

# The missisquoiid trilobite *Parakoldinioidia* Endo 1937 in the uppermost Cambrian of Oklahoma and Texas, and its biostratigraphic significance

STEPHEN R. WESTROP & JONATHAN M. ADRAIN

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Missisquoiid trilobites are widespread in Laurentian North America but most occurrences have been reported under a single name, *Missisquoia typicalis* Shaw 1951 (now = *Parakoldinioidia stitti* Fortey 1983). The base of the *Parakoldinioidia* Zone (= *Missisquoia typicalis* Subzone of older publications) is usually defined by the first appearance of the eponymous genus. In central Texas, the type area of the zone, three species have been recorded, and only one species is reported from correlative strata in Oklahoma. Restudy of archival collections from southern Oklahoma made by J.H. Stitt, as well as type and figured material from Texas and western Canada, revealed unexpected diversity of missisquoiid species. Our revision shows that there are at minimum ten species of *Parakoldinioidia* and three species of *Lunacrania* recorded in the uppermost Furongian successions of the southern Midcontinent and the southern Canadian Rocky Mountains. This indicates that Missisquoiidae underwent a significant radiation following the extinction interval at the base of the *Eureka apopsis* Zone. It also demonstrates the potential for a high-resolution species based zonation of at least regional utility. New species are *Parakoldinioidia akerfeldti*, *P. lindgreni*, *P. mendezi*, *P. lopezi* and *P. akessoni*; three additional new species are placed in open nomenclature.

Stephen R. Westrop (swestrop@ou.edu), Oklahoma Museum of Natural History and School of Geology and Geophysics, University of Oklahoma, Norman, Oklahoma 73072, USA; Jonathan M. Adrain (jonathan-adrain@uiowa.edu), Department of Earth and Environmental Sciences, University of Iowa, Iowa City, Iowa 52242, USA. Received 23 August 2013.

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TRILOBITES of the family Missisquoiidae Hupé 1955 occur throughout Laurentian North America in a relatively narrow interval of what is now the latest Cambrian succession (e.g., Shaw 1951; Winston & Nicholls 1967; Stitt 1971, 1977; Taylor & Halley 1974; Ludvigsen 1982; Fortey 1983; Westrop 1986; Dean 1989). Although widely distributed, both geographically and environmentally, missisquoiid trilobites have been assigned traditionally to a small number of species of *Missisquoia* Shaw 1951. However, Fortey (in Fortey *et al.* 1982) argued that *Lunacrania* Kobayashi 1955 was a valid genus (see Dean 1977 for an alternative interpretation), and later (1983) proposed that *Missisquoia* was a junior synonym of *Parakoldinioidia* Endo 1937. Fortey's views prevailed, albeit slowly (e.g., Adrain in Jell & Adrain 2003; Westrop in Landing *et al.* 2011), and Lee *et al.* (2008) expanded the roster of Laurentian missisquoiid genera further by removing *Tangshanaspis* Zhou & Zhang 1978 from synonymy with *Parakoldinioidia* (see Ludvigsen 1982).

Despite these revisions to the supraspecific systematics, the number of missisquoiid species reported from the Laurentian uppermost Cambrian strata remains low. Nowhere is this more obvious than in the classic succession of Oklahoma, which was collected in fine stratigraphic detail by Stitt (1971, 1977). Through an interval of 61 metres in the Joins Ranch section (JoR-1058—JoR-1257; Stitt 1971), Stitt viewed Missisquoiidae as represented by only two species, *Tangshanaspis depressa* (Stitt 1971) and *Parakoldinioidia*

*stitti* Fortey 1983 (= *Missisquoia typicalis* of Stitt). The latter species has been recorded throughout Laurentia under the name, *Missisquoia typicalis* Shaw (e.g., Shaw 1951; Winston & Nicholls 1967; Stitt 1971, 1977; Taylor & Halley 1974; Fortey *et al.*, 1982; Westrop 1986; Dean 1989). However, Lee *et al.* (2008) noted that this taxon likely represents more than one species, and were unable to code it for phylogenetic analysis. Westrop (in Landing *et al.* 2011) agreed with Lee *et al.*, and restricted *P. stitti* to its variably deformed type material from Vermont (Shaw 1951).

Westrop (2013) recently evaluated the record of *Tangshanaspis* in Laurentia and concluded that Stitt (1971) erroneously associated sclerites of two distinct species when he named *Missisquoia depressa*. Moreover, isolated pygidia suggested that there might be as many as four species of *Tangshanaspis* represented in the Signal Mountain Formation of Oklahoma. Here, we continue the revision of Laurentian Missisquoiidae from restudy of Stitt's (1971, 1977) collections from Oklahoma, as well as type material from Texas and western Canada. Our results change the history of Laurentian missisquoiids from relative stasis to a significant radiation following the terminal Sunwaptan (base of *Eureka apopsis* Zone) extinction interval. *Parakoldinioidia* is represented in Oklahoma and Texas by far more species than recognised previously, and this has significant biostratigraphic implications. Moreover, restudy of figured and associated material from collection CC-93 from the Wilberns Formation at Calf Creek, Texas

(Winston & Nicholls 1967) demonstrates that as many as five missisquoid species [*Parakoldinioidia inflata* (Winston & Nicholls); *Lunacrania nasuta* (Winston & Nicholls); *P. sp. nov. A*; *P. cf. sp. nov. A*; *P. n. sp. C*] co-occur in a single sample.

Our study also demonstrates the value of high-resolution digital photography in the revision of archival collections. It is now possible to produce publication quality images quickly in large numbers and, not surprisingly, this leads to new interpretations of material that was studied half-a-century ago largely with light microscopy.

## MATERIAL AND LOCALITIES

This study is based largely on archival material from the J.H. Stitt collection housed at the Oklahoma Museum of Natural History. Changes in land ownership have prevented access to classic localities in the Arbuckle Mountains sampled by Stitt (1971), so that previously unfigured sclerites from his field collections are the only source of new information on trilobite faunas of this part of southern Oklahoma. Much of the material in these collections is only partly prepared, and further excavation of sclerites revealed unanticipated diversity of species of *Parakoldinioidia* (Figs 4–15, 25). Restudy of missisquoids from Texas (Winston & Nicholls 1967; Figs 2, 3, 16–19, 24) and western Canada (Kobayashi 1955; Dean 1977, 1989; Figs 18I–K, 20–24) also demonstrates surprising taxonomic complexity.

*Southern Oklahoma.* Stitt's (1971, 1977, 1983) monographs present the results of detailed stratigraphic sampling of sections in the Arbuckle Mountains and in the limestone hills on the north flank of the Wichita Mountains. Although the collections are closely spaced stratigraphically, most include only a handful of sclerites of variable quality of preservation. Missisquoids (*Parakoldinioidia*; *Lunacrania*) occur in the upper Signal Mountain Formation, a succession of shallow water carbonates that include bioclastic wacke- and packstone, intraclastic and oolitic packstone, and intraclastic rudstone; tongues of dolostone may interrupt the succession in both the lower (Royer Dolomite) and the upper (Butterfly Dolomite) Signal Mountain (Stitt 1971). The best preserved and most abundant sclerites of *Parakoldinioidia* come from the Joins Ranch section (Stitt 1971, p. 59), Murray County. At this locality, species of *Parakoldinioidia* enter the succession at 339.5 m (collection JoR–1114) above the base of the section and have their highest occurrence at 383.0 m above the base (collection JoR–1257). However much of this material is poorly preserved and resists preparation, particularly where neomorphism has converted lime mud into microspar. Sclerites suitable for systematic work at the species level are restricted to six collections (JoR–1125, 1153, 1171, 1187, 1190 and 1199) between 342.9 m and 365 m above the base, but even here, small sample sizes present difficulties. No useful material was recovered from collections from Stitt's (1971) US Highway 77 section, also in Murray County. Preservation of sclerites of *Parakoldinioidia* in the Chandler Creek section, Comanche County (Stitt 1977), is generally very poor, to the point that species level identifications are usually impossible. Two collections, CC–1547 and CC–1605, 471.5 m and 489.2 m above the base of the section, yielded specimens that are included in this study. Taken together, the collections indicate that a minimum of six species of *Parakoldinioidia* (*P. akerfeldti* sp. nov., *P. lindgreni* sp. nov., *P. mendezi* sp. nov., *P. lopezi* sp. nov., *P. akessonii* sp. nov. and, possibly,

*P. inflata* Winston & Nicholls 1967) and one species of *Lunacrania* occur in the upper Signal Mountain Formation in southern Oklahoma. All of this material was identified as *Missisquoia typicalis* by Stitt (1971, 1977).

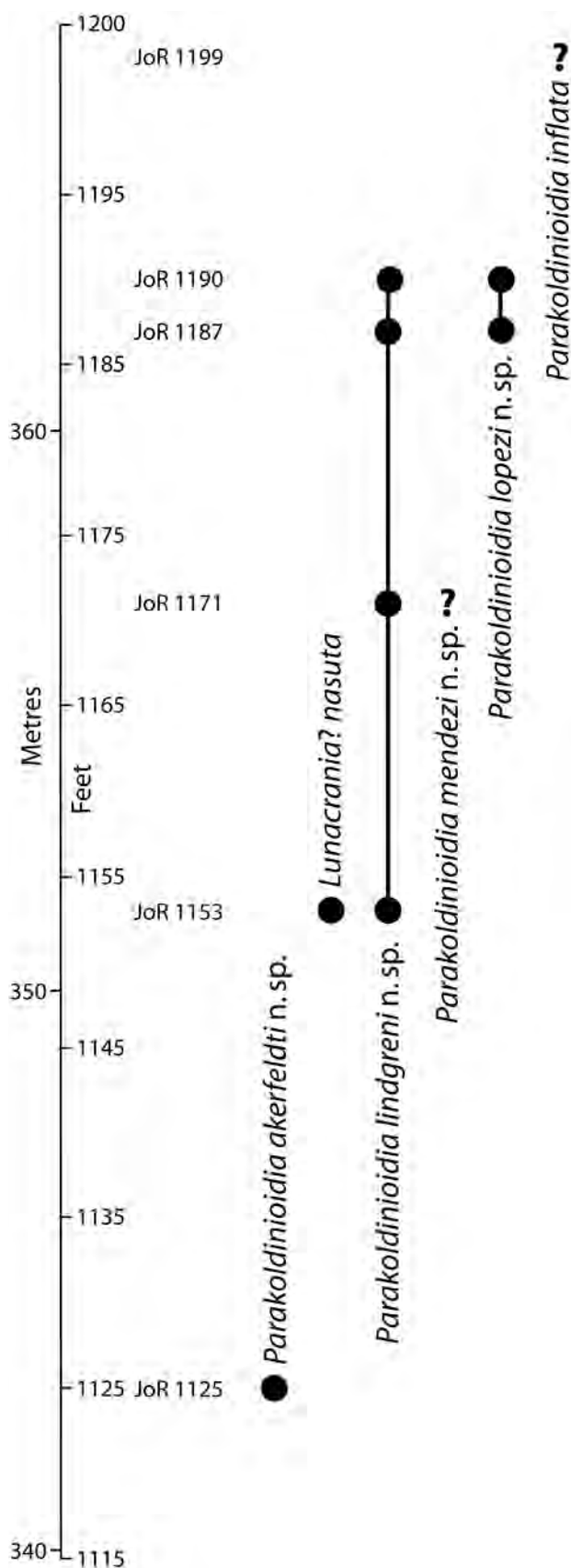
*Central Texas.* Missisquoid trilobites were first described from the San Saba Member of the Wilberns Formation of Mason and McCulloch counties by Winston & Nicholls (1967), who assigned their material to three species of *Missisquoia*. Although stratigraphic and geographic occurrence data (Winston & Nicholls 1967, p. 89) indicate that missisquoids occurred in numerous samples through their study area, all but two of the figured specimens are from the Calf Creek section, Mason County, and most of these come from a single horizon, CC–93. All are reillustrated here, along with some previously unfigured sclerites that were associated with figured specimens. *Parakoldinioidia inflata* (Winston & Nicholls 1967) and *Lunacrania nasuta* (Winston & Nicholls 1967) are valid species, and we can show that at least five additional species of *Parakoldinioidia* (*P. lindgreni*, *P. sp. nov. A*, *P. cf. sp. nov. A*, *P. sp. nov. B*, *P. sp. nov. C*) are represented in the San Saba Member.

*Alberta and British Columbia.* Species of *Parakoldinioidia* and *Lunacrania* from Alberta that are included in the study are mostly from the Basal Silty Member of the Survey Peak Formation at Wilcox Pass, Jasper National Park, and were illustrated previously by Dean (1977, 1989). This unit is composed of shale and storm-influenced carbonates that include bioclastic pack- and grainstone, and intraclastic rudstone; small thrombolitic buildups are also present (Westrop 1989). We also reillustrate two cranidia from uppermost Cambrian strata to the north of Jasper National Park, and several types from the McKay Group at Jubilee Mountain, near Harrogate, British Columbia (Kobayashi 1955). At least two species of *Lunacrania* and one species of *Parakoldinioidia* are represented among Dean's figured material from Wilcox Pass, but they are placed in open nomenclature, largely because of uncertainties regarding the correct sclerite associations. The cranidium and pygidium illustrated by Westrop (1986, pl. 1, figs. 35–37) from the Basal Silty Member at Wilcox Peak almost certainly represents an additional new species of *Parakoldinioidia*.

## BIOSTRATIGRAPHY

The study interval comprises the uppermost Furongian (global "Stage 10"; Babcock & Peng 2007), which corresponds to the lower Skullrockian of the Laurentian nomenclature (Landing *et al.* 2011, fig. 1). Traditionally, the Skullrockian was the lowest part of the Ordovician in Laurentia (Ross *et al.* 1997) but recent revisions of global nomenclature (Babcock & Peng 2007) now place the lower part of it in the uppermost Cambrian. Winston & Nicholls (1967) assigned these strata to the *Missisquoia* Zone, which was modified by Stitt (1977) to comprise a lower *M. depressa* Subzone and an upper *M. typicalis* Subzone. Changes to generic nomenclature led Landing *et al.* (2011) to modify this two-fold division into a *Tangshanaspis* Zone and an overlying *Parakoldinioidia* Zone.

Revision of *Tangshanaspis* by Westrop (2013) has shown that the *Tangshanaspis* Zone may ultimately be replaced by two species based zones. Recognition that *Parakoldinioidia* is represented in Oklahoma and Texas by at least eight species (see below; see also Lee *et al.* 2008, p. 324, table 4), some of which are shared between these regions, suggests



**Figure 1.** Stratigraphic ranges of species of *Parakoldinioidia* in the most fossiliferous interval of the upper Signal Mountain Formation, Joins Ranch section, Murray County, Oklahoma (Stitt, 1971, p. 58).

that there is as yet unrealised potential for a species based zonation for the remainder of the Furongian.

In Oklahoma, the most fossiliferous interval of the upper Signal Mountain Formation at the Joins Ranch section (Fig. 1) begins with the appearance of *P. akerfeldti* sp. nov., with *P. lindgreni* sp. nov. and *Lunacrania nasuta* entering eight and a half metres higher in succession. The upper three metres of this fossiliferous interval has yielded *P. lopezi* sp. nov. and, possibly, *P. inflata*.

*Parakoldinioidia lindgreni*, *P. inflata* and *L. nasuta* are also present in Wilberns Formation of central Texas (see below). The latter two species co-occur in collection CC-93 at Calf Creek, and *P. lindgreni* occurs about a metre lower in the same section (collection CC-90). Unfortunately, taxonomic problems (see below) mean that the full ranges of *P. lindgreni* and *L. nasuta* cannot be determined from the data presented by Winston & Nicholls (1967). However, with more information from Texas and Oklahoma, it seems likely that it will be possible to replace the *Parakoldinioidia* Zone of the southern midcontinent with a set of two or more species assemblage zones. *Parakoldinioidia* sp. nov. C also occurs in collection CC-93 and is very similar to *P. cf. sp. nov. C* from Alberta (compare Figs 19 and 21). This indicates that it may be possible to broadly correlate any zonation developed for the midcontinent to other regions of Laurentia.

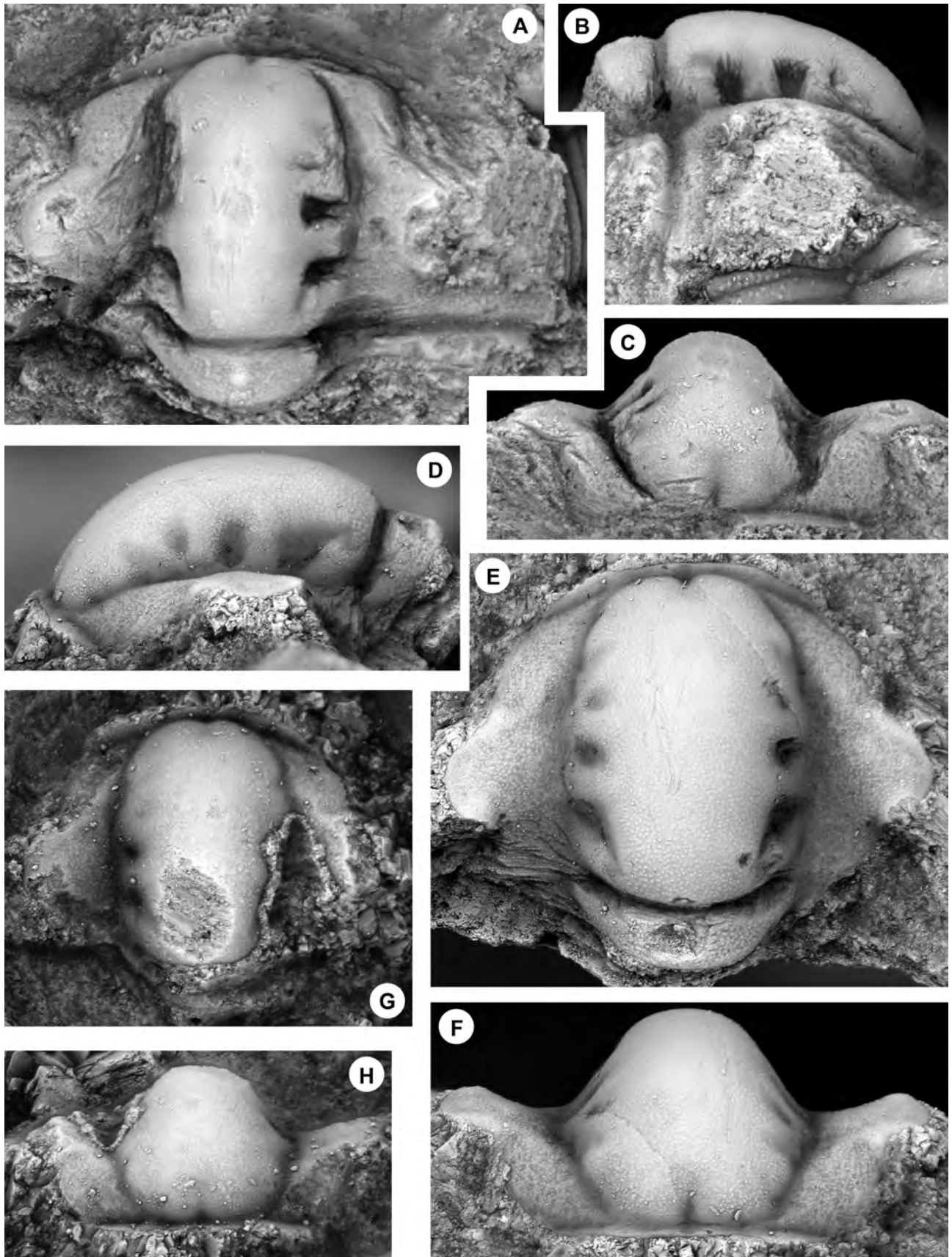
#### SYSTEMATIC PALAEOLOGY

Illustrated material is housed at the Geological Survey of Canada, Ottawa (GSC), the Oklahoma Museum of Natural History (OMNH), and the National Museum of Natural History, Washington, DC (USNM). To maximise depth of field, all digital images were rendered from stacks of images focused at 100 micron intervals using Helicon Focus 4.0 for the Macintosh <<http://www.heliconsoft.com>>. 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 LEIOSTEGIOIDEA Bradley 1925  
Family MISSISQUOIIDAE Hupé 1955

*Discussion.* Lee *et al.* (2008) presented the most comprehensive revision of Missisquoidae attempted to date, and we have used some of their generic concepts and parts of their diagnoses. We will comment on their phylogenetic analysis elsewhere, in conjunction with an analysis of our own. Suffice to say that placement in their cladograms of a species of the oryctocephalid *Oryctocephalus* Walcott 1886 within Missisquoidae as a sister to either *Tangshanaspis* or *Tasmanocephalus* Kobayashi 1936 (Lee *et al.* 2008, fig. 5) indicates that there are issues of taxon selection and likely character coding that need to be addressed. An outgroup for phylogenetic analysis should be sought within Leiostegioidea.

We follow Lee *et al.* (2008) in considering Missisquoidae to include *Parakoldinioidia*, *Tasmanocephalus*, *Pseudokoldinioidia* Endo 1944 and *Tangshanaspis*; we treat *Lunacrania* as an unequivocal missisquoid, but agree with Lee *et al.* that there are some doubts about the affinities of *Hardyia* Walcott 1924, largely because there is so little reliable information on the anatomy of this genus. *Parakoldinioidia* encompasses a wide range of cranial and, particularly, pygidial morphologies (e.g., Figs 3F–H,



**Figure 2.** *Parakoldinioidia inflata* (Winston & Nicholls 1967), San Saba Member, Wilberns Formation, Calf Creek section, Mason County, central Texas. All cranidia from collection CC-93 and all x20; **A–C**, USNM 185932 (paratype), dorsal, lateral and anterior views; **D–F**, USNM 185931 (holotype), lateral, dorsal and anterior views; **G, H**, USNM 560652 (previously unfigured, associated with USNM 185928), dorsal and anterior views.

