sculpture of fine tubercles restricted to distal portions of fixigenae and crest of glabella.

DISCUSSION: As recognized by Palmer (1965), Frederickson's (1949, pl. 68, fig. 17; Fig. 9*j*) paratype of *Oligometopus minutus* belongs to *Cheilocephalus*, so that this species is now known only from the holotype. Stitt (1977, pl. 2, fig. 1; Figs. 10*k*–10*m*) illustrated a single pygidium from his Chandler Creek section in the Wichita Mountain that we assign to *Oligometopus* (see *Oligometopus*. sp.indet. later in the text). Clearly, far more data are needed to determine if it belongs to *O. minutus*.

Oligometopus contractus Palmer, 1965 Figs. 9*d*–9*f*

Oligometopus contractus Palmer 1965, p. 31, pl. 1: 5.

HOLOTYPE: An incomplete cranidium (USNM 141507) from the Corset Spring Shale, Shingle Pass, Nevada (Figs. 9*d*–9*f*).

DIAGNOSIS: *Oligometopus* with narrow palpebral area of fixigena equal to 27% of glabellar width at SO. Glabella relatively broad, so that width at SO is nearly 90% of glabellar length. Palpebral lobe equal to about one-third of glabellar length.

DISCUSSION: Despite extensive collecting at the type locality at Shingle Pass, Nevada, we have not discovered additional material of this species, which is known only from the holotype. This specimen (Figs. 9*d*–9*f*) is clearly differentiated from both *O. contractus* and *O. minutus* by possessing a