7, 21), and it is likely that additional monophyletic groups will emerge from further phylogenetic analysis of the family. For example, *Parakoldinioidea inflata* (Winston & Nicholls 1967) is closely related to *P. lopezi* sp. nov. from Oklahoma (see below), and material identified as *P. inflata* from Alberta (Loch *et al.* 1993) may prove to represent a third member of this group. These species may well represent a missisquoiid clade characterised by a strongly inflated glabella standing well above the level of weakly convex fixigenae, an abbreviated anterior cranial border, and a pygidium that possesses a long median spine. However, lingering uncertainties over sclerite associations (see below) prevent formal naming of this group at this time.

#### **Parakoldinioidea** Endo 1937

*Type species.* *Parakoldinioidea typicalis* Endo 1937 from the Yenchou Formation, Liaoning, China (by original designation).

*Diagnosis.* Convex, cylindrical to anteriorly tapered glabella outlined fully by axial and preglabellar furrows. Pygidium subtriangular in outline, strongly arched and with well developed axial ring furrows and pleural furrows.

*Discussion.* Monophyly of several missisquoid genera is supported by potentially apomorphic character states. Species of *Tangshanaspis* share such traits as a weakly convex glabella that is constricted medially, partial to complete effacement of the librigenal border and a broad, relatively flat, semielliptical pygidium (Westrop 2013). As discussed later, *Lunacrania* can be diagnosed by a suite of cranial and pygidial characters. Autapomorphies of *Tasmanocephalus* include posteriorly positioned palpebral lobes, conspicuous palpebral ridges, an anterior border that widens abaxially around the anterior margin of the glabella, and broad genal spines (e.g., Jell & Stait 1985, p. 43, pl. 16). Following Lee *et al.* (2008), *Pseudokoldinioidea* consists of species that are united by a convex glabella that expands anteriorly to a nearly truncate margin (“inverted trapezoidal glabella” of Lee *et al.*, p. 324) and which lacks a median furrow at the anterior margin (e.g., Zhou & Zhang 1985, pl. 24, figs 5, 6; Lu & Zhou 1990, pl. 16, figs 1, 3–5). Unlike other missisquoids, the pygidium of *Pseudokoldinioidea* (e.g., Qian in Chen 1986, pl. 70, fig. 8) has a narrow, rim-like border along much of the lateral and posterior margins, and the pleural field is traversed by firmly impressed interpleural and, particularly, pleural furrows.

In contrast, monophyly of *Parakoldinioidea* seems less secure, and the diagnosis presented above is provisional. Diagnostic characters identified by Lee *et al.* (2008, p. 321) may be plesiomorphic, and the status of the genus is ambiguous. For example, glabellar outline is shared with some species of *Lunacrania*, as is the presence of a median furrow anteriorly (Fig. 24). *Lunacrania* is also characterised by effacement of the axial ring, pleural and interpleural furrows over much of the pygidium, so that the more furrowed configuration of species assigned to *Parakoldinioidea* may represent the plesiomorphic condition (e.g., compare Fig. 7 and Fig. 251). At the same time, there may be additional phylogenetic structure obscured by the current broad concept of *Parakoldinioidea* (see above) and this underscores the need for further phylogenetic analysis of Missisquoidae.

**Parakoldinioidea inflata** (Winston & Nicholls 1967) (Fig. 2, ?Fig. 3, ?Fig. 4)

1967 *Missisquoia inflata*; Winston & Nicholls, p. 89, pl. 13, figs. 4, 7

?1967 *Missisquoia typicalis* Shaw; Winston & Nicholls, p. 88, pl. 13, fig. 18 [only; fig. 2 = indet. trilobite; fig. 5 = *Parakoldinioidea lindgreni* sp. nov.; fig. 6 = *P. sp. nov.* B; figs. 10, 12 = *P. sp. nov.* C; fig. 15 = *P. sp. nov.* A?].

1971 *Missisquoia inflata* Winston & Nicholls; Hu, p. 108.

? 1993 *Missisquoia inflata* Winston & Nicholls; Loch *et al.*, p. 509, fig. 8.11, 8.12.

1997 *Missisquoia inflata* Winston & Nicholls; Ross *et al.*, p. 16, fig. 8.

2000 *Missisquoia inflata* Winston & Nicholls; Yuan & Yin, p. 252.

2003 *Missisquoia inflata* Winston & Nicholls; Miller *et al.*, p. 53.

2007 *Missisquoia inflata* Winston & Nicholls; Lee & Choi, p. 1460.

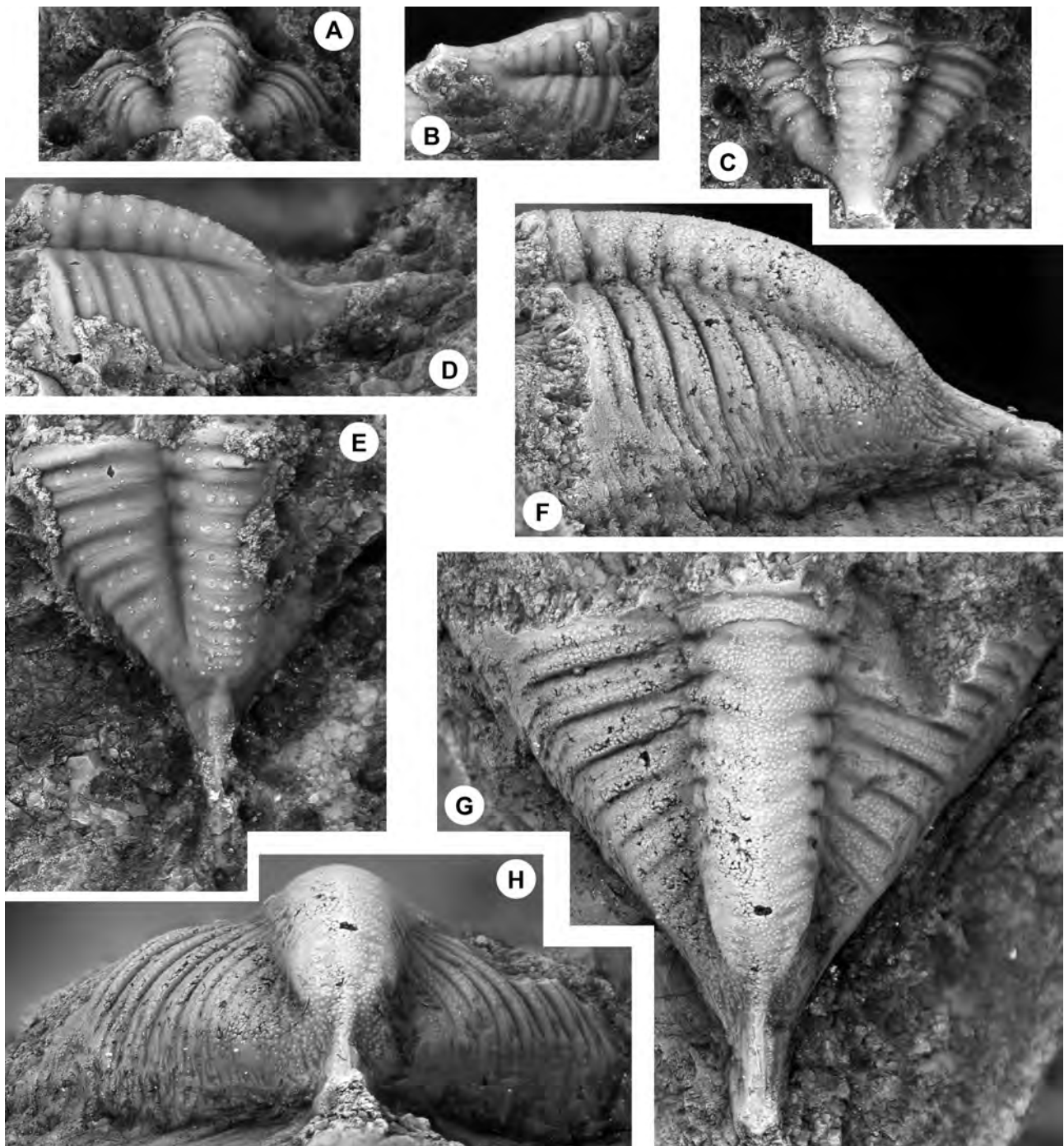
2008 *Lunacrania? inflata* (Winston & Nicholls); Lee *et al.*, p. 332, appendix 1

*Diagnosis.* Cranium with very short anterior border equal to about 4% of cranial length. Axial furrows bowed gently outwards. Glabella strongly convex, raised well above gently upsloping palpebral area of fixigena; S1 and S2 firmly impressed, S3 pit-like. Cranial sculpture with closely spaced granules (Fig. 2E) over entire surface except for glabellar furrows, anterior border and palpebral lobes. Pygidial assignment uncertain, although all completely preserved candidates possess a long marginal spine behind the axis.

*Holotype.* A cranium (USNM 185931; Fig. 2D–F) from the San Saba Member, Wilberns Formation, Mason County, Texas.

*Occurrence.* San Saba Member, Wilberns Formation, Calf Creek section, Mason County, central Texas (Winston & Nicholls 1967), collection CC–93; possibly Signal Mountain Formation, Joins Ranch Section, Murray County, Oklahoma (Stitt 1971, p. 59), collection JoR–1199 (Fig. 4); possibly Basal Silty Member, Survey Peak Formation, Mount Wilson, Banff National Park, Alberta (Loch *et al.* 1993).

*Discussion.* Lee *et al.* (2008) assigned *Parakoldinioidea inflata* questionably to *Lunacrania*. However, it is almost certainly unrelated to *Lunacrania* as it lacks synapomorphies of that group (see below), and it is more likely related to species of *Parakoldinioidea*. The paratype cranium of *P. inflata* has undergone additional, rather clumsy preparation (compare Fig. 1A–C with Winston & Nicholls 1967, pl. 13, fig. 7) that removed part of the left side of the glabella and enlarged the remaining lateral glabellar furrows. It is unclear when this preparation took place. Winston (in Winston & Nicholls 1967, p. 66) indicated that he published plates constructed by Nicholls in the late 1950s as part of his unfinished M.A. thesis research, so that preparation likely occurred at a later date; perhaps during the summers of 1963 and 1964, when Winston noted that he restudied the collections. Fortunately, the holotype (Fig. 1D–F) was left untouched, and we also illustrate a previously unfigured, small, incomplete cranium (Fig. 2G, H) from the same collection (CC–93), associated with the holotype



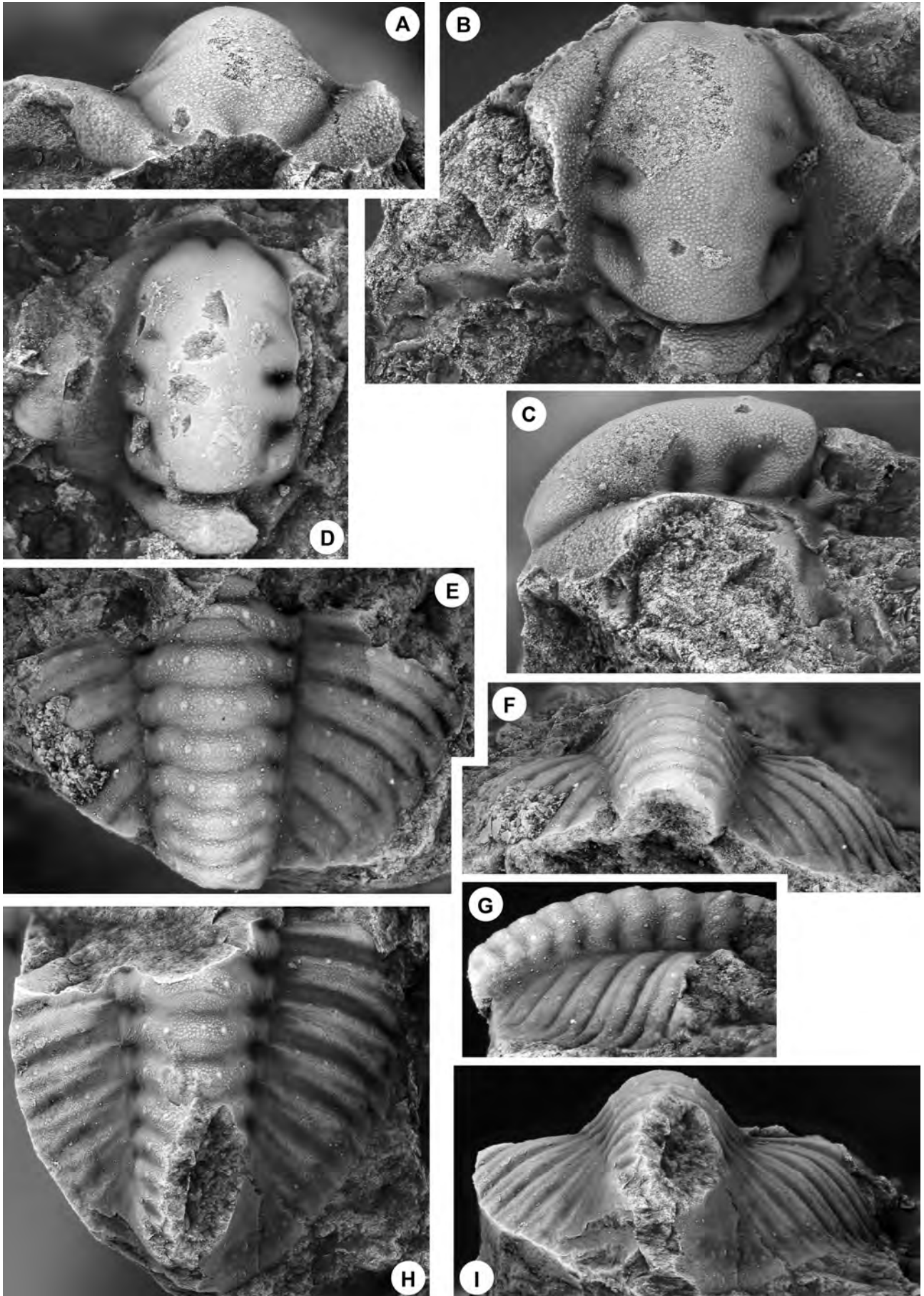
**Figure 3.** *Parakoldinioidia inflata* (Winston & Nicholls 1967)?, San Saba Member, Wilberns Formation, Calf Creek section, Mason County, central Texas. All pygidia from collection CC-93 and assigned questionably to the species. A–C, USNM 560653 (previously unfigured, associated with USNM 185922), posterior, lateral and dorsal views, x20; D, E, USNM 560654 (previously unfigured, associated with USNM 185922), lateral and dorsal views, x20; F–H, USNM 185930 (illustrated previously as *Missisquoia typicalis* Shaw by Winston and Nicholls 1967, pl. 13, fig. 18), lateral, dorsal and posterior views, x14

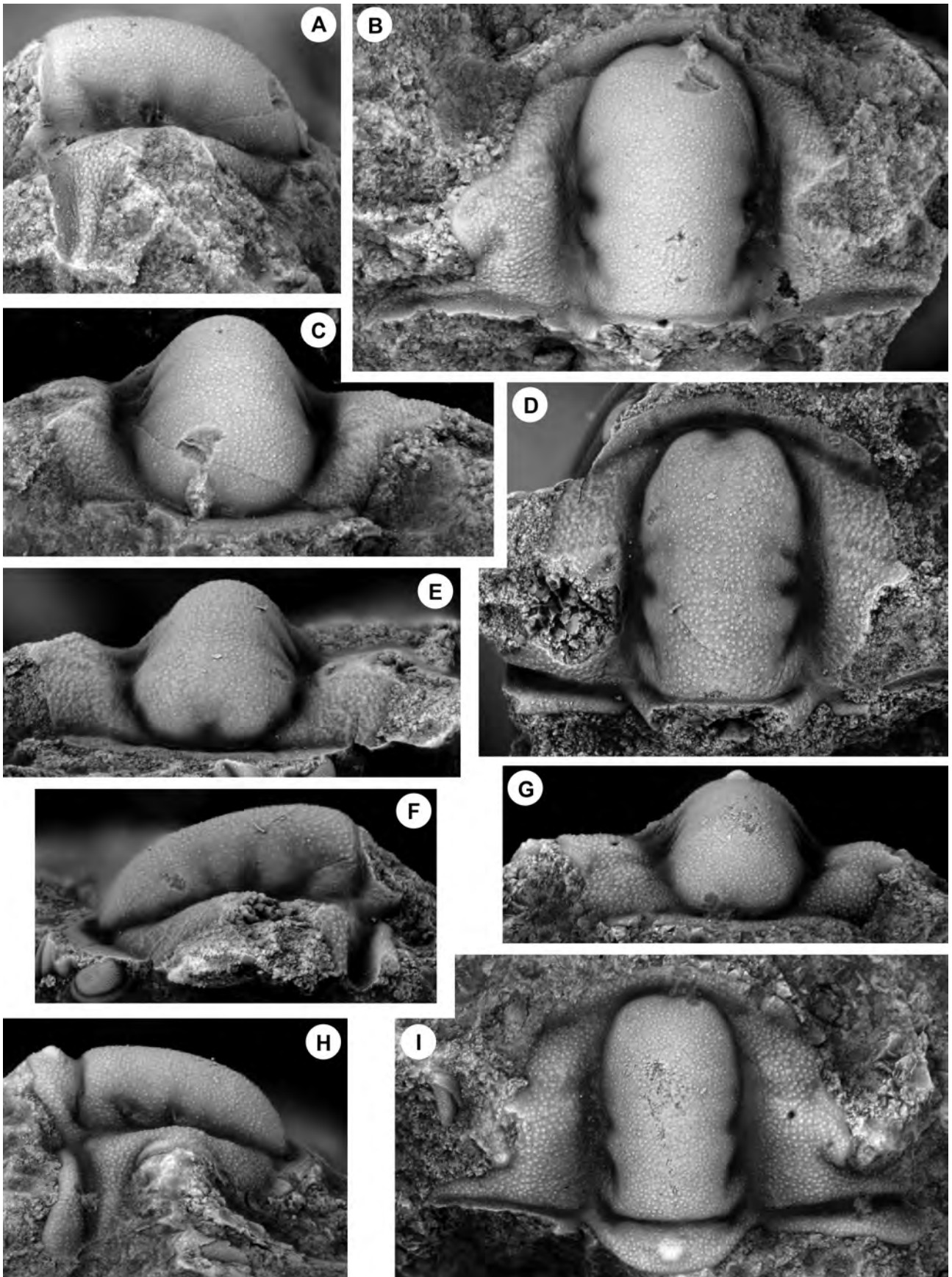
of *Lunacrania nasuta* (Winston & Nicholls 1967), to provide additional information on glabellar morphology.

Loch *et al.* (1993, p. 509) were the first to suggest that *P. inflata* possessed a spinose pygidium, and noted that cranidia of this species were associated with “spined, densely

granulated pygidia” in Texas. Three spinose pygidia (Fig. 3) occur with the type cranidia in collection CC-93 at Winston & Nicholls’ (1967) Calf Creek section. Only the smallest of these (Fig. 3A–C; previously unfigured) appears to conform to the description by Loch *et al.* (1993, p. 509) in having

**Figure 4** (opposite). *Parakoldinioidia inflata* (Winston & Nicholls 1967)?, Signal Mountain Formation, Joins Ranch Section, Murray County, Oklahoma. All from collection JoR-1199 and assigned questionably to the species. A–C, cranidium, OU 13199, anterior, dorsal and lateral views, x18; D, cranidium, OU 13200, dorsal view, x20; E–G, pygidium, OU 13201, dorsal, posterior and lateral views, x18; H, I, pygidium, OU 13202, dorsal and posterior views, x11.





**Figure 5.** *Parakoldinioidia akerfeldti* sp. nov., Signal Mountain Formation, Joins Ranch Section, Murray County, Oklahoma. All cranidia from collection JoR-1125 (Stitt 1971, p. 59) and all x20. **A–C**, OU 13203, lateral, dorsal and anterior views; **D–F**, OU 13204, dorsal, anterior and lateral views; **G–I**, OU 13205 (holotype), anterior, lateral and dorsal views.



only one well defined axial ring, and only three distinct pleurae with firmly impressed pleural furrows. However, the sculpture of barely perceptible, widely separated granules on the pleural bands and axial rings contrasts with the closely packed granules of the holotype cranium (Fig. 2D–F).

The largest pygidium from CC–93 (Fig. 3F–H; Winston & Nicholls 1967, pl. 13, fig. 18) is more convex with a long, multisegmented axis that includes one well incised, complete axial ring furrow anteriorly, six additional rings that are clearly defined only at the axial furrows, and at least six more short, ill defined segments are present posteriorly. The pleural field is crossed by at least six firmly impressed pleural furrows, and a distinct post-axial ridge extends onto a narrowly based (tr.) median spine. We doubt that this specimen is conspecific with the smallest pygidium, as it would imply that dramatic morphological changes take place during the holaspis stage. The sculpture of closely spaced granules matches the sculpture of the holotype cranium, and on this basis is perhaps the most likely candidate for the pygidium of *P. inflata*.

An intermediately sized sclerite from CC–93 (Fig. 3D, E; not previously figured) is an alternative candidate for the pygidium of *P. inflata*. The sculpture is closest to the small pygidium (Fig. 3A–C), although the granules on the posterior pleural band and axial rings are much more clearly defined. It is, however, relatively longer than the small pygidium, with twice as many pleural furrows on the pleural field, and at least ten segments clearly defined on the axis; a post-axial ridge extends onto the marginal spine, but this feature is not present on the smaller specimen (Fig. 3A). It is possible that the small and intermediately sized specimens are conspecific, although this hypothesis also demands considerable allometric change during the holaspis period. Possible crania of *P. inflata* from Oklahoma (see below) are associated with pygidia with long, multi-segmented axes and at least a half dozen firmly impressed pleural furrows; sculpture that resembles that of the intermediately sized pygidium from CC–93, although the coarse granules on the axial ring and pleural bands are augmented with closely spaced smaller granules (Fig. 4E–G). A larger specimen (Fig. 4H, I) from the same collection is more complete posteriorly, although is damaged immediately behind the axis; if present, any median spine would be very narrowly based. We conclude that there is some doubt regarding the sclerite associations of *P. inflata*, although we agree with Loch *et al.* (1993) that it is most likely that the pygidium possesses a median spine, and this is noted in the diagnosis. An improved understanding of the anatomy of this species must await discovery of more material.

Two incomplete crania from Oklahoma (Fig. 4A–D) may represent *P. inflata*, although the small sample size precludes a definitive identification; they may also represent the unpublished record of the species in Oklahoma mentioned by Stitt (in Loch *et al.* 1993, p. 509). They share the convex glabella with outwardly bowed lateral margins, deep S1 and S2, pit-like S3, and a short but conspicuous anterior median furrow. Like *P. inflata*, they appear to possess large palpebral lobes centred opposite L2 (Fig. 4D), the anterior border is short, and the sculpture comprises closely spaced granules. Aside from an apparently deeper anterior border furrow, we can discern no appreciable differences.

*Parakoldinioidia inflata* has also been recorded from the Basal Silty Member of the Survey Peak at Mount Wilson, Alberta. With only a single cranium illustrated in dorsal view and a pygidium in lateral view (Loch *et al.* 1993, fig. 8.11, 8.12), this occurrence cannot be evaluated critically.

The cranium has a short border, but the glabella seems to be evenly tapered, rather than weakly barrel-shaped as in the types of *P. inflata*, and the glabellar furrows are relatively shallow. We doubt that it is conspecific with *P. inflata*, but clearly more material is needed to be sure. As noted above, the pygidium is similar to the smallest spinose pygidium from Texas. It appears to possess a more slender spine but, in the absence of a dorsal view, little more can be said.

*Parakoldinioidia* sp. A and *P. cf. P. sp. A* of Fortey (1983, pl. 25, figs 5, 6 and 4, respectively) are each represented by a single cranium from the Shallow Bay Formation, western Newfoundland, that possesses a very short anterior border reminiscent of *P. inflata*. Both have gently tapered glabellae and, in the case of *P. sp. A*, much narrower (tr.) posterolateral projections than *P. inflata* (e.g., Fig. 2A, B). Other sclerites of *Parakoldinioidia* from western Newfoundland (e.g., Fortey in Fortey *et al.* (1982, pl. 2, fig. 3–4) are too incompletely preserved for meaningful discussion.

#### ***Parakoldinioidia akerfeldti* sp. nov. (Figs 5–7)**

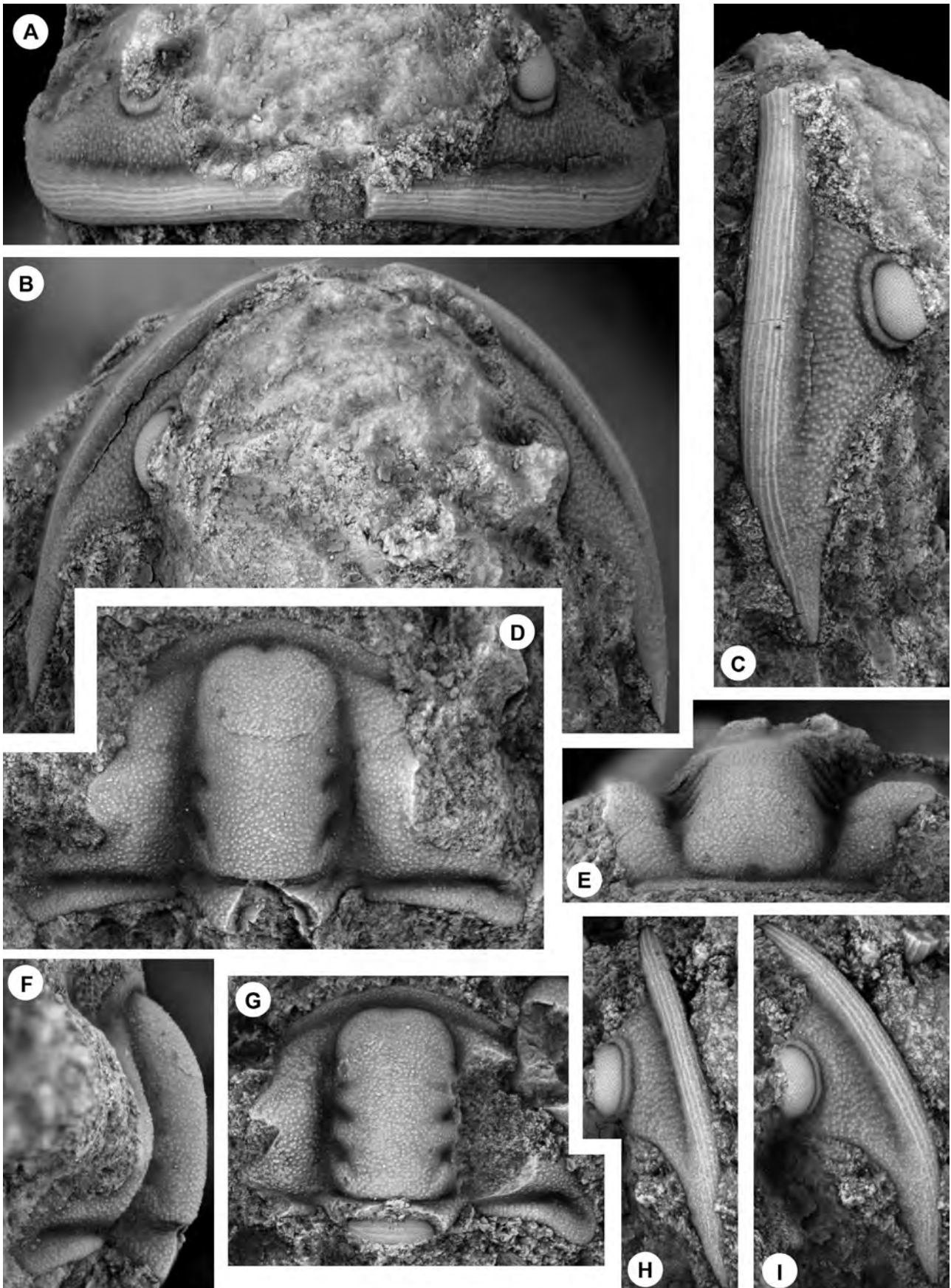
**Diagnosis.** Palpebral area of fixigena nearly flat. Cranium relatively broad, so that cranial length is less than 90% (87%; 85–88) of cranial width across palpebral lobes. Librigena with strongly convex lateral border and border furrow that shallows posteriorly, terminating short of genal spine. Pygidium relatively narrow, with length equal to about 80% of maximum width (81%; 80–84) and sharply triangular in outline; pleural field flexed steeply downward to lateral margin with four pairs of free spines that decrease in size towards the rear.

**Holotype.** A cranium (OU 13205; Fig. 5G–I) from the Signal Mountain Formation, Murray County, Oklahoma.

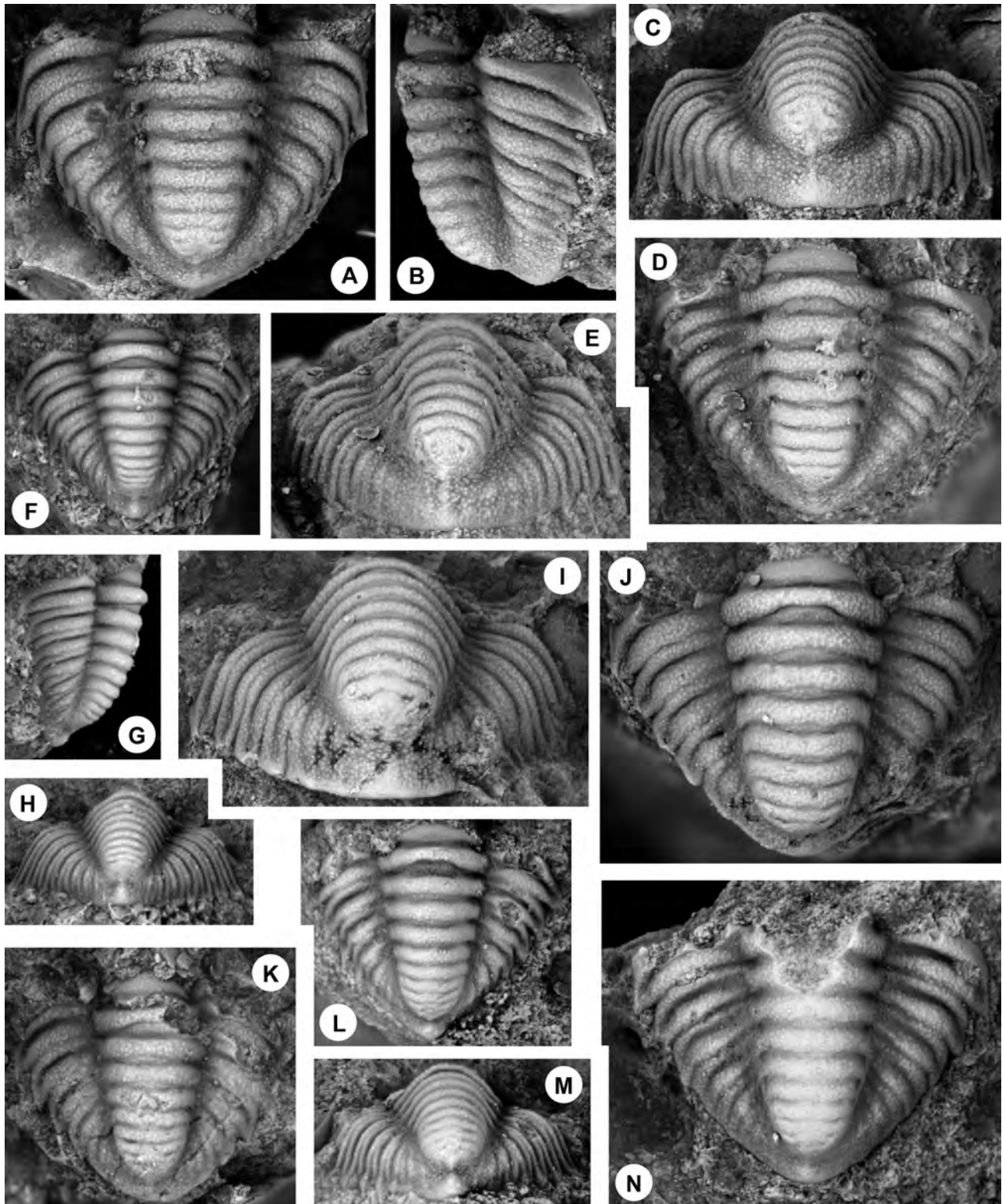
**Name.** For Mikael Åkerfeldt.

**Occurrence.** Signal Mountain Formation, Joins Ranch Section, Murray County, Oklahoma (Stitt 1971, p. 59), collection JoR–1125.

**Description.** Excluding posterolateral projection, strongly arched cranium subrectangular in outline with forwardly curved anterior margin; cranial length equal to 87% (85–88%) of width across palpebral lobes. Glabella convex, raised well above fixigenae, outlined by well defined axial and preglabellar furrows, and occupies 91% (91–92) of cranial length; nearly parallel-sided but becomes tapered anteriorly, with rounded anterior margin (more transverse in smaller specimens; Fig. 6G) interrupted by short median furrow that may give margin weakly bilobate appearance (Fig. 5D). LO accounts for 18% of glabellar length; SO is finely etched groove, nearly transverse medially but deflected forward abaxially. Lateral glabellar furrows short (tr.) and expressed only near glabellar margin. S1 firmly impressed, oriented obliquely backward; S2 also well incised but more transverse; S3 faint on at least larger crania (Fig. 5B, D) and oriented obliquely forward. Lateral glabellar lobes without independent convexity; L1 shorter than LO, occupying 13% (12–14) of glabellar length; L2 equal in length to L1, but longer than L3. Anterior border flat, arcuate band, accounting for 9% (8–9) of cranial length in front of glabella; anterior border is finely etched groove. Palpebral area of fixigenae nearly flat; palpebral lobe semielliptical flap, length (exsag.) equal to 34% (33–35) of preoccipital



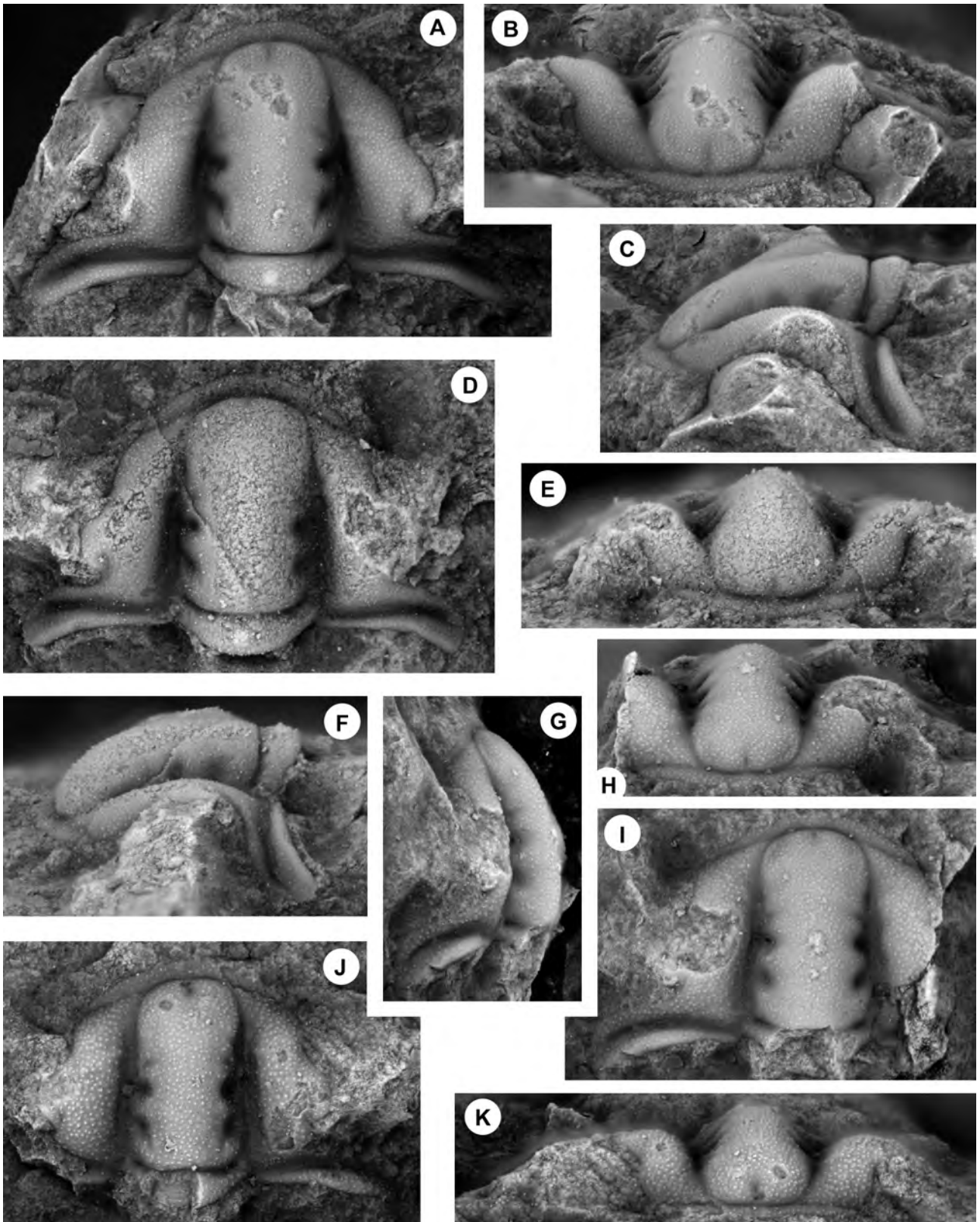
**Figure 6.** *Parakoldinioidia akerfeldti* sp. nov., Signal Mountain Formation, Joins Ranch Section, Murray County. All from collection JoR-1125 (Stitt 1971, p. 59) and all x20. **A–C.** Yoked librigenae, OU 13206, anterior, dorsal and lateral views; **D–F,** cranium, OU 13207, dorsal, anterior and lateral views. **G,** cranium, OU 13208, dorsal view; **H, I,** librigena, OU 13209, lateral and dorsal views.



**Figure 7.** *Parakoldinioidia akerfeldti* sp. nov., Signal Mountain Formation, Joins Ranch Section, Murray County, Oklahoma. All pygidia from collection JoR-1125 (Stitt 1971, p. 59) and all x20. A–C, OU 13210, dorsal, lateral and posterior views; D, E, OU 13211, dorsal and posterior views; F–H, OU 13212, dorsal, lateral and posterior views; I, J, OU 13213, posterior and dorsal views; K, OU 13214, dorsal view; L, M, OU 13215, dorsal and posterior views; N, OU 13216, dorsal view.

glabellar length and centred opposite L2; without palpebral furrow, but with narrow rim-like band identifiable by reduction in size of granulate sculpture (e.g., Fig. 5B). Palpebral ridge weak, proceeds obliquely forward across fixigena to reach axial furrow just in front of S3. Anterior

branches of facial sutures converge gradually forward to anterior border furrow before curving inward along anterior cranial margin; posterior branches abruptly divergent before swinging abruptly backwards to reach posterior cranial margin. Posterolateral projection broad (tr.), so



**Figure 8.** *Parakoldinoidea lindgreni* sp. nov., Signal Mountain Formation, Joins Ranch Section, Murray County, Oklahoma (Stitt 1971). **A–C**, cranidium, OU 13217 (holotype), dorsal, anterior and lateral views, collection JoR–1187, x20; **D–F**, cranidium, OU 13218, dorsal, anterior and lateral views, collection JoR–1190, x20; **G–I**, cranidium, OU 13219, lateral, anterior and dorsal views, collection JoR–1153, x20; **J, K**, cranidium, OU 13220, dorsal and anterior views, collection JoR–1153.

that cranial width across palpebral lobes is 71% (70–72) of width across posterolateral projection; length (exsag.) behind palpebral lobe equal to 22% (21–22) of cranial length (sag.). Posterior border furrow well incised, nearly transverse; posterior border expands abaxially, maximum length (exsag.) at distal tip equal to 13% (12–14) of cranial length (sag.), so that posterior cranial margin deflected backward. External surface with sculpture of closely spaced coarse granules; granules arrayed along low caecal ridges on preocular field of fixigena (e.g., Fig. 5D, E). Conspicuous medial tubercle on LO (Fig. 5I).

Librigenae yoked anteriorly; anterior cephalic margin strongly curved; stout genal spine present. Small visual surface of eye mounted on convex eye socle; eye socle furrow lightly impressed. Lateral border convex, separate from short, steeply sloping librigenal field by shallow border furrow that terminates short of genal spine; position of border marked on spine only by band of terrace ridges. Border with sculpture of coarse terrace ridges running parallel to cephalic margin; remainder of librigena with granulose sculpture, arrayed along ridges of caecal network on librigenal field (e.g., Fig. 6C).

Pygidium subtriangular in outline, strongly convex, and relatively narrow, with length equal to 81% (80–84) of maximum width. Axial furrows shallow. Axis conspicuous, raised far above pleural field, accounting for 91% (88–93) of pygidial length and 43% (39–45) of pygidial width at first axial ring; tapers backwards, so that width at sixth ring is 67% (65–70) of width at first ring. Weak postaxial ridge evident on some smaller specimens (e.g., Fig. 7F). Articulating half-ring semielliptical, comprises 10% (9–12) of axis; articulating furrow firmly impressed, short (sag.) medially but lengthens abaxially. First five or six axial rings separated by well incised, complete, transverse ring furrows; first furrow curves forward medially, widening (sag., exsag.) so that first ring narrows medially; posteriorly at least four additional segments crowded together and separated by shallow, incomplete furrows. Pleural field nearly flat near axis but flexed steeply downward abaxially to lateral margin with four pairs of free spines that decrease in size towards the rear. Pleural furrows deep grooves but interpleural furrows lightly impressed; anterior and posterior pleural bands roughly equal in length. Entire surface aside from articulating half-ring with closely spaced coarse granules.

**Discussion.** *Parakoldinioidia akerfeldti* sp. nov. is most similar to *P. maddowae* Westrop (in Landing *et al.* 2011, figs 11, 12). The cranidium of *P. akerfeldti* is relatively wider across the palpebral lobes, so that cranial length is less than 90% of width (87%; 85–88) across palpebral lobes, whereas cranial length is roughly equal to width (97%; 93–100) in *P. maddowae*. The difference in width is even more pronounced at the posterolateral projection (compare Fig. 5B, I, with Landing *et al.* 2011, fig. 11B). During cranial ontogeny, the glabellae of both species tend to become more tapered and rounded anteriorly, but this trend is more pronounced in *P. akerfeldti* (compare Figs 5B, D, I and 6G) than in *P. maddowae* (compare Landing *et al.* 2011, fig. 11b, e, o). Cephalic sculpture of coarse granules is better expressed in *P. akerfeldti*, and the comparison is particularly striking for the librigenae (compare Fig. 6C, H, I with Landing *et al.* 2011, fig. 12f, g). In addition, lateral borders are better defined on librigenae of *P. akerfeldti*. Complete preparation of one specimen revealed that the librigenae of *P. akerfeldti* were yoked anteriorly (Fig. 6A–C).