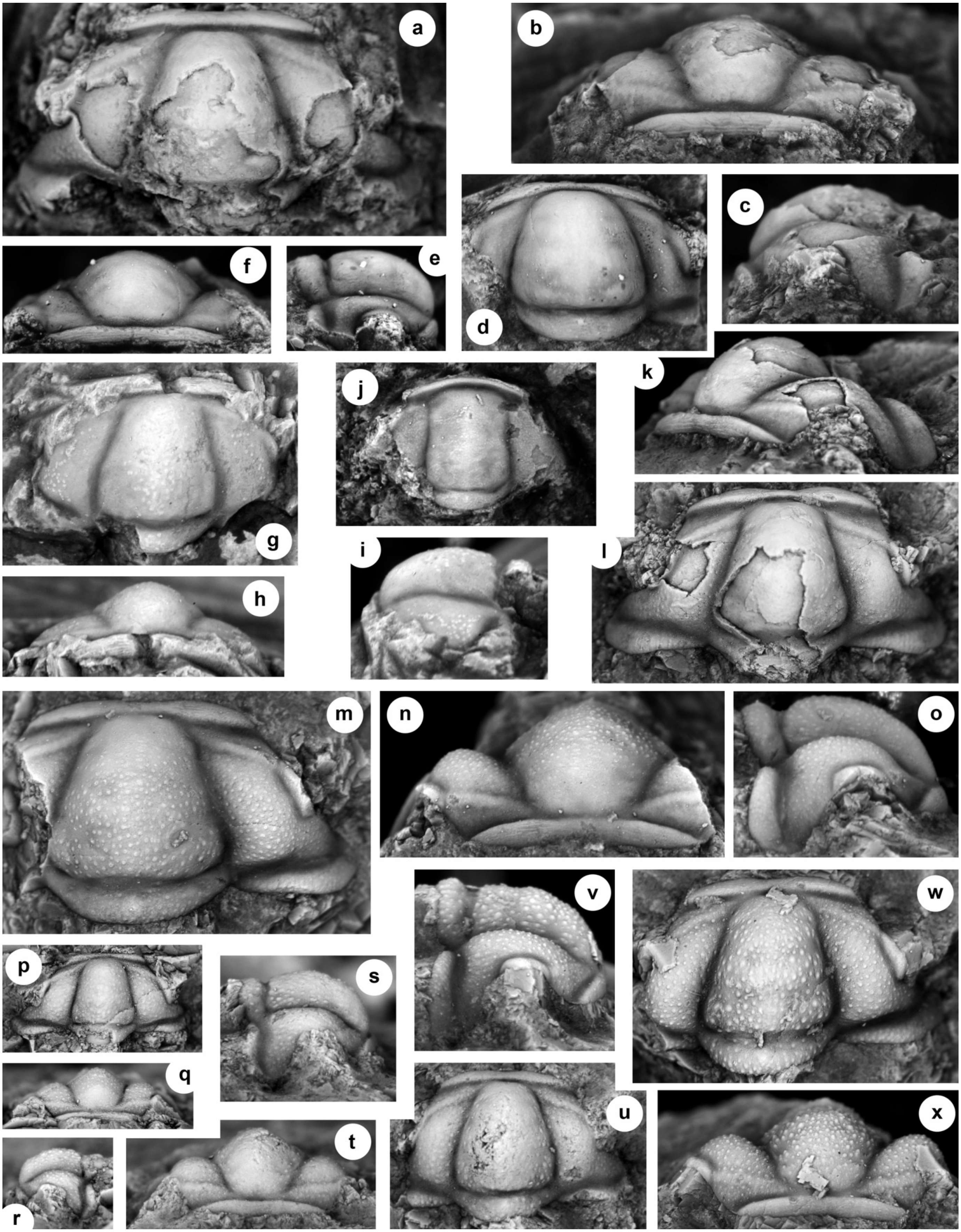

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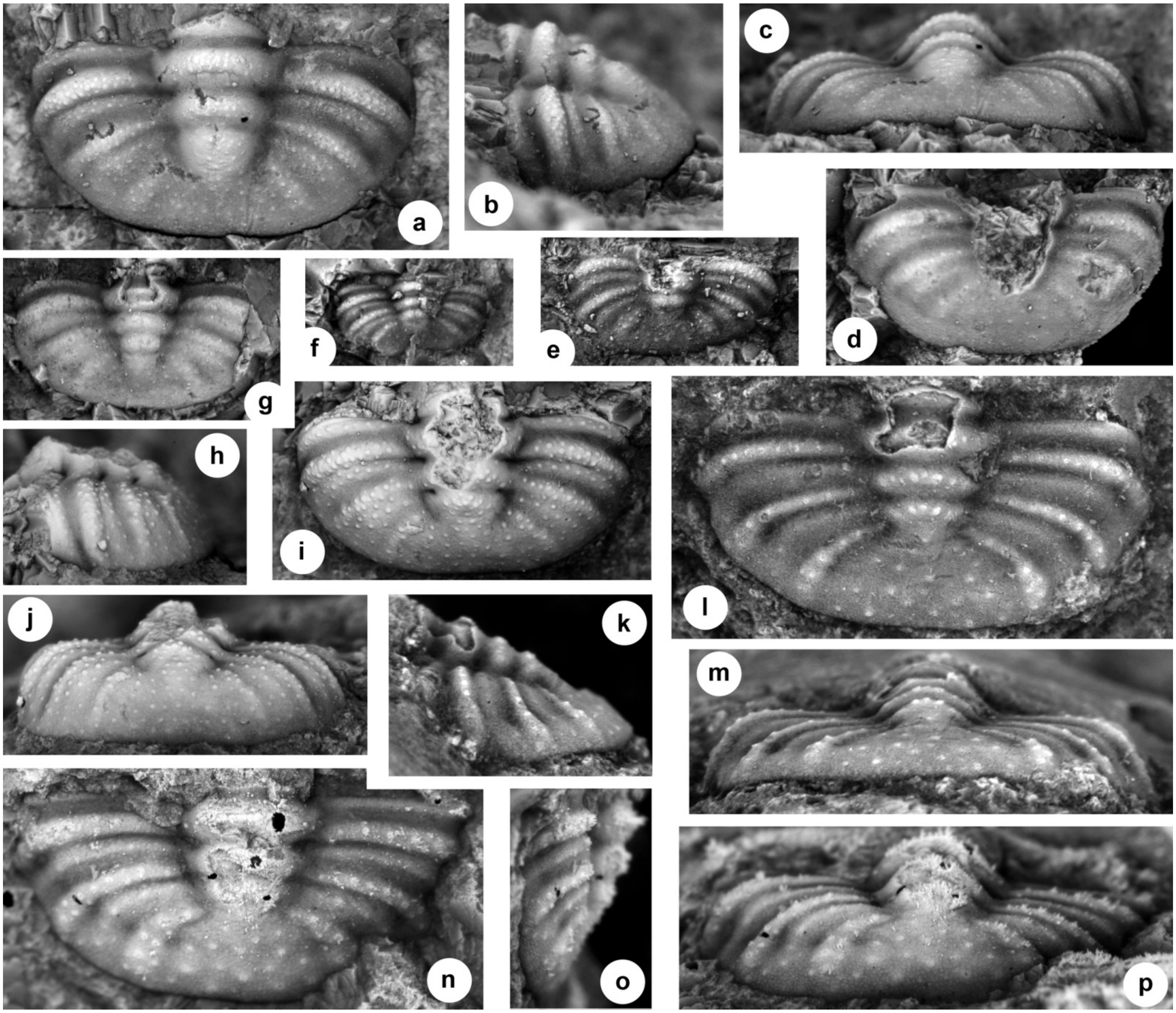
Fig. 10. *Oligometopus* from Nevada, Oklahoma, and Pennsylvania. (***a–j***) *Oligometopus breviceps* (Walcott, 1884), from the Corset Spring Shale, section SHP, Shingle Pass, south Egan Range, Nevada. All from collection SHP 18.25, except (*h*)–(*j*) (SHP 18.6). (***a–c***) pygidium, OU 12392, (*a*) dorsal, (*b*) lateral, and (*c*) posterior views, × 12. (***d***) pygidium, OU 12393, dorsal view, × 12. (***e***) pygidium, OU 12394, dorsal view, × 12. (***f***) pygidium, OU 12395, dorsal view, × 12. (***g***) Pygidium, OU 12396, dorsal view, × 12. (***h–j***) pygidium, OU 12397, (*h*) lateral, (*i*) dorsal, and (*j*) posterior views, × 12. (***k–p***) *Oligometopus* sp. indet. (***k–m***) pygidium, OU 8209, (*k*) posterior, (*l*) lateral, and (*m*) dorsal views, Honey Creek Formation, Chandler Creek, Wichita Mountains, Oklahoma, collection CC 319 × 12. (***n–p***) pygidium (latex cast from external mould), YPM 18601, (*n*) dorsal, (*o*) lateral, and (*p*) posterior views, Ore Hill Member, Gatesburg Formation, Potter Creek, Pennsylvania, collection 47–5w.8a, × 12.