Pygidia of *P. akerfeldti* are proportionately longer and narrower, particularly at smaller sizes (compare Fig. 7F, L with Landing *et al.* 2011, fig. 12c, h, i); pygidial length is about 75% (73%; 69–75) of maximum width in *P. maddowae*, and is about 80% (82; 81–84) in *P. akerfeldti*.

*Parakoldinioidia akerfeldti* has a relatively flat palpebral area of the fixigenae. Among other species that share this condition, *P. mendezi* sp. nov. (Fig. 10, ?Fig. 11) has a distinctive, relatively short (exsag.) posterolateral projection, and the glabella is weakly tapered anteriorly. Pygidia of *P. akerfeldti* and *P. mendezi* are similar, but the pleural fields of the former are flexed downward more steeply (e.g., compare Figs 7C and 10N). *Parakoldinioidia* sp. nov. C (Fig. 19) has a longer anterior border on the cranidium, which is nearly smooth aside from scattered, ill-defined granules. The pygidium attributed *P.* sp. nov. C (Fig. 19E–G) is dramatically different from *P. akerfeldti*, with broad pleural fields that flatten distally at eight pairs of broad, bluntly rounded marginal spines.

#### **Parakoldinioidia lindgreni** sp. nov. (Figs 8, 9, 18D–F)

1967 *Missisquoia typicalis*; Winston & Nicholls, p. 88, pl. 13, fig. 5 [only; fig. 2 = indet. trilobite; fig. 6 = *Parakoldinioidia* sp. nov. B; figs. 10, 12 = *P.* sp. nov. C; fig. 15 = *P.* sp. nov. A?; fig. 18 = *P. inflata*?].

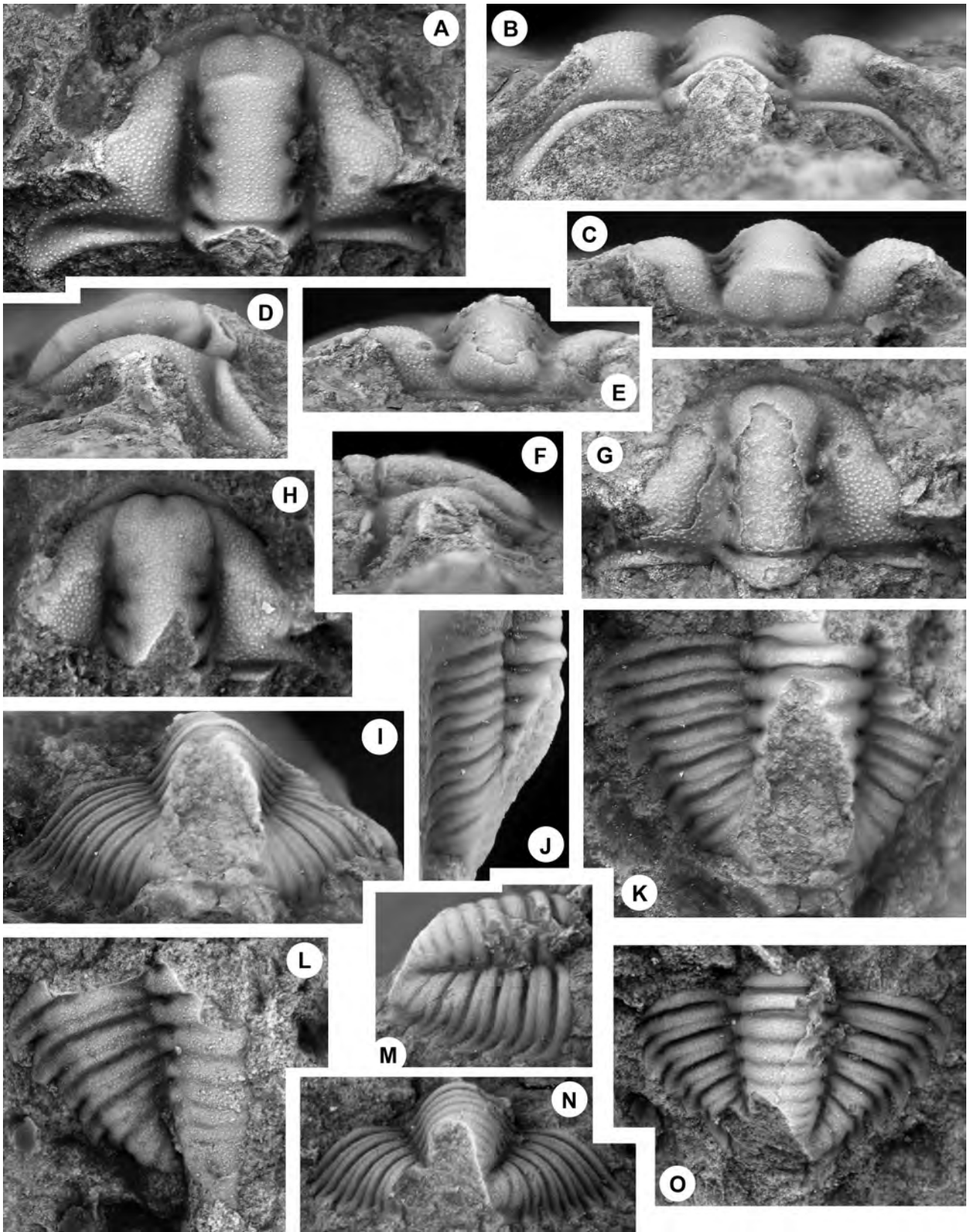
**Diagnosis.** Strongly upsloping palpebral area of fixigena; palpebral lobe elevated well above axial furrow. Axial furrows narrow and shallow markedly in front of S3, but glabella remains clearly defined anteriorly. Anterior cranial border narrows abaxially. Posterolateral projection short (exsag.) and broad (tr.), flexed gently backward abaxially. Pygidium with five pairs of conspicuous marginal spines.

**Holotype.** A cranidium (OU 13217; Fig. 8A–C) from the Signal Mountain Formation, Murray County, Oklahoma.

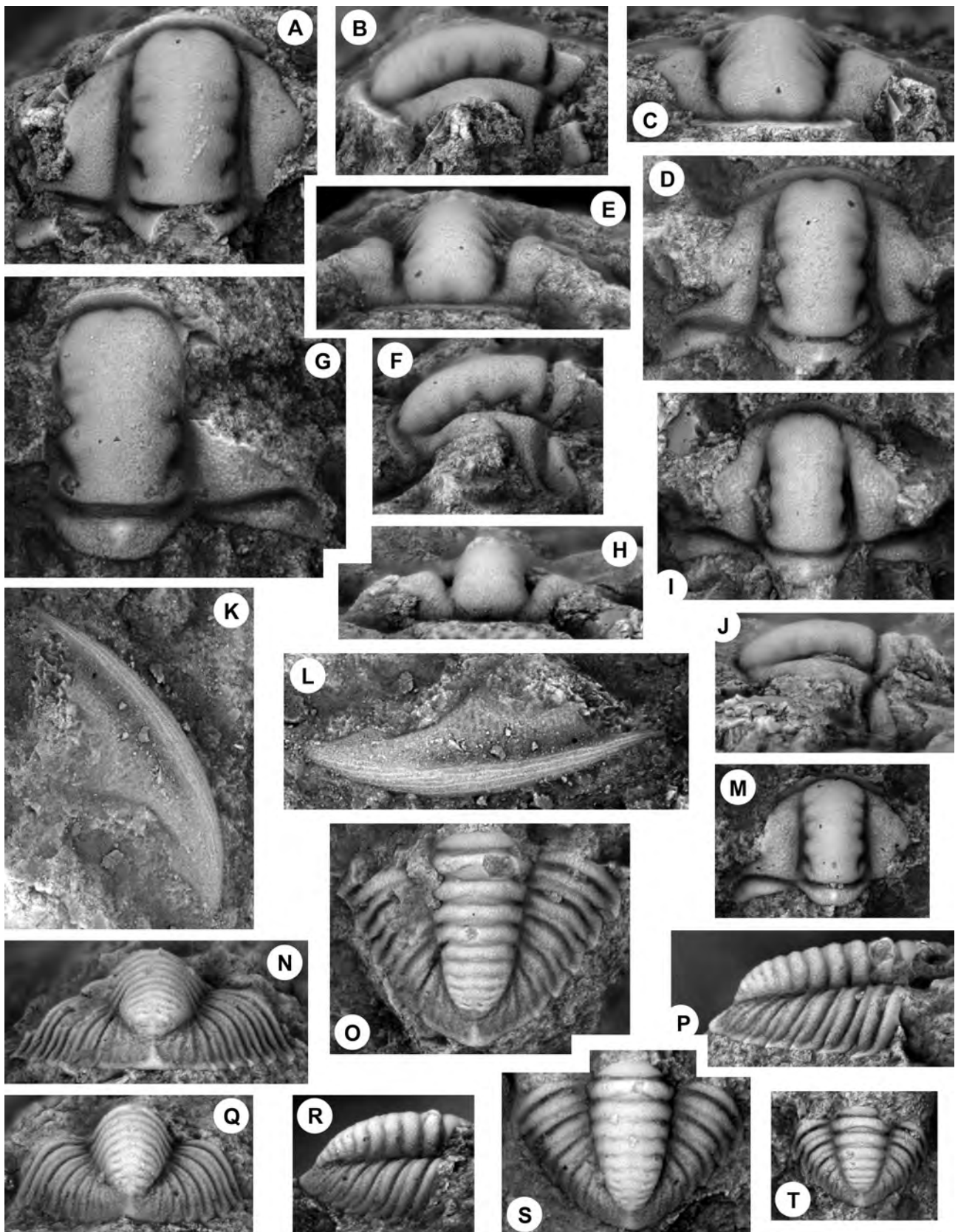
**Name.** For Peter Lindgren.

**Occurrence.** Signal Mountain Formation, Joins Ranch Section, Murray County, Oklahoma (Stitt 1971, p. 59), collections JoR–1153, 1187, 1190. San Saba Member, Wilberns Formation, Calf Creek section, Mason County, central Texas (Winston & Nicholls 1967), collection CC–90.

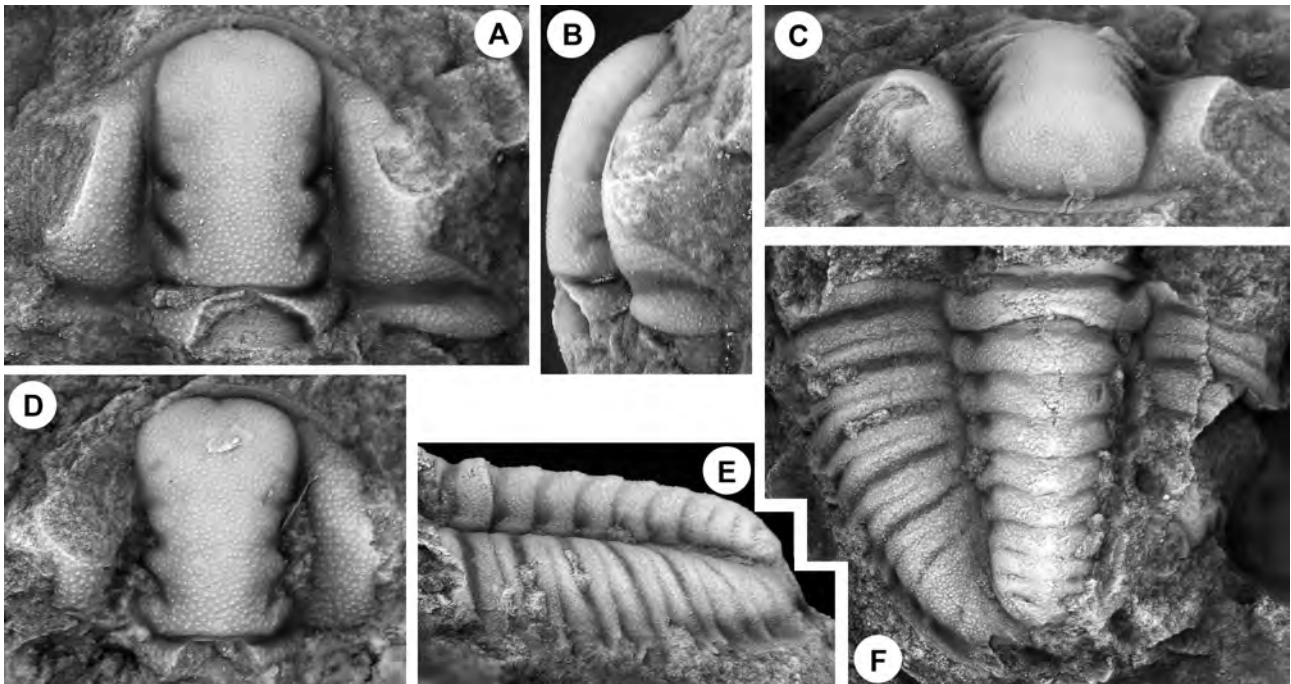
**Description.** Cranidium subpentagonal in outline with strong convexity, length equal to 84% (79–86) of cranial width across palpebral lobes. Glabella outlined by firmly impressed axial furrows posteriorly; in front S3, axial furrows shallow, but glabella remains well defined; strongly arched, standing well above axial furrows; parallel-sided but well rounded anteriorly, occupies 93% (91–94) of cranial length and 40% (38–44) of cranial width between palpebral lobes. LO curved gently backwards, comprises 16% (15–18) of glabellar length. SO well incised, transverse across most of glabellar width but deflected forward near axial furrows. Lateral glabellar furrows narrow (tr.) and confined to flanks of glabella. S1 oblique, S2 nearly transverse, and both deeply incised; S3 barely perceptible. L1 occupies 13% (12–14) of glabella length; L2 and, particularly, L3 shorter. Median anterior glabellar furrow short (sag.), variably expressed (e.g., Figs 8A, I, 9H); where firmly impressed, anterior glabellar margin bilobate. Anterior cranial border flat, curved strongly forward, and narrows abaxially, becoming



**Figure 9.** *Parakoldinioidia lindgreni* sp. nov., Signal Mountain Formation, Joins Ranch Section, Murray County, Oklahoma. All from collection JoR-1153, except L-O (JoR-1187) (Stitt 1971, p. 59) and all x20. A-D, cranidium, OU 13221, dorsal, posterior, anterior and lateral views; E-G, cranidium, OU 13222, anterior, lateral and dorsal views; H, cranidium, OU 13223, dorsal view; I-K, pygidium, OU 13224, posterior, lateral and dorsal views; L, pygidium, OU 13225, dorsal view; M-O, pygidium, OU 13226, lateral, posterior and dorsal views.



**Figure 10.** *Parakoldinioidia mendezi* sp. nov., Signal Mountain Formation, Chandler Creek Section, Comanche County, Oklahoma. All from collection CC-1547 (Stitt 1977, p. 53), and all x20. A–C, cranidium, OU 13227 (holotype), dorsal, lateral and anterior views; D–F, cranidium, OU 13228, dorsal, anterior and lateral views; G, cranidium, OU 13229, dorsal view; H–J, cranidium, OU 13230, anterior, dorsal and anterior views; K, L, librigena, OU 13231, dorsal and lateral views; M, cranidium, OU 13232, dorsal view; N–P, pygidium, OU 13233, posterior, dorsal and lateral views; Q–S, pygidium, OU 13234, posterior, lateral and dorsal views; T, pygidium, OU 13235, dorsal view.



**Figure 11.** *Parakoldinioidia mendezi* sp. nov.?, Signal Mountain Formation, Joins Ranch Section, Murray County, Oklahoma. All from collection JoR-1171 (Stitt 1971, p. 59). **A–C**, cranidium, OU 13236, dorsal, lateral and anterior views, x20; **D**, cranidium, OU 13237, dorsal view, x20; **E, F**, pygidium, OU 13238, lateral and dorsal views, x16.

nearly obsolete at anterior corners of cranidium in most specimens (e.g., Figs 8A, 9H, 18F); anterior border furrow lightly impressed and merges with preglabellar furrow. Palpebral area of fixigena, strongly upsloping, width (including palpebral lobe) equal to 72% (66–79) of glabellar width at L2; palpebral lobe arcuate band defined adaxially by barely perceptible palpebral furrow; length equal to 34% (32–37) of preoccipital glabellar length and centred opposite L2; elevated well above axial furrow. Anterior branches of facial suture converge forward before curving inward along anterior cranial margin; posterior branches roughly transverse near palpebral lobe but become increasingly curved backward distally. Posterolateral projection short (exsag.), length behind palpebral lobe equal to 11% (7–14) of cranial length (sag.) and wide, with cranial width at palpebral lobes equal to 70% (66–76) of width at posterior; flexed backward distally. Posterior border furrow well incised, transverse along much of length, but swings backward near abaxial tip; posterior border expands slightly abaxially, maximum length (exsag.) equal to 19% (16–21) of cranial length (sag.). External surface aside from furrows with sculpture of coarse granules (e.g., Fig. 8J); conspicuous median tubercle on LO.

All available pygidia incomplete posteriorly but are broadly subtriangular in outline and strongly arched (e.g., Fig. 9M–O). Convex axis occupies about one-third of pygidial width at anterior. Five axial rings defined by shallow, transverse ring furrows that extend across full width of axis, deepening appreciably near axial furrows; at least four additional segments posteriorly, separated by incomplete furrows. Pleural field flexed steeply downward to lateral margin with at least five pairs of conspicuous marginal spines that show little change in size towards rear. Interpleural furrows fine grooves, but pleural furrows deeply incised, terminating at inner edges of marginal spines. External surface with closely packed fine granules (e.g., Fig. 9O).

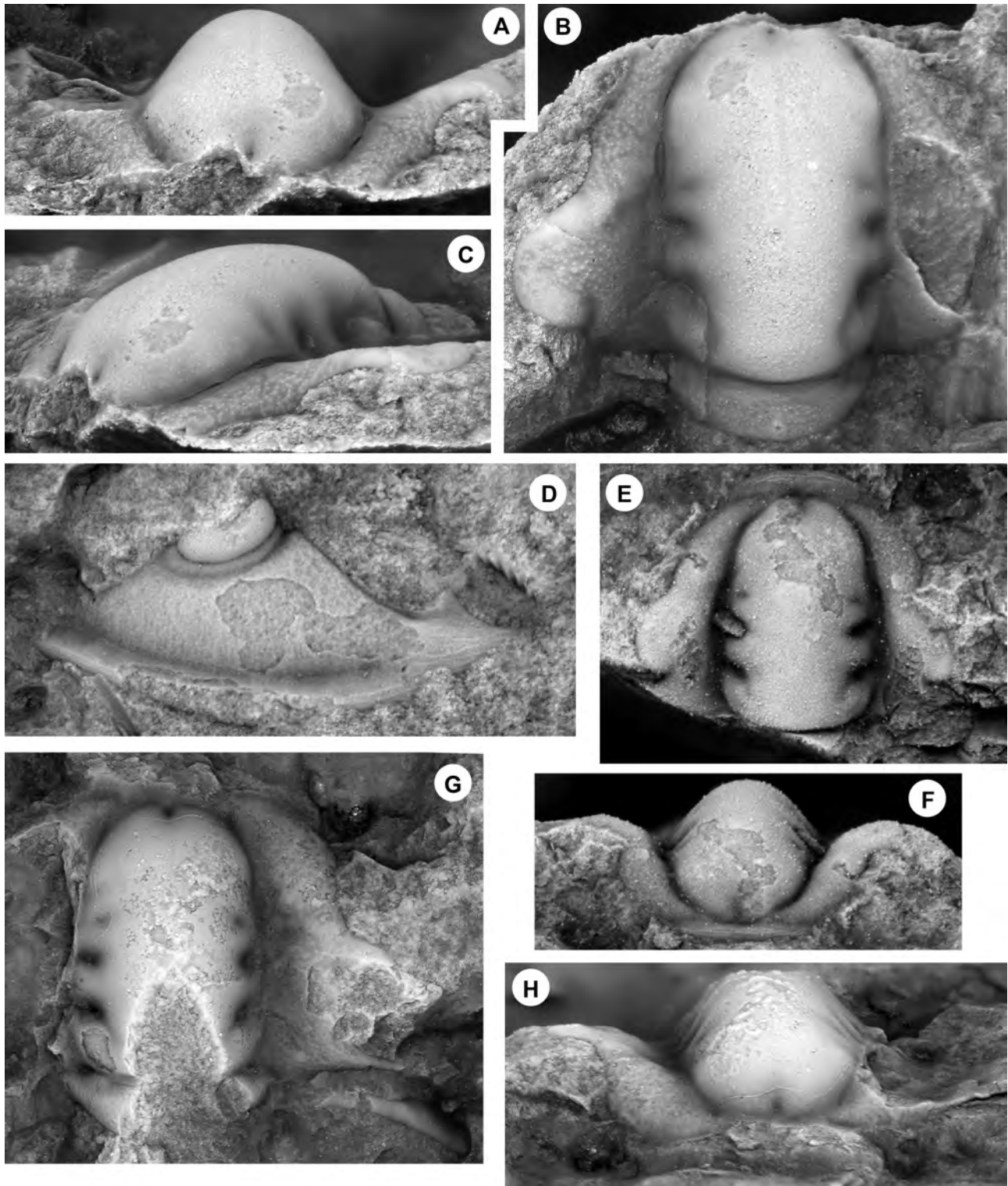
*Discussion.* *Parakoldinioidia lindgreni* sp. nov. occurs in both Oklahoma and Texas. The inflated, upsloping palpebral areas of the fixigenae that rise well above the axial furrows contrast with the nearly flat palpebral areas of *P. akerfeldti* sp. nov. (e.g., Fig. 5C, G), *P. madowae* Westrop (in Landing *et al.* 2011; e.g. fig. 11a) and *P. mendezi* (e.g., Fig. 10C, E, H). Pygidia of *P. akerfeldti*, *P. madowae* and *P. mendezi* all possess relatively small free spines along the margin that decrease in size posteriorly (e.g., Figs 7, 10N–T; Landing *et al.* 2011, fig. 12a–e, h–m) whereas the five large spines of *P. lindgreni* show no appreciable change in size towards the rear (e.g., Fig. 9J, K).

Compared to *P. lindgreni*, cranidia of *P. inflata* (Winston & Nicholls; Fig. 2A, E, G) have shorter anterior borders, axial furrows that are bowed gently outwards, less steeply sloping palpebral areas, and posterolateral projections that are nearly transverse (Fig. 2A, B), rather than curved backwards. Candidates for the pygidium of *P. inflata* (Fig. 3) all possess long, median marginal spines, as does the pygidium of *P. lopezi* sp. nov. (Fig. 13); cranidia of the latter (Fig. 12) have less steeply upsloping palpebral areas, larger, more strongly curved palpebral lobes, and a sculpture of finer, less conspicuous granules. Finally, the pygidium from the Survey Peak Formation, Alberta, which was illustrated by Westrop (1986, pl. 1, fig. 35), is similar to *P. lindgreni* in gross aspect, but appears to have much smaller marginal spines, and narrower pleural fields. The associated cranidium (Westrop 1986, pl. 1, figs 36–37) has nearly flat palpebral areas of the fixigenae, shallower lateral glabellar furrows, and a very short anterior border.

#### ***Parakoldinioidia mendezi* sp. nov. (Fig. 10, ?11)**

*Diagnosis.* Narrow (tr.) posterolateral projection. Glabella parallel sided to slightly expanded anteriorly. Anterior cranial border short and nearly flat. Pygidium with at least





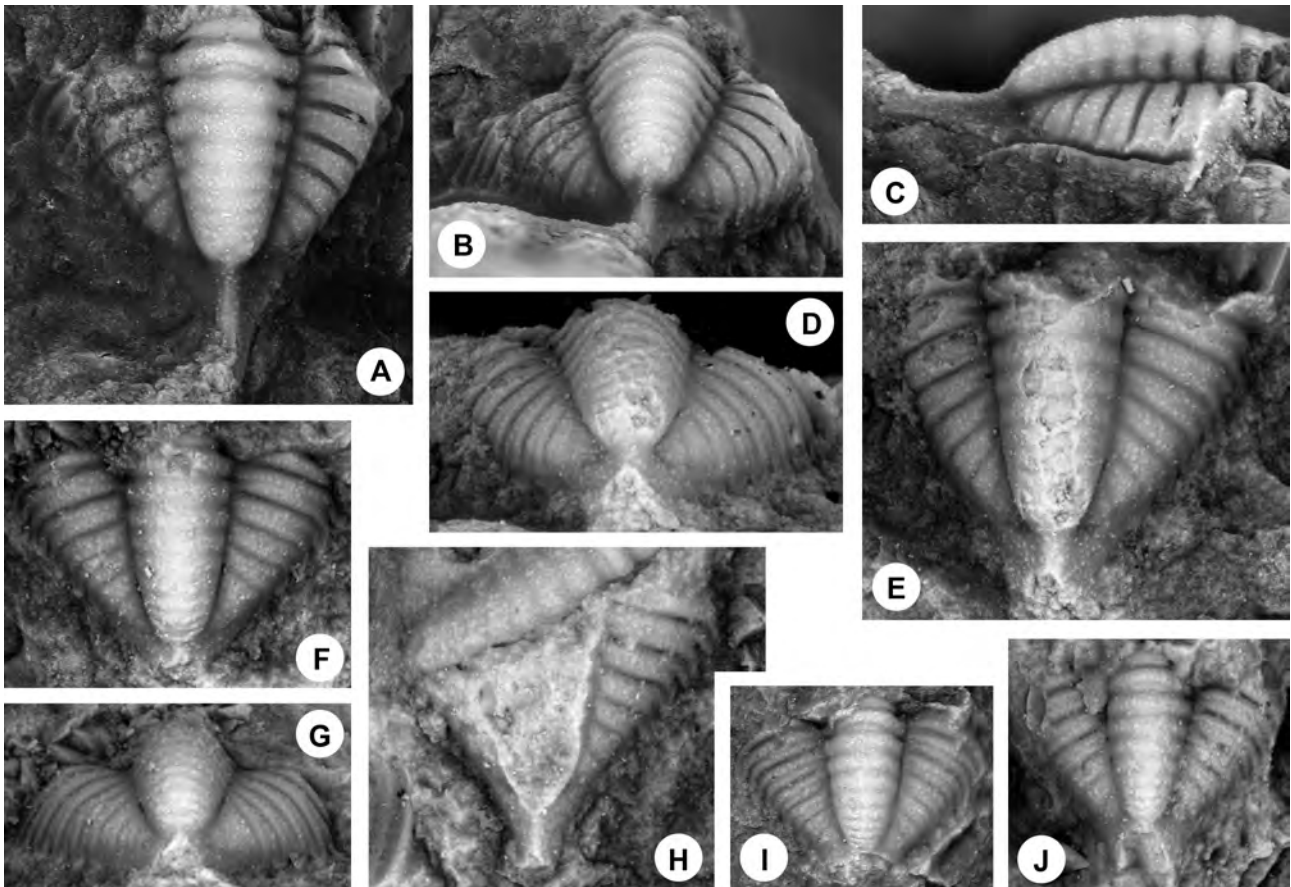
**Figure 12.** *Parakoldinioidia lopezi* sp. nov., Signal Mountain Formation, Joins Ranch Section, Murray County, Oklahoma. All x20 from collection JoR-1187 (Stitt 1971, p. 59) except A–C (from JoR-1190 and x18). A–C, cranium, OU 13239 (holotype), anterior, dorsal and anterior-oblique views; D, librigena, OU 13240, lateral-oblique view; E, F, cranium, OU 13241, dorsal and anterior views; G, H, cranium, OU 12356, dorsal and anterior views.

four pairs of clearly defined marginal spines.

*Holotype.* A cranium (OU 13227; Fig. 10A–C) from the Signal Mountain Formation, Comanche County, Oklahoma.

*Name.* For Martin Mendez.

*Occurrence.* Signal Mountain Formation, Chandler Creek Section, Comanche County, Oklahoma (Stitt 1977, p. 53), collection CC-1547; ? Signal Mountain Formation, Joins



**Figure 13.** *Parakoldinioidia lopezi* sp. nov., Signal Mountain Formation, Joins Ranch Section, Murray County, Oklahoma. All from collection JoR-1190 (Stitt 1971, p. 59) and except A-C (JoR-1187). All pygidia and x20. A-C, OU 12357, dorsal, posterior and lateral views; D, E, OU 13242, posterior and dorsal views; F, G, OU 13243, dorsal and posterior views; H, OU 13244, dorsal view; I, OU 13245, dorsal view; J, OU 12358, dorsal view.

Ranch Section, Murray County, Oklahoma (Stitt 1971, p. 59), collection JoR-1171.

**Discussion.** *Parakoldinioidia mendezi* occurs in the Signal Mountain Formation at the Chandler Creek section (Fig. 10), and material from the Joins Ranch section (Fig. 11) is also assigned questionably to this species. Sclerites from Joins Ranch are larger than those from Chandler Creek, making comparisons difficult. The cranidia (Fig. 11A-D) differ from the smaller specimens from Chandler Creek only in having a rather more inflated palpebral areas, a slightly shorter anterior border and coarser sculpture, particularly on the glabella.

*Parakoldinioidia mendezi* closely resembles *P. maddowae* Westrop (in Landing *et al.* 2011; Figs 11, 12), from the Little Falls Formation of New York, and a comparison is presented in lieu of a full description. These two species share relatively flat palpebral areas of the fixigenae, narrow (tr.) posterolateral projections, and there are no appreciable differences in the librigenae, aside from the presence of conspicuous terrace ridges on the lateral border of *P. mendezi*. Cranidia of *P. mendezi* have shorter anterior borders and glabellae that are parallel-sided or even expand slightly anteriorly. The glabella of *P. maddowae* becomes anteriorly tapered during holaspid ontogeny (e.g., see Landing *et al.* 2011, fig. 11i, o and b). Pygidia are quite similar, although those of *P. maddowae* tend to be relatively wider, and have three pairs of well developed marginal spines, whereas those of *P. mendezi* have at least four (e.g., Fig. 10N-P).

Morphology of *P. mendezi* is compared with *P. akerfeldti* and *P. lindgreni* under the discussion of those species. *Parakoldinioidia cyclochila* (Hu 1971, pl. 20), from the Deadwood Formation, Wyoming, has a narrow (tr.) posterolateral projection and a parallel-sided glabella that are comparable to those of *P. mendezi*. However, *P. cyclochila* has a semielliptical pygidium that is unusual for the genus; so much so that Lee *et al.* (2008) assigned this species questionably to *Pseudokoldinioidia*.

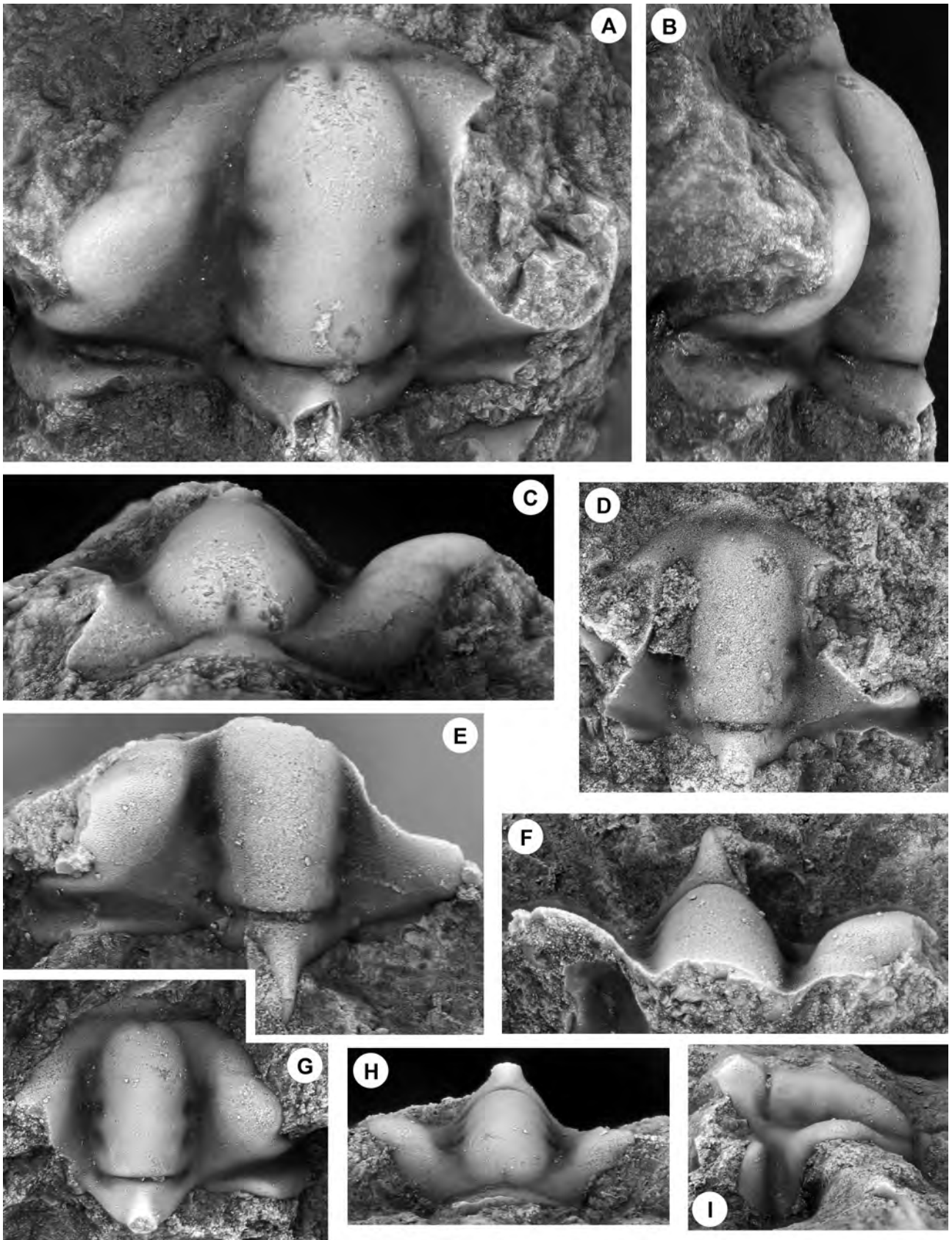
#### ***Parakoldinioidia lopezi* sp. nov. (Figs 12, 13)**

**Diagnosis.** Glabella parallel sided but well rounded anteriorly. Well incised, slot-like S1 and S2 furrows; S3 faint. Palpebral area of fixigenae upsloping; palpebral lobe large and centered opposite L2. Pygidium subtriangular in outline with stout median spine. External surfaces of cranium, librigena and pygidium finely granulate, augmented by caecae on librigenal field.

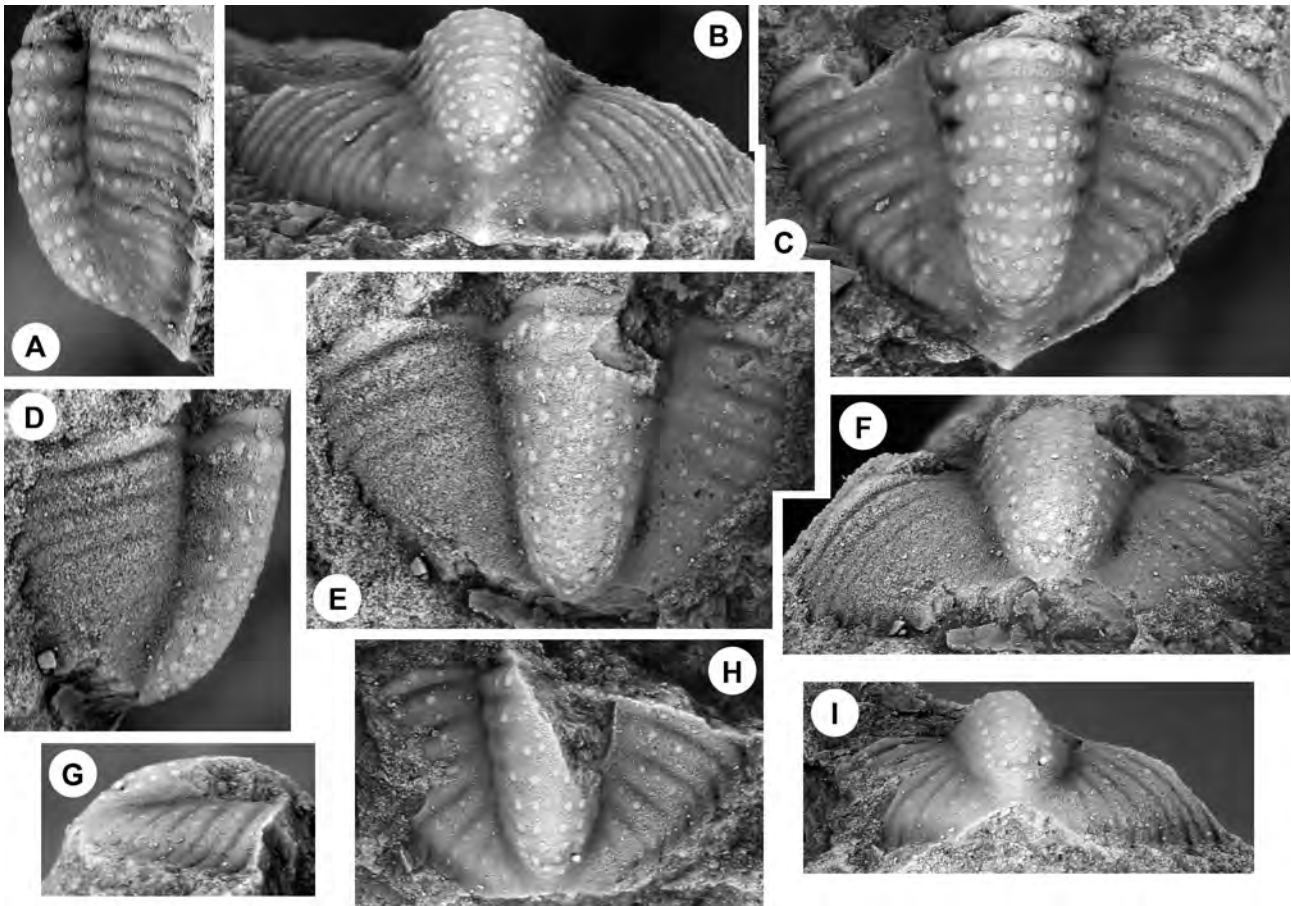
**Holotype.** A cranidium (OU 13239; Fig. 12A-C) from the Signal Mountain Formation, Murray County, Oklahoma.

**Name.** For Martin Lopez.

**Occurrence.** Signal Mountain Formation, Joins Ranch Section, Murray County, Oklahoma, collection JoR-1190.



**Figure 14.** *Parakoldinioidia akessoni* sp. nov., Signal Mountain Formation, Chandler Creek Section, Comanche County, Oklahoma. All cranidia from collection CC-1605 and all x20. A–C, OU 13246 (holotype), dorsal, lateral and anterior views; D, OU 13247, dorsal view; E, F, OU 13248, dorsal and anterior views; G–I, OU 13249, dorsal, anterior and lateral views.



**Figure 15.** *Parakoldinioidia akessoni* sp. nov., Signal Mountain Formation, Chandler Creek Section, Comanche County, Oklahoma. All pygidia from collection CC-1605 and all x20. A–C, OU 13250, lateral, posterior and dorsal views; D–F, OU 13251, lateral, dorsal and posterior views; G–I, OU 13252, lateral, dorsal and posterior views.

*Discussion.* *Parakoldinioidia lopezi* is similar enough to *P. inflata* (Winston & Nicholls; Fig. 2) to permit a comparison between them rather than a full description. The cranidium of *P. lopezi* has a larger, more posteriorly positioned palpebral lobe and, consequently, a more slender (exsag.) posterolateral projection. Glabella margins are nearly straight between LO and L3, and the anterior border is relatively longer than *P. inflata* (compare Fig. 12E, F and Fig. 2E). Weak granulose sculpture on glabella, fixigenae, librigenal field of librigena, and entire surface of pygidium support the sclerite association. The pygidium of *P. lopezi* (Fig. 13) has a post-axial ridge that extends onto a stout median marginal spine. The pleural field is crossed by five or six well defined pleural furrows; interpleural furrows are weak, particularly posteriorly. The axis has at least 10 segments, although axial ring furrows are weak over the posterior half. Pygidial assignment is uncertain for *P. inflata*, but all potential candidates possess well developed median spines. The most likely of these (Fig. 3F–H) is much larger than those of *P. lopezi*, limiting comparisons. It is more strongly arched, and is proportionately longer and wider.

***Parakoldinioidia akessoni* sp. nov.** (Figs 14, 15)

*Diagnosis.* Long, slender occipital spine and smooth cranial surface. Anterior border bluntly pointed, narrowing abaxially and with conspicuous arch in anterior view. Palpebral area of fixigena strongly inflated, upsloping, flattening abaxially to form narrow (tr.) semielliptical, flap-

like palpebral lobe. Posterolateral projection dips steeply downward; appears narrow (tr.) in dorsal view. Associated pygidium subtriangular in outline, with very short median spine. Prominent tuberculate sculpture on axial rings and coarse granules to fine tubercles best expressed on posterior pleural bands of pleural field (Fig. 15C, H).

*Holotype.* A cranidium (OU 13247; Fig 14A–C) from the Signal Mountain Formation, Chandler Creek Section, Comanche County, Oklahoma.

*Name.* For Fredrik Åkesson.

*Occurrence.* Signal Mountain Formation, Chandler Creek Section, Comanche County, Oklahoma (Stitt 1977, p. 53), collection CC-1605.

*Description.* Cranidium subtrapezoidal in outline, with bluntly pointed anterior margin, length equal to 82% (72–85) of width across palpebral lobes; strongly convex in anterior and lateral views. Glabella with long, slender occipital spine; occupies 90% of cranial length (excluding spine) and 37% (35–40) of cranial width at palpebral lobes; strongly arched and parallel-sided between SO and S3, but tapered and well rounded anteriorly. Short median furrow defines bilobate anterior margin. Excluding spine, LO accounts for 22% (19–26; higher values in smaller specimens) of glabellar length; SO finely etched groove bowed gently backwards; lateral glabellar furrows narrow (tr.), and only S1 and S2

expressed clearly; S1 oblique and S2 nearly transverse; barely perceptible, transverse S3 evident on some specimens (e.g., Fig. 14A). Anterior border furrow shallow and curved very gently forward; anterior border subtriangular and arched downward abaxially in anterior view (Fig. 14C). Palpebral area of fixigena strongly inflated, upsloping, flattening abaxially to form narrow (tr.) semielliptical, flap-like palpebral lobe centred opposite S2 and equal to 32% (30–35) of preoccipital glabellar length; palpebral furrow obsolete. Anterior branches of facial sutures converge forward before swinging inward along anterior cranial margin; posterior branches diverge abruptly, before turning sharply backward to intersect posterior margin of cranium. Posterolateral projection flexed downward and narrow (tr.) in dorsal view, so that cranial width at palpebral lobes is 84% of width at posterior margin; long (exsag.), with length behind palpebral lobe equal to 25% (24–27) of cranial length (sag). Posterior border furrow deep and transversely oriented. Posterior border expands abaxially, reaching maximum length (exsag) equal to 13% of cranial length (sag.); consequently, posterior margin of cranium deflected backward before curving forward along sutural margin. External surface of cranium smooth (apparent granulation on some specimens is a preservational feature, particularly Fig. 14D, E).