much narrower palpebral area of the fixigena (Fig. 11*b*). Compared to these species, the glabella is relatively broader and less tapered anteriorly, and the palpebral lobe is somewhat larger.

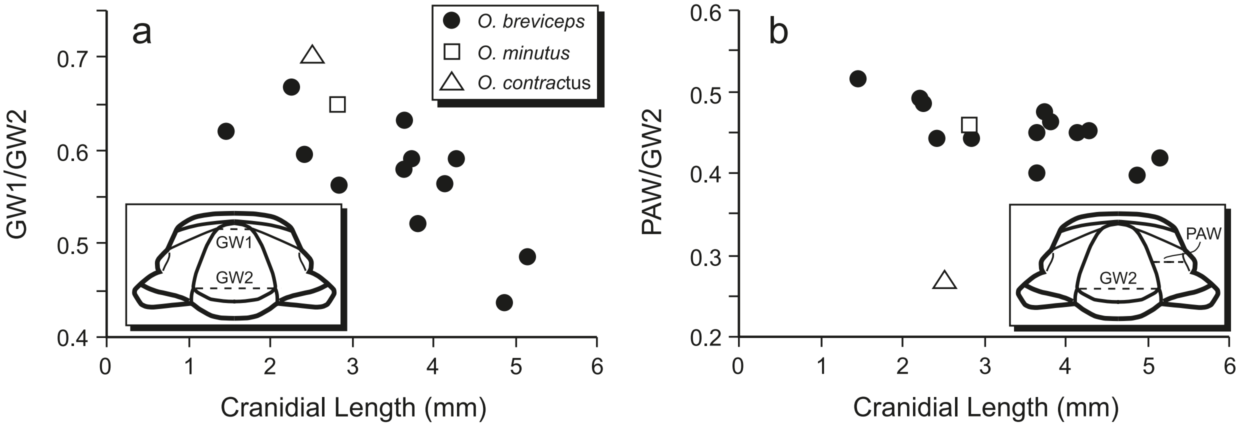
Oligometopus sp. indet. Figs. 10*k*–10*p*

Unassigned pygidium L; Wilson, 1951, p. 650, pl. 95, fig. 14

Unassigned pygidium L; Wilson, Stitt 1977, p. 50, pl. 2, fig. 1

DISCUSSION: Stitt (1977) identified a pygidium (Figs. 10*k*–10*m*) from the Honey Creek Formation, Wichita Mountains, Oklahoma, as "unassigned pygidium L" Wilson 1951, which was based on a single specimen (Figs. 10*n*–10*p*) from the Ore Hill Member of the Gatesburg Formation. Neither Wilson nor Stitt was able to assign these pygidia to a genus, but they are regarded herein as representing an indeterminate species of *Oligometopus*. They share several features with similarly sized pygidia of *O. breviceps* (Figs. 9*a*–9*c*, 9*h*–9*j*), including a short axis with three segments, firmly impressed pleural furrows that define convex, subeq-

Fig. 11. Bivariate plots of cranidial parameters of *Oligometopus*. (*a*) Plot of the ratio between glabella width opposite palpebral ridges (GW1) and glabella width at SO (GW2) against cranidial length. For *Oligometopus breviceps* (Walcott), this ratio declines with increasing cranidial length as the extent of anterior taper of the glabella increases. (*b*) Plot of the ratio between palpebral area width (PAW) and glabellar width at SO (GW2) against cranidial length. The only known cranidium of *O. contractus* Palmer is a distinct outlier characterized by a relatively narrow palpebral area.



ual pleural bands, the absence of a border, and tuberculate sculpture. They differ from *O. breviceps* in having relatively broader pleural fields that are less strongly flexed downward distally (e.g., compare Figs. 10*n* and 10*p* with Fig. 10*j*), and shorter axes. Unlike similarly sized pygidia of *O. breviceps*, the third pair of pleural furrows and pleural bands are well defined (in this respect, they resemble small pygidia of *O. breviceps*; Figs. 10*e*, 10*f*), and the pleural furrows deepen distally to form pit-like terminations (e.g., Figs. 10*l*–10*n*).

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