Pygidium subtriangular in outline, length equal to about 70% of maximum width, with short medial spine at posterior margin. Axis convex, raised well above pleural field and outlined by faint axial furrows; occupies about 85% of pygidial length and slightly more than one third of pygidial width at first axial ring; barely perceptible post-axial ridge present. Axial ring furrows shallow to obsolete over crest of axis but deepen at axial furrows; seven axial rings defined largely by presence of tuberculate sculpture, with at least one additional segment forming terminal piece. Pleural and interpleural furrow barely perceptible to entirely effaced near axis but deepen abaxially. Anterior and posterior pleural bands variably expressed, but roughly equal in length. Posterior pleural bands with fine tubercles; sculpture subdued on anterior bands. Pleural, interpleural and axial rings furrows lack sculpture; axial rings with coarse to fine tubercles.

*Discussion.* *Parakoldinioidia akessoni* is unique in possessing a long, slender occipital spine. The cranidia (Fig. 14) have smooth external surfaces whereas associated pygidia (Fig. 15) have conspicuous tuberculate sculpture on the axial rings, and coarse granules to fine tubercles on the posterior pleural bands of pleural field. Because of this marked contrast in sculpture, the pygidial assignment is provisional.

Cranidia are also characterised by a bluntly pointed anterior border that narrows abaxially. The palpebral area of the fixigena is strongly inflated and upsloping, flattening abaxially to form a simple, semielliptical flap-like palpebral lobe. The posterolateral projection dips steeply downward, and appears narrow (tr.) in dorsal view.

*Parakoldinioidia* sp. nov. B from Texas (Fig. 18A–C) is closest to *P. akessoni* in possessing a smooth external surface and strongly upsloping palebral areas of fixigenae. The anterior border is shorter, less tapered abaxially and, unlike *P. akessoni*, it is not arched downward in dorsal view (compare Figs 14C and 18C). The glabellae are comparable in outline and in the expression of S1, S2 and anterior median glabellar furrows; *P. sp. nov. B* lacks an occipital spine. The palpebral lobe of *P. sp. nov. B* is relatively longer, extending beyond the level of S2, and the posterolateral projection is

both shorter (exsag.) and wider (tr.), and dips downward at a shallower angle.

The pygidium is convex, subtriangular in outline, with a long, strongly arched axis of at least eight rings. A short nub of a medial marginal spine and sculpture suggest affinities with pygidial morphotypes associated with *P. inflata* (Fig. 3) and *P. lopezi* (Fig. 13).

#### **Parakoldinioidia** sp. nov. A (Figs 16 A–F, ?17)

1967 *Missisquoia nasuta*; Winston & Nicholls, p. 89, pl. 13, fig. 9 [only; figs 1, 2, = *Lunacrania nasuta*].

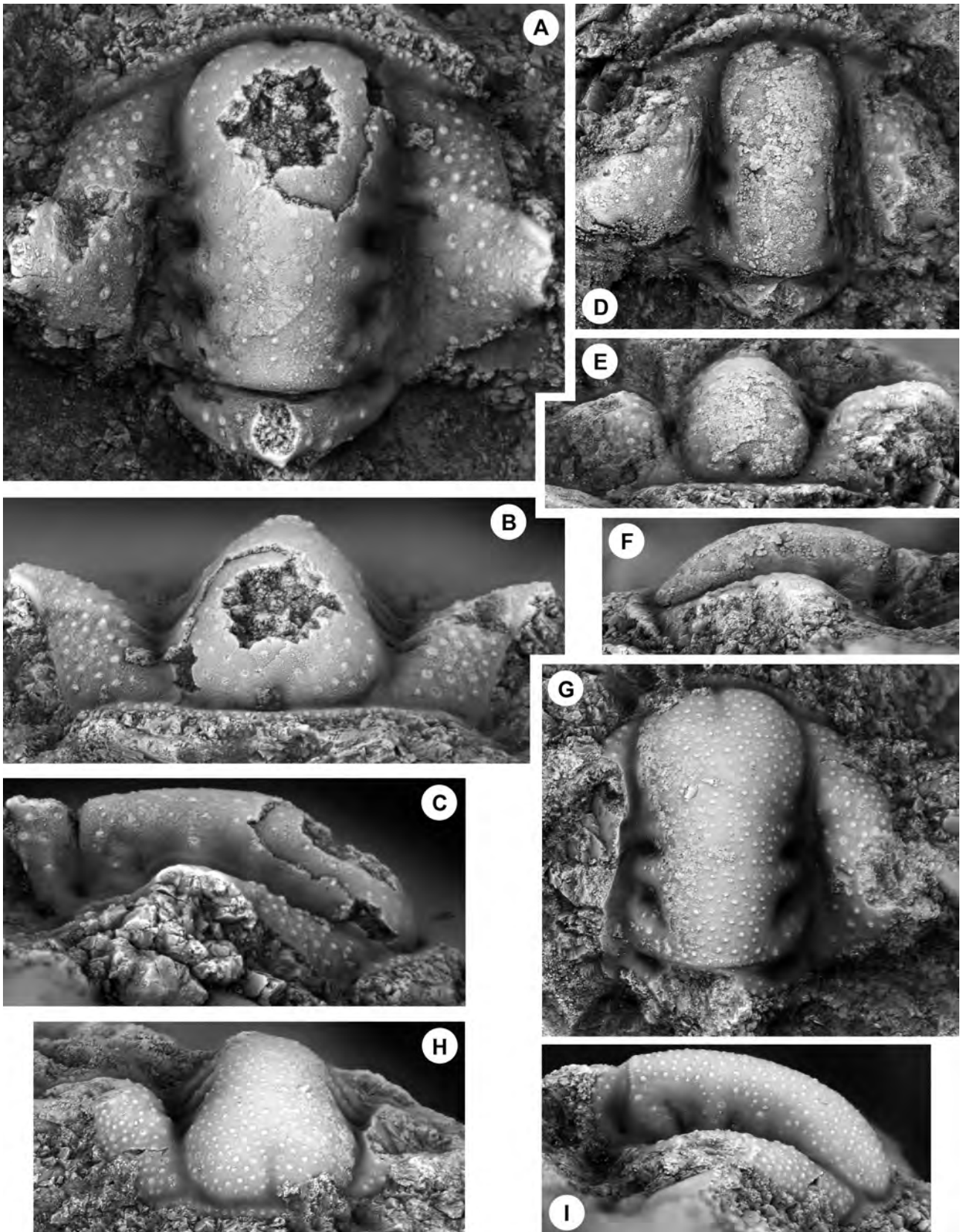
?1967 *Missisquoia typicalis*; Winston & Nicholls, p. 88, pl. 13, fig. 15 [only; fig. 2 = indet. trilobite; fig. 5 = *Parakoldinioidia lindgreni* sp. nov.; fig. 6 = *P. sp. nov. B*; figs 10, 12 = *P. sp. nov. C*; fig. 18 = *P. inflata*?].

*Occurrence.* San Saba Member, Wilberns Formation (Winston & Nicholls 1967), Calf Creek section, Mason County, collection CC–93; Camp San Saba section, McCulloch County, central Texas, collection SS–432.

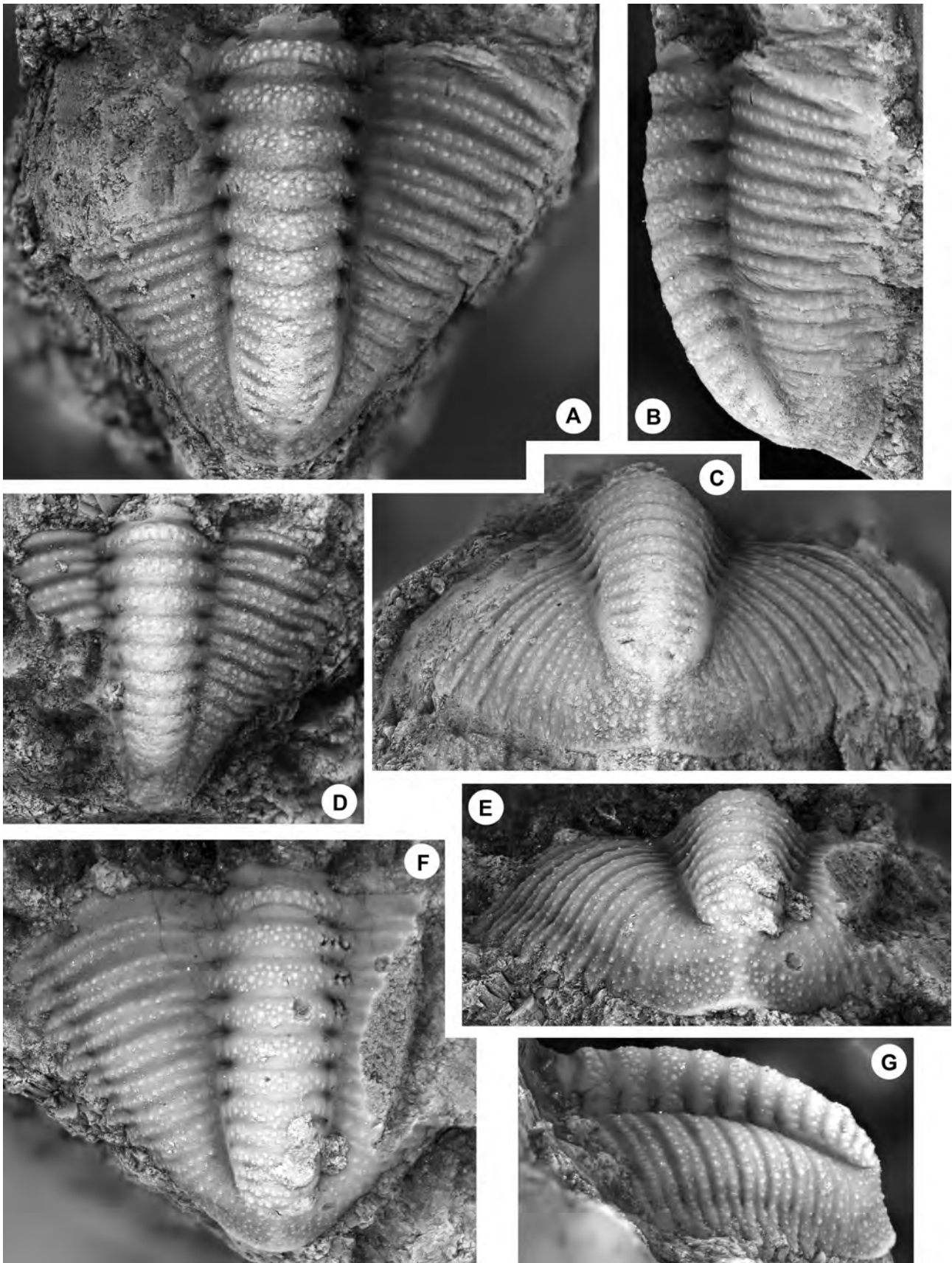
*Discussion.* A paratype cranidium of *Lunacrania nasuta* (Winston & Nicholls) from the Camp San Saba section (Fig. 16 A–C) is clearly not conspecific with the other types (Fig. 24A–C, G–I) from the Calf Creek and Threadgill Creek sections (see also Lee *et al.* 2008, appendix 1, p. 332, who described this specimen as “difficult to assess”). Indeed, this cranidium possesses characters that indicate that it is a new species of *Parakoldinioidia* rather than *Lunacrania*. It has a sculpture of widely spaced coarse granules to fine tubercles that becomes closely packed on the anterior border. The convex, parallel-sided glabella is outlined completely by axial furrows and has narrow (tr.) but firmly impressed S1 and S2 furrows. Fixigenae are strongly upsloping so that the palpebral lobes are elevated well above the axial furrows, and are centred opposite L2. A smaller, previously unfigured cranidium from collection CC–93 at Calf Creek (Fig. 16D–F) undoubtedly represents the same species as the larger cranidium, differing only in having a relatively narrower glabella and in lacking the palpebral ridge.

Pygidia from CC–93 are assigned only questionably to *P. sp. nov. A* because there is another coarsely granulose cranial morph in this collection (see *P. cf. sp. nov. A*, below). They are subtriangular in outline, with length about 75% of maximum width and strongly convex; eight pairs of marginal spines are present in front of a short (exsag.) posterior sector with an entire margin. The convex axis is very weakly tapered, and occupies about 90% of pygidial length and slightly more than 25% of maximum pygidial width; a low postaxial ridge is present on some specimens (Fig. 17A, C). Anteriorly, seven axial rings are defined by complete, transverse ring furrows that deepen abruptly near the axial furrow. The rear quarter of the axis has shallower, incomplete ring furrows that separate at least six additional segments. Pleural furrows are deep oblique grooves that do not extend onto the marginal spines and divide pleurae into short (exsag.), anterior and posterior pleural bands; pleural furrows are narrower (exsag.) and lightly impressed. External surface, aside from furrows, has sculpture of closely spaced fine tubercles and coarse granules (e.g., Fig. 17A).

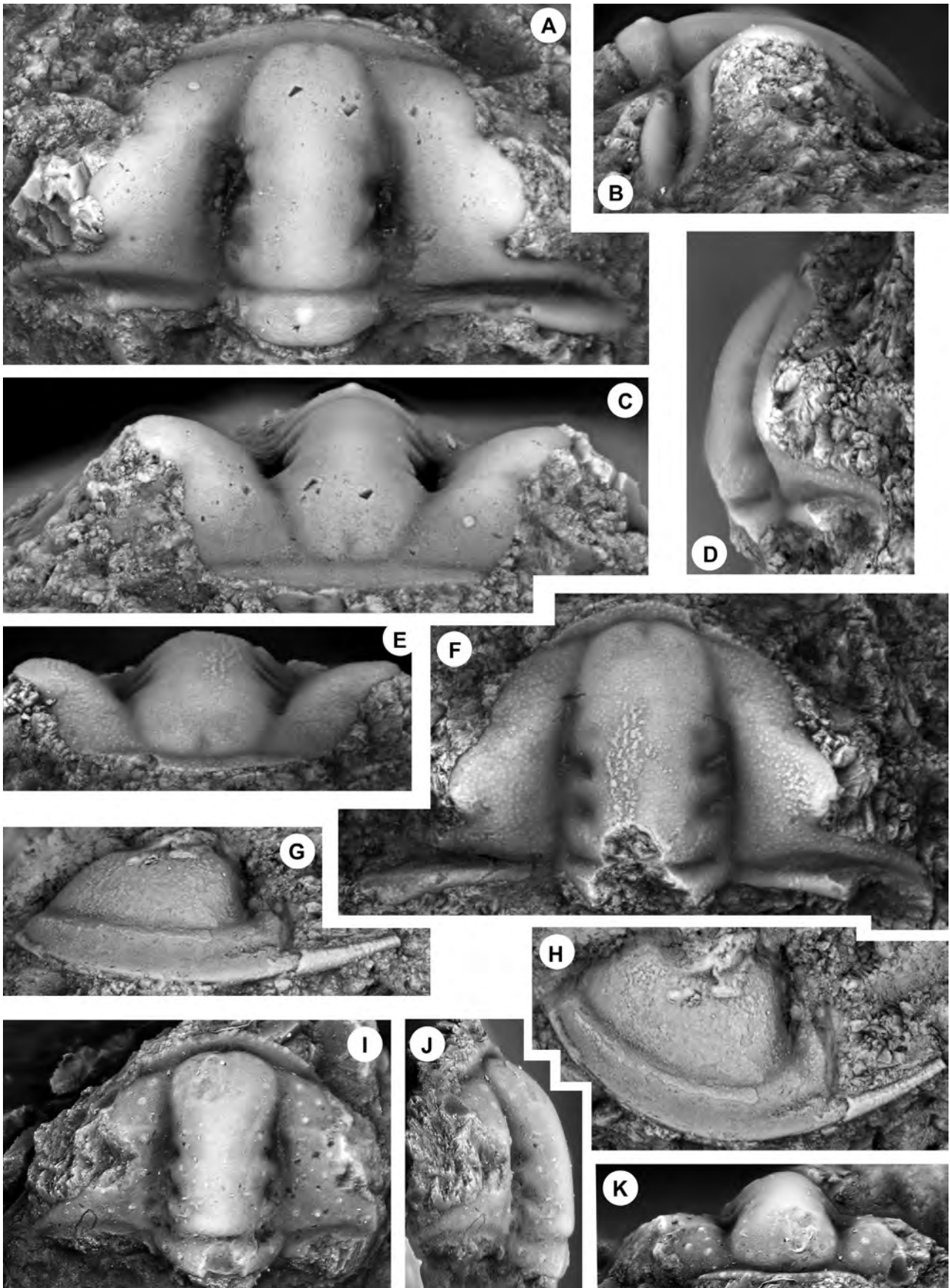
Although unusual among Laurentian species, coarsely granulose to tuberculate sculpture is present in *Parakoldinioidia* from Queensland, Australia (Shergold 1975, 1980). *Parakoldinioidia bigranulosa* Shergold



**Figure 16.** *Parakoldinioidia* spp. from the San Saba Member, Wilberns Formation, central Texas. All from Calf Creek section, Mason County, except A–C (San Saba Section, McCulloch County). All cranidia and all x16 except A–C (x14) A–F, *Parakoldinioidia* sp. nov. A. A–C, USNM 185923 (illustrated previously as a paratype of *Missisquoia nasuta* Winston & Nicholls 1967, pl. 13, fig. 9), lateral, dorsal and anterior views, collection SS–432; D–F, USNM 560655 (previously unfigured, associated with USNM 185922), dorsal, anterior and lateral views, collection CC–93; G–I, *Parakoldinioidia* cf. sp. nov. A., USNM 560656 (previously unfigured, associated with USNM 185922), dorsal, anterior and lateral views, collection CC–93.



**Figure 17.** *Parakoldinioidia* n. sp. A.? from the San Saba Member, Wilberns Formation, Calf Creek section, Mason County, central Texas. All pygidia from collection CC-93, and all x14 except D (x18). A–C, USNM 185929, dorsal, lateral and posterior views; D, USNM 560657 (previously unfigured, associated with USNM 185928), dorsal view; E–G, USNM 560658 (previously unfigured, associated with USNM 185930), dorsal, posterior and lateral views.



**Figure 18.** *Parakoldinioidia* spp. All from the San Saba Member, Wilberns Formation, central Texas, except I–J (uppermost Cambrian strata, Swift’s Ranch, Alberta). A–C, *Parakoldinioidia* sp. nov. B, cranidium, USNM 185926, dorsal, lateral and anterior views, Camp San Saba section, McCulloch County, collection SS–432, x18 (illustrated previously as *Missisquoia typicalis* Shaw (*continued opposite*))



(1975, pl. 45, figs 2–5), from the Chatsworth Limestone at Black Mountain, has a denser covering of granules and fine tubercles than *P. sp. nov. A*, particularly over the glabella. In addition, the anterior cranial border is longer and, in the smaller cranidium (Shergold 1975, pl. 45, fig. 3), there is a conspicuous medial projection (“anterior prong” of Shergold). The glabella of *P. bigranulosa* differs in being constricted at L2 and has deeper S1 and S2 furrows that continue abaxially to the axial furrow. The associated pygidia are shorter and narrow than the pygidia tentatively attributed to *P. sp. nov. A*, and have fewer segments evident on both the axis and pleural field.

Shergold (1980, p. 80) noted that *Parakoldinioidia sp. aff. P. bigranulosa*, from the type section of the Chatsworth Limestone at Lily Creek, likely represents more than one species. The most completely preserved cranidium (Shergold 1980, pl. 30, fig. 2) has a shorter, more sharply triangular anterior border than *P. sp. nov. C*, and the remarkably large and inflated palpebral lobe contrasts sharply with the simple, semielliptical, flap-like lobes of all Laurentian species described to date. The glabella is slightly expanded at L1, whereas other cranidia are parallel-sided (Shergold 1980, pl. 30, fig. 3) or slightly constricted at L2 (Shergold 1980, pl. 30, fig. 4). Pygidia (Shergold 1980, pl. 30, figs 5–10) vary in outline but, on both testate and exfoliated surfaces, all have deep, slot-like pleural furrows and shallow interpleural furrows unlike that in *P. sp. nov. A?* described above.

#### **Parakoldinioidia cf. P. sp. nov. A (Fig. 16G–I)**

*Occurrence.* San Saba Member, Wilberns Formation, Calf Creek section, Mason County (Winston & Nicholls 1967), collection CC–93.

*Discussion.* A single cranidium differs from *Parakoldinioidia sp. nov. A*, with which it co-occurs, in having a far greater density of granules, particularly on the glabella, and appears to have possessed an even shorter anterior border. The palpebral area of the fixigena is narrower, so that the palpebral lobe (broken off) seems to have been closer to the glabella; palpebral ridges are absent. We doubt very much that this specimen is conspecific with *P. sp. nov. A*, but more material is needed for a definitive decision. It is an alternate candidate for association with the pygidia assigned questionably to *P. sp. nov. A* (Fig. 17).

Granulose to tuberculate species of *Parakoldinioidia* from Australia (Shergold 1975, pl. 45, figs. 2–5; 1980, pl. 30) all have longer, nasute rather than anteriorly rounded, anterior borders and much wider palpebral areas of fixigenae than *P. cf. P. sp. nov. A*.

#### **Parakoldinioidia sp. nov. B (Fig. 18A–C)**

1967 *Missisquoia typicalis*; Winston & Nicholls, p. 88, pl. 13, fig. 6 [only; fig. 2 = indet. trilobite; fig. 5 = *Parakoldinioidia lindgreni sp. nov.*; figs 10, 12 = *P. sp. nov. C*; fig. 15 = *P. sp. nov. A?*; fig. 18 = *P. inflata?*].

*Occurrence.* San Saba Member, Wilberns Formation, Camp

San Saba section, McCulloch County, central Texas (Winston & Nicholls 1967), collection SS–432.

*Discussion.* We are confident that a single cranidium from the Camp San Saba section, central Texas, records a new species. It is relatively broad, with length (sag.) equal to about 75% of maximum width across the palpebral lobes, and has a smooth external surface. The glabella is relatively narrow, with shallow S1 and S2 furrows, and barely perceptible L3; palpebral areas of fixigenae are strongly upsloping, and the elevated palpebral lobes are long, equal to one-third of glabella length, and centered opposite S2.

*Parakoldinioidia sp. nov. B* is most like *P. akessoni* from Oklahoma, and is compared to that species above. It is also similar to *P. lindgreni* (e.g., Fig. 18E, F), but has a relatively wider cranidium with a less rounded anterior margin, larger palpebral lobes, more elevated fixigenae, and a smooth, rather than granulose surface.

#### **Parakoldinioidia sp. nov. C (Fig. 19)**

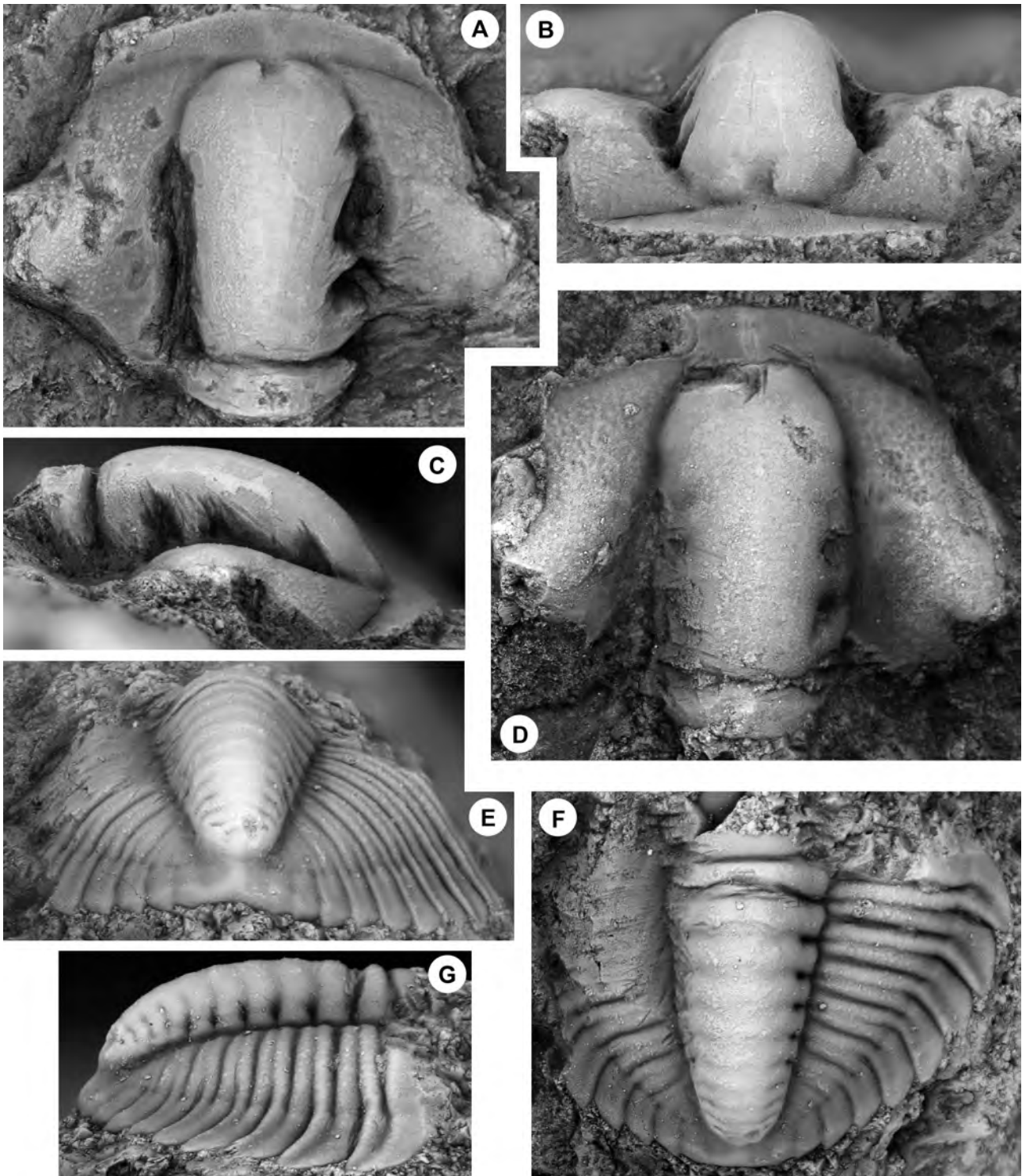
1967 *Missisquoia typicalis*; Winston & Nicholls, p. 88, pl. 13, figs 10, 12 [only; fig. 2 = indet. trilobite; fig. 5 = *Parakoldinioidia lindgreni sp. nov.*; fig. 6 = *P. sp. nov. B*; fig. 15 = *P. sp. nov. A?*; fig. 16 = *P. inflata?*].

*Occurrence.* San Saba Member, Wilberns Formation, Calf Creek section, Mason County, central Texas (Winston & Nicholls 1967), collection CC–93.

*Discussion.* A distinctive semielliptical pygidium with eight pairs of bluntly pointed marginal spines is associated with a cranidium with a relatively long, gently down-sloping anterior border because both have nearly smooth surfaces. Both sclerite types were considered to be part of a highly variably species that Winston & Nicholls (1967) identified as “*Missisquoia typicalis*”. Like paratypes of *P. inflata* (see above) and *L. nasuta* (Fig. 24A–C), the cranidium illustrated by Winston & Nicholls (1967, pl. 13, fig. 10) has suffered from subsequent, heavy-handed preparation that, in this case, removed part of the left side of the glabella and over-deepened the lateral glabellar furrows (Fig. 19A–C). Fortunately, a previously unfigured specimen from the same collection (Fig. 19D) shows that S1 and S2 are in fact short (tr.) but well incised, and S3 is barely perceptible.

The pygidium is semielliptical in outline, with length equal to about 65% of width, strongly arched, and despite the spinose margin, is well rounded. The axis is convex, standing well above the pleural field, which is flexed steeply down distally; it occupies about 95% of pygidial length and about 30% of width at the first axial ring. The first six axial rings are defined by axial ring furrows that are well incised at the axial furrows but quickly and abruptly shallow adaxially, and are gently impressed over most of the axis; at least five additional segments are outlined by ring furrows that are weakly expressed over their entire width (tr.). Bluntly pointed spines at pleural tips are broad (exsag.) anteriorly but become smaller towards the rear of the pygidium, and are curved backward; spines are absent from the region behind the

by Winston & Nicholls 1967, pl. 13, fig. 6); **D–F**, *Parakoldinioidia lindgreni sp. nov.*, cranidium, USNM 18925, lateral, anterior and dorsal views, Calf Creek section, Mason County, collection CC–90, x20 (illustrated previously as *Missisquoia typicalis* Shaw by Winston & Nicholls 1967, pl. 13, fig. 5). **G, H**, indet. librigena, USNM 185924, lateral and dorsal views, collection CC–93, x16 (illustrated previously as *Missisquoia typicalis* Shaw by Winston & Nicholls 1967, pl. 13, fig. 2); **I–K**, *Parakoldinioidia sp. indet.*, cranidium, GSC 9377a (identified as *Hardyia mention* Walcott by Kindler 1929), anterior, dorsal and anterior views, x20.



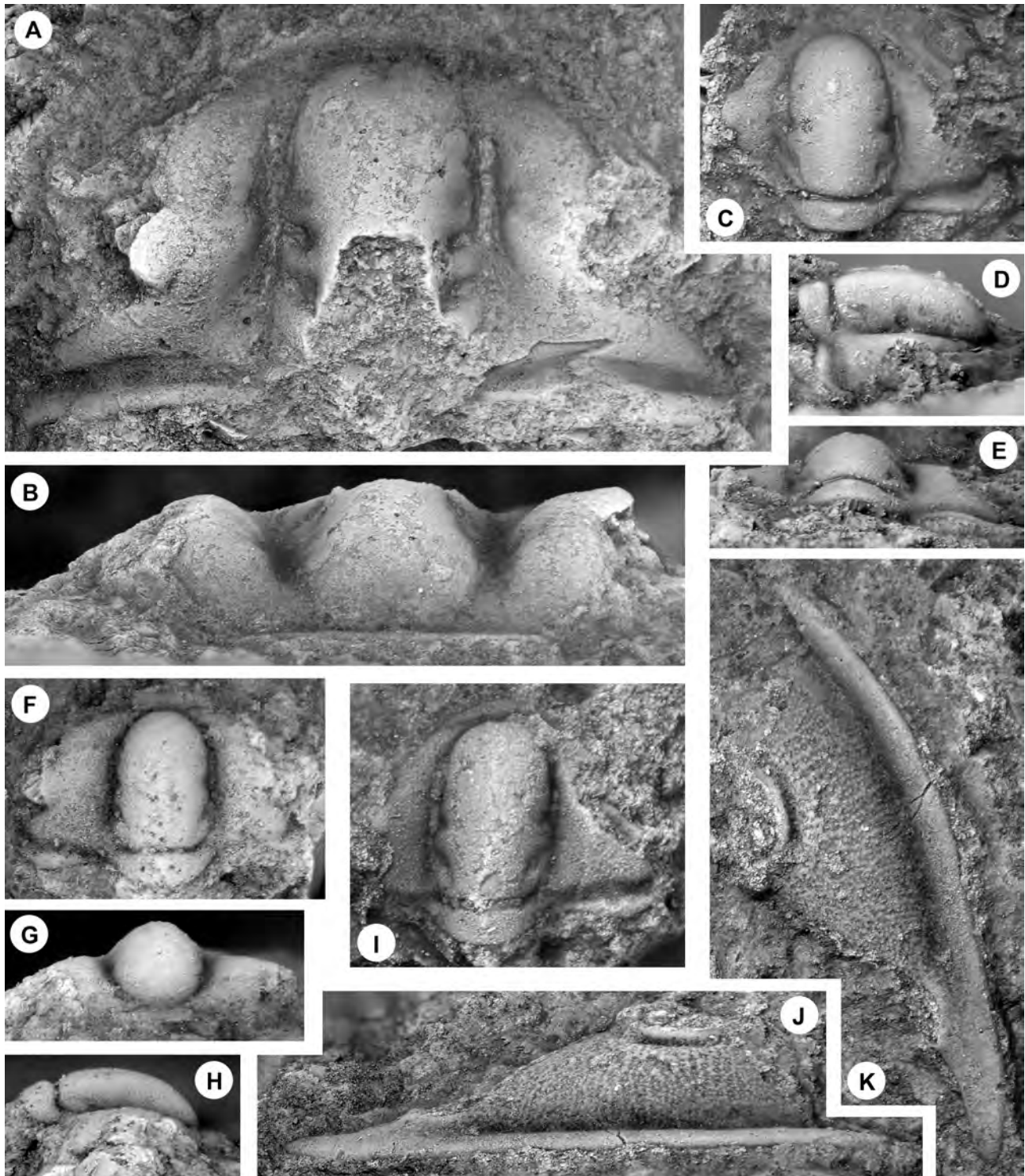
**Figure 19.** *Parakoldinioidia* sp. nov. C from the San Saba Member, Wilberns Formation, Calf Creek section, Mason County, central Texas. All from collection CC-93. A–C, cranidium, USNM 185925 (figured previously as *Missisquoia typicalis* Shaw by Winston & Nicholls 1967, pl. 13, fig. 10), dorsal, anterior and lateral views, x15. D, cranidium, USNM 560659 (previously unfigured, associated with USNM 185928), dorsal view, x14; E–G, pygidium, USNM 185928 (figured previously as *Missisquoia typicalis* Shaw by Winston & Nicholls 1967, pl. 13, fig. 12), posterior, dorsal and lateral views, x15.

axis. Pleural furrows are well defined adaxially but shallow at a distinct paradoublural furrow, and extend onto spines; interpleural furrows are more finely etched but still distinct.

***Parakoldinioidia* cf. *P.* sp. nov. C (Figs. 20A–E, 21)**

1977 *Missisquoia typicalis*; Dean, p. 4, pl. 1, figs 5, 9, 12, 15 [only; figs. 4, 7 = *Lunacrania* sp. indet.].

1989 *Missisquoia typicalis*; Dean, p. 31, pl. 19, figs 1, 2, 5,



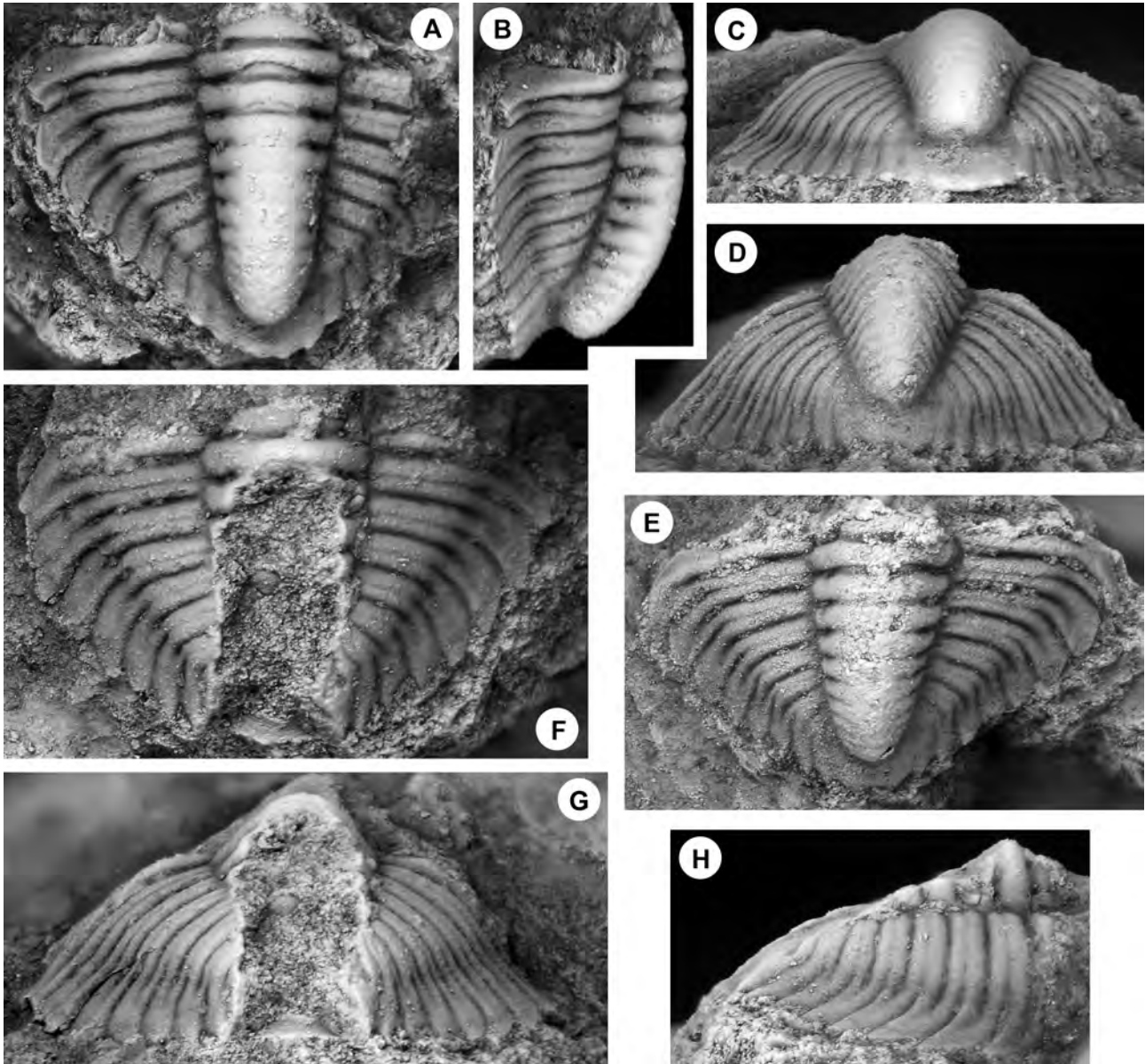
**Figure 20.** *Parakoldinioidia* spp. from the Basal Silty Member, Survey Peak Formation, Wilcox Pass, Alberta (Dean 1977, 1989). **A–E**, *Parakoldinioidia* cf. *P. sp. nov.* **C. A, B**, cranium, GSC 47974, dorsal and anterior views, GSC loc. 92223 x14 (figured previously as *Missisquoia typicalis* Shaw by Dean 1977, pl. 1, figs. 12, 15). **C–E**, cranium, GSC 47973, dorsal, lateral and posterior views, GSC loc. 92223, x20 (figured previously as *Missisquoia typicalis* Shaw by Dean 1977, pl. 1, fig. 9); **F–K**, *Parakoldinioidia* sp. indet. **F–H**, cranium, GSC 62222, dorsal, anterior and lateral views, GSC loc. 89269, x 20 (figured previously as *Missisquoia typicalis* Shaw by Dean 1989, pl. 13, fig. 4); **I**, cranium, GSC 137485 (previously unfigured), dorsal view, GSC loc. 92223, x20; **J, K**, librigena, GSC 62226, lateral and dorsal views, GSC loc. 89269, x15 (figured previously as *Missisquoia typicalis* Shaw by Dean 1989, pl. 13, fig. 13).

7 (only; figs 3, 4, 13 = *Parakoldinioidia* sp. indet.).

(Dean 1977, 1989).

**Occurrence.** Basal Silty Member, Survey Peak Formation, Wilcox Pass, Jasper National Park, Alberta, GSC loc. 92223

**Discussion.** Pygidia illustrated previously by Dean from the Survey Peak Formation, Alberta (Fig. 21) are very similar to



**Figure 21.** *Parakoldinioidia* cf. *P. sp. C* from the Basal Silty Member, Survey Peak Formation, Wilcox Pass, Alberta (Dean 1977, 1989). A–C, pygidium, GSC 62220, dorsal, lateral and posterior views, GSC loc. 92223, x20 (figured previously as *Missisquoia typicalis* Shaw by Dean 1989, pl. 13, figs 5, 7); D, E, pygidium, GSC 47972, posterior and dorsal views, GSC loc. 92223, x20 (figured previously as *Missisquoia typicalis* Shaw by Dean 1977, pl. 1, fig. 5); F–H, pygidium, GSC 62219, dorsal, posterior and lateral views, GSC loc. 92223, x20 (figured previously as *Missisquoia typicalis* Shaw by Dean 1989, pl. 13, fig. 1).

the pygidium of *P. sp. nov. C* from the Wilberns Formation, Texas (Fig. 19E–G). They differ from the latter in having a more tapered, subtriangular outline and an additional three pairs of small marginal spines along the posterior margin. Poor preservation and small sample size limits knowledge of the associated cranidia, but the anterior border is appreciably shorter than in *P. sp. nov. C*, as is the palpebral lobe (compare Fig. 19A–C and Fig. 20A, B).

Two cranidia and a librigena assigned to “*M. typicalis*” by Dean (1989; Fig. 20F–K) are from a different collection (GSC locs. 89269) from the sclerites that we assign to *P. cf. P. sp. nov. C*. One of the cranidia (Fig. 20F–H) in particular has much wider fixigenae than the others. In the absence of associated pygidia, these specimens are viewed as an indeterminate species of *Parakoldinioidia*.

#### *Parakoldinioidia* sp. indet. (Fig. 18I–K)

1929 *Hardyia metion*; Kindle, p. 146, pl. 1, fig. 17 [only; fig. 16 = *Lunacrania* cf. *L. trisecta*].

*Occurrence.* Uppermost Cambrian strata, Swift’s Ranch, seven miles north of Jasper National Park, Alberta (Kindle 1929).

*Discussion.* The sculpture of widely spaced tubercles and the weak palpebral ridge ally an incomplete cranidium from the Jasper region, Alberta, with *Parakoldinioidia* sp. nov. A, from which it differs most obviously in having weakly inflated palpebral areas of the fixigenae (compare Fig. 16B, E and Fig. 18K).

**Lunacrania** Kobayashi 1955

*Type species.* *Lunacrania trisecta* Kobayashi 1955 from the McKay Group, Jubilee Mountain, Harrogate region, British Columbia (by original designation).

*Diagnosis.* Glabellar furrows shallowing anteriorly, so that anterior portion of glabella is poorly differentiated from adjacent fixigenae. Palpebral lobe small to minute. Pygidium with convex axis with ring furrows largely to completely effaced, aside from one firmly impressed furrow at anterior. Pleural field with four pairs of segments expressed anteriorly, with one or two well incised pleural furrows; remainder of pleural furrows becomes effaced towards the rear.

*Discussion.* In removing *Lunacrania* from synonymy with *Parakoldinioidia*, Fortey (in Fortey *et al.* 1982) left unanswered the question of whether it might be a junior synonym of *Macroculites* (see Dean 1977), which has page priority. He later (Fortey 1983) noted that the holotype cranidium of *Macroculites enigmaticus* Kobayashi 1955 is poorly preserved, and also claimed that it is impossible to determine the size of the palpebral lobes on this specimen; a character which he (Fortey in Fortey *et al.* 1982) viewed as pivotal in distinguishing *Lunacrania* from *Parakoldinioidia*. Our new images of this specimen (Fig. 22A–C) confirm its dismal condition, although the size of the broken area on the most elevated portion of the right fixigena suggests that the palpebral lobe was small, and thus shares a potential synapomorphy with other species of *Lunacrania*. Even so, we recommend that *L. enigmatica* be treated as a *nomen dubium* that is restricted to the holotype; other cranidia that have been assigned to this species in the past (e.g., Westrop 1986; Fig. 22D–F) are placed in open nomenclature.

The holotype and only known specimen of *L. trisecta* from the type area in British Columbia is far better preserved than *L. enigmatica*, although our new images (Fig. 22J–L) indicate that the palpebral lobes, although likely very small, are not actually preserved. A few previously illustrated sclerites from Alberta (Fig. 22D–I, M, 23A–C, G, K–M) have had a chequered nomenclatural history (e.g., Dean 1977; Westrop 1986, p. 67) but are assigned here to *Lunacrania*. Although they are not easy to interpret, they provide some guidance on the likely pygidial anatomy of the genus. Two cranidia from different localities (Fig. 22G–I, M) are larger than, but possibly conspecific with, *L. trisecta*, sharing the short, subtriangular anterior border, axial furrows that become largely effaced anteriorly, and small, forwardly placed palpebral lobes; characters that were included in the diagnosis of *Lunacrania* by Lee *et al.* (2008). They differ from the holotype in having weak yet clearly defined S1 and S2 furrows. Although this could be a function of the difference in size, given the extremely small sample, we prefer to err on the side of caution and place the specimens from Alberta in open nomenclature (*Lunacrania* cf. *L. trisecta*). Both cranidia differ from *Lunacrania enigmatica* (Fig. 22A–C) in possessing much shorter anterior borders and less convex glabellae.

As noted by Dean (1977), the holotype pygidium of *Rhamphopyge altipolium* Kobayashi 1955 is from the same locality as both *L. trisecta* and *L. enigmatica*. He also mentioned (1977, p. 3) that, “material almost identical with the holotype has been collected from GSC loc. 89273”. A pygidium from this collection was figured by Dean (1989, pl. 13, figs 8, 10) and is reillustrated here (Fig. 23A–C). It

differs minimally from the much smaller holotype in having a longer axis, and less convex border behind an anterior region with four pairs of marginal spines. One of the cranidia of *L. cf. L. trisecta* occurs at GSC loc. 89273 (Fig. 22M), and we suggest that the pygidium belongs to this species. This further suggests that the holotype of *R. altipolium* may belong to *L. trisecta*. If the types of *R. altipolium* and *L. trisecta* are associated correctly, a case could be made for treating *L. trisecta* and *L. cf. L. trisecta* as a single species, given the close similarities between their respective cranidia and pygidia.

A second species of *Lunacrania* from the Survey Peak Formation at Wilcox Pass is represented by two pygidia (Fig. 23H–M). Dean (1977, pl. 1, figs 4, 7) illustrated one of these under the name *Missisquoia typicalis*, but Westrop (1986) suggested that it might belong to the species identified here as *L. cf. L. enigmatica* (Fig. 22D–F). The long posterior border of the pygidium is similar in proportions to the anterior border of the cranidium of *L. cf. L. enigmatica*, but as they are not known to occur together in the same collection, a confident assignment cannot yet be made.

All pygidia assigned to *Lunacrania* from western Canada have convex axes with one deeply incised axial ring furrow anteriorly, but the rest of the ring furrows are mostly to completely effaced. On the pleural field, four pairs of segments are expressed anteriorly, with one or two firmly impressed pleural furrows, and the remainder become effaced. *Lunacrania nasuta* (Winston & Nicholls 1967) from Texas and Oklahoma shares these pygidial characters (Fig. 25G–I) and provides further support for the sclerite assignments of the material from Alberta and British Columbia. The cranidium of *Lunacrania nasuta* displays the anterior shallowing of axial furrows that occurs in *L. trisecta*, *L. cf. trisecta* and *L. cf. L. enigmatica* and, like these species, the frontal glabellar lobe is poorly differentiated from the adjacent regions of the fixigenae. It differs in retaining a vestigial median anterior glabellar furrow (Fig. 24C, G) and has larger palpebral lobes. The pygidium attributed to *L. nasuta* (Fig. 25G–I) is a little less effaced than pygidia from western Canada. In addition, it has small spines that are expressed along the lateral margin at least as far back as the level of the tip of the axis (Fig. 25H), whereas other species have entire margins posteriorly (e.g., Fig. 23A, E, K).

Lee *et al.* (2008) assigned *Parakoldinioidia inflata* (Winston & Nicholls 1967) questionably to *Lunacrania*. However, the cranidium of this species (Fig. 2) has large palpebral lobes and a glabella that is convex anteriorly and outlined fully by axial and preglabellar furrows. All candidates for the pygidium of this species (Fig. 3) have a completely furrowed pleural field; axial ring furrows are variably expressed along the length of the axis, but are at minimum identifiable on the sides of the axis, near the axial furrows. It is here returned to *Parakoldinioidia*.

**Lunacrania trisecta** Kobayashi 1955 (Fig. 22J–L, ?23D–F)

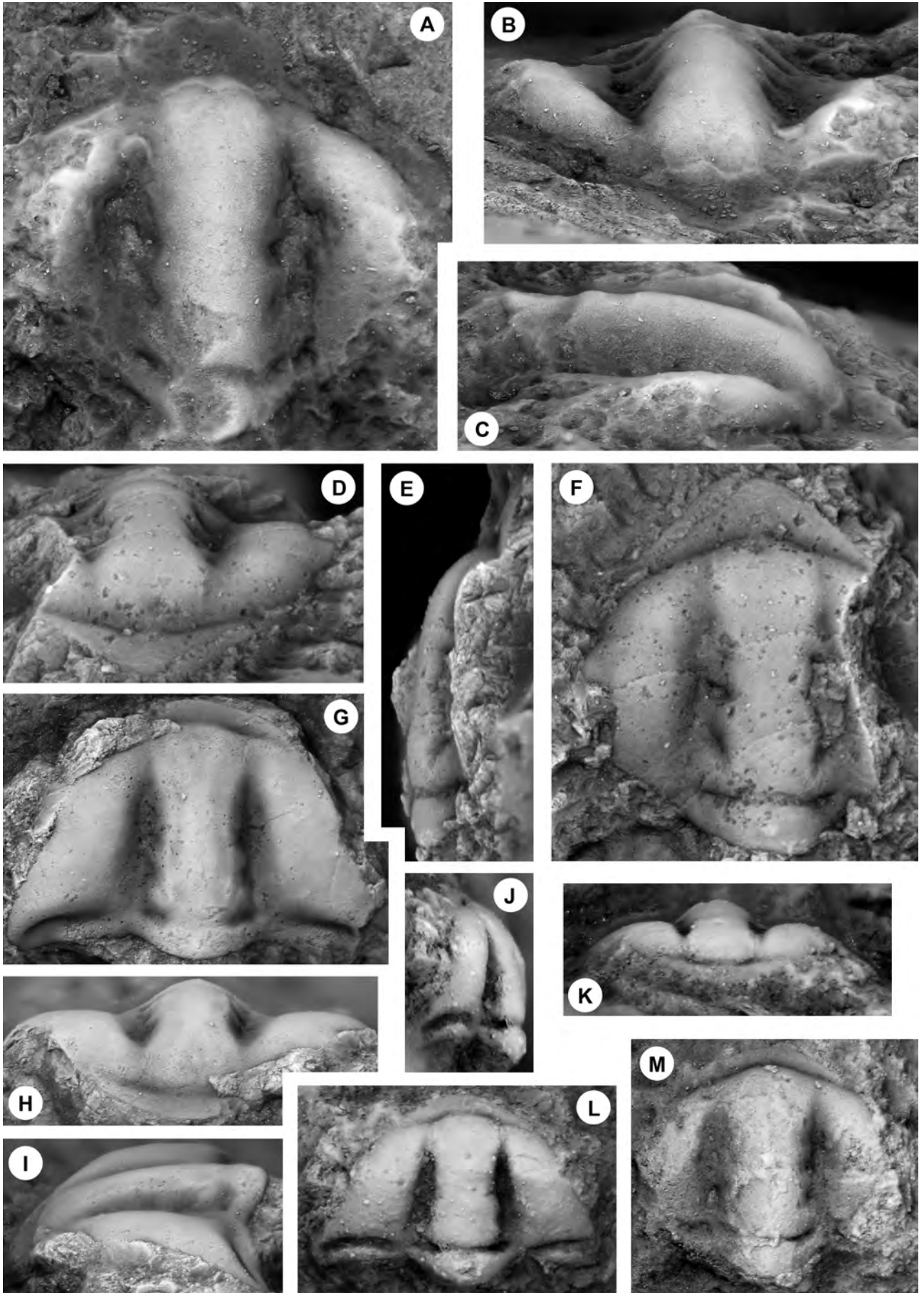
1955 *Lunacrania trisecta*; Kobayashi, p. 472, pl. 7, fig. 7, pl. 8, fig. 10.

?1955 *Rhamphopyge antipolum*; Kobayashi, p. 473, pl. 6, figs. 9a, b, pl. 9, fig. 8.

?1977 *Missisquoia enigmatica* (Kobayashi); Dean, p. 4, pl. 1, figs 2, 3.

1977 *Missisquoia enigmatica* (Kobayashi); Dean, p. 4, pl. 1, fig. 8 [only].

1982 *Lunacrania trisecta* Kobayashi; Fortey in Fortey *et*



*al.*, p. 112.

1983 *Lunacrania trisecta* Kobayashi; Fortey, p. 196.

1989 *Lunacrania trisecta* Kobayashi; Dean, p. 31.

2008 *Lunacrania trisecta* Kobayashi; Lee *et al.*, p. 332, appendix 1.

**Diagnosis.** Palpebral lobes very small. Anterior border short, equal to about 10% of glabellar length. Posterior margin of fixigenae nearly transverse. Lateral glabellar furrows faint. External surface of cranidium smooth. Pygidium (assigned questionably) with four pairs of short marginal spines anteriorly; remainder of margin in the form of weakly convex border. One deep axial ring furrow at anterior end of axis that is otherwise almost completely unfurrowed. Four pairs of oblique pleural furrows that become progressively shallower towards rear.

**Holotype.** A cranidium (GSC 12743; Fig. 22J–L) from the McKay Group, Jubilee Mountain, British Columbia (locality 24 of Evans 1933).

**Discussion.** As discussed above, the holotype pygidium of *Rhamphopyge antipolum*, is assigned questionably to *L. trisecta*, with which it co-occurs with at Evans' (1933) locality 24.

In establishing *Lunacrania spicata* for sclerites from the Shallow Bay Formation, Newfoundland, Fortey (1983, p. 196) included the presence of an occipital spine, the backwardly curved posterior tips of the fixigenae and the very short anterior border as characters that separated it from *L. trisecta*. Our new images of *L. trisecta* (Fig. 22J–L) also show that, unlike *L. spicata*, the lateral glabellar furrows are barely perceptible, and the external surface of the cranidium is smooth, rather than granulose. Small cranidia from the Shallow Bay Formation illustrated under the name *Lunacrania cf. L. trisecta* by Fortey (in Fortey *et al.* 1982, pl. 2, figs 1, 2) are likely assigned correctly to the genus, but the small sizes of the images limit further evaluation. The well defined lateral glabellar furrows and broad rectangular glabella (in particular, see Fortey *et al.* 1982, pl. 2, fig. 2) suggest that these specimens are not closely related to *L. trisecta*, nor to the sclerites illustrated here as *L. cf. L. trisecta* (Fig. 22G–I, M).

Fortey (1983) also included *Paranumia triangulata* Hu 1973 (pl. 1, figs 1–23), from the Deadwood Formation of South Dakota, in *Lunacrania*. All of Hu's figured specimens are very small and are difficult to interpret. The palpebral lobes are certainly small and located far from the glabella. However, the glabella differs from *L. trisecta* and other species that we assign to the genus in being convex anteriorly, outlined fully by axial and preglabellar furrows, and well differentiated from adjacent areas of the fixigenae. Some of the pygidia (e.g., Hu 1973, pl. 1, figs 19, 20) could perhaps be interpreted as immature, more furrowed versions of larger

sclerites that we assign to *Lunacrania* (e.g., Fig. 23J), but the larger specimens (Hu 1973, pl. 1, fig. 23) are, as far as we can tell from the dorsal views, more like *Parakoldinoidea*. Without information from larger holaspids, we consider the affinities of *Paranumia triangulata* to be uncertain.

**Lunacrania cf. L. trisecta** Kobayashi 1955 (Figs 23G–I, M, 24A–C, G)

1929 *Hardyia metion*; Kindle, p. 146, pl. 1, fig. 16 [only; fig. 17 = *Parakoldinoidea* sp. indet.].

cf. 1955 *Lunacrania trisecta*; Kobayashi, p. 472, pl. 7, fig. 7, pl. 8, fig. 10.

1977 *Missisquoia typicalis*; Dean, p. 4, pl. 1, fig. 5 (smaller pygidium only; larger specimen = *Parakoldinoidea* cf. P. sp. nov. C)

non 1982 *Lunacrania cf. L. trisecta*; Fortey in Fortey *et al.*, p. 112, pl. 2, figs 1, 2.

1989 *Missisquoia enigmatica*; Dean, p. 31, pl. 13, figs 6, 8, 10.

**Occurrence.** Basal Silty Member, Survey Peak Formation, Wilcox Pass Jasper National Park, Alberta, GSC locs. 89273, 92223 (Dean 1977, 1989). Unnamed uppermost Cambrian strata, Swift's Ranch, seven miles north of Jasper National Park, Alberta (Kindle 1929).

**Discussion.** As noted earlier, sclerites assigned to *L. cf. L. trisecta* are similar to the respective holotypes of *L. trisecta* and *R. antipolum*, and should larger samples become available, it may be possible to show that they all represent a single species.

**Lunacrania enigmatica** Kobayashi 1955 (Fig. 22A–C)

1955 *Macroculites enigmaticus*; Kobayashi, p. 460, pl. 6, fig. 14.

1977 *Missisquoia enigmatica* (Kobayashi); Dean, p. 4, pl. 1, fig. 6 [only]

non 1986 *Missisquoia enigmatica* (Kobayashi); Westrop, p. 67, pl. 1, fig. 38

1989 *Missisquoia enigmatica* (Kobayashi); Dean, p. 32.

?1993 *Missisquoia enigmatica* (Kobayashi); Loch *et al.*, p. 509, fig. 8.13, 8.14.

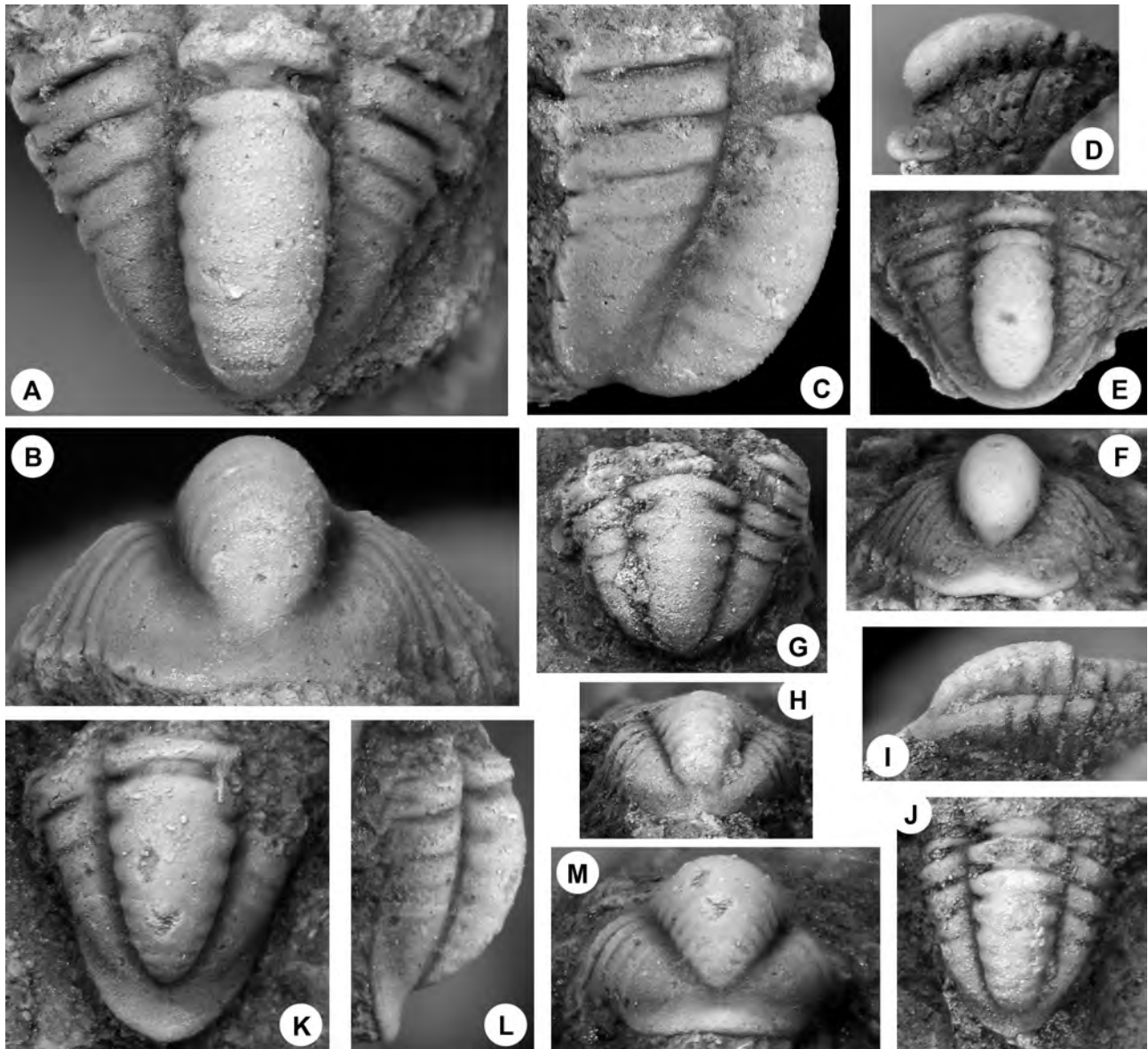
2003 *Missisquoia enigmatica* (Kobayashi); Miller *et al.*, p. 52.

2008 *Lunacrania? enigmatica* (Kobayashi); Lee *et al.*, p. 332, appendix 1.

**Holotype.** A cranidium (GSC 12716; Fig. 22A–C) from the McKay Group, Jubilee Mountain, British Columbia (locality 24 of Evans 1933).

**Discussion.** As discussed above, *Lunacrania enigmatica* is

**Figure 22. *Lunacrania* spp.**, uppermost Cambrian strata, Alberta and British Columbia. **A–C, *Lunacrania enigmatica*** Kobayashi, 1955, cranidium, GSC 12716 (holotype of *Macroculites enigmaticus* Kobayashi, 1955), dorsal, anterior and lateral views, McKay Group, Jubilee Mountain, British Columbia (locality 24 of Evans 1933), x20; **D–F; *Lunacrania cf. L. enigmatica*** (Kobayashi 1955), cranidium, GSC 75234, anterior, lateral and dorsal views, Basal Silty Member, Survey Peak Formation, Wilcox Peak Alberta, collection W319, x20 (figured previously by Westrop 1986, pl. 1 fig. 38). **G–I, M, *Lunacrania cf. L. trisecta*** Kobayashi 1955. **G–I**, cranidium, GSC 9377, dorsal, anterior and lateral views, uppermost Cambrian strata, Swift's Ranch, Alberta, x20 (figured previously by Dean 1977, pl. 1, fig. 1 as *Missisquoia enigmatica* [Kobayashi]); **M**, cranidium, GSC 62223, dorsal view, Basal Silty Member, Survey Peak Formation, Wilcox Pass, Alberta, GSC loc. 89273, x20; (figured previously by Dean 1989, pl. 13, fig. 6 as *Missisquoia enigmatica* [Kobayashi]); **J–L, *Lunacrania trisecta*** Kobayashi 1955, cranidium, GSC 12743 (holotype), lateral, anterior and dorsal views, McKay Group, Jubilee Mountain, British Columbia (locality 24 of Evans 1933), x20 (figured by Dean 1977, pl. 1, fig. 8 as *Missisquoia enigmatica* [Kobayashi]).



**Figure 23.** *Lunacrania* spp. latest Cambrian strata, Alberta and British Columbia. **A–C, G,** *Lunacrania* cf. *L. trisecta* Kobayashi 1955, Basal Silty Member, Survey Peak Formation, Wilcox Pass, Alberta. **A–C,** pygidium, GSC 62224, dorsal, posterior and lateral views, GSC loc. 89273, x20 (figured previously by Dean 1989, pl. 13, figs 8, 10 as *Missisquoia enigmatica* [Kobayashi]); **G,** pygidium, GSC 47973, dorsal view, GSC loc. 92223, x20 (figured previously by Dean 1977, pl. 1, fig. 8 as *Missisquoia enigmatica* [Kobayashi]); **D–F,** *Lunacrania trisecta* Kobayashi 1955?, pygidium, GSC 12744 (holotype of *Rhamphopyge altipolum* Kobayashi 1955), McKay Group, Jubilee Mountain, British Columbia (locality 24 of Evans 1933); **H–M,** *Lunacrania* sp. indet., Basal Silty Member, Survey Peak Formation, Wilcox Pass, Alberta. **H–J,** pygidium, GSC 137486 (not previously figured) posterior, lateral and dorsal views, , GSC loc. 89269, x20; **K–M,** pygidium, GSC 47971, dorsal, lateral and posterior views, GSC loc. 92223, x28.

best treated as a *nomen dubium* and restricted to the holotype.

***Lunacrania* cf. *L. enigmatica*** (Kobayashi 1955) (Fig. 22D–F)

1986 *Missisquoia enigmatica*; Westrop, p. 67, pl. 1, fig. 38.

*Occurrence.* Basal Silty Member, Survey Peak Formation, Wilcox Peak, Alberta, collection W319 (Westrop 1986).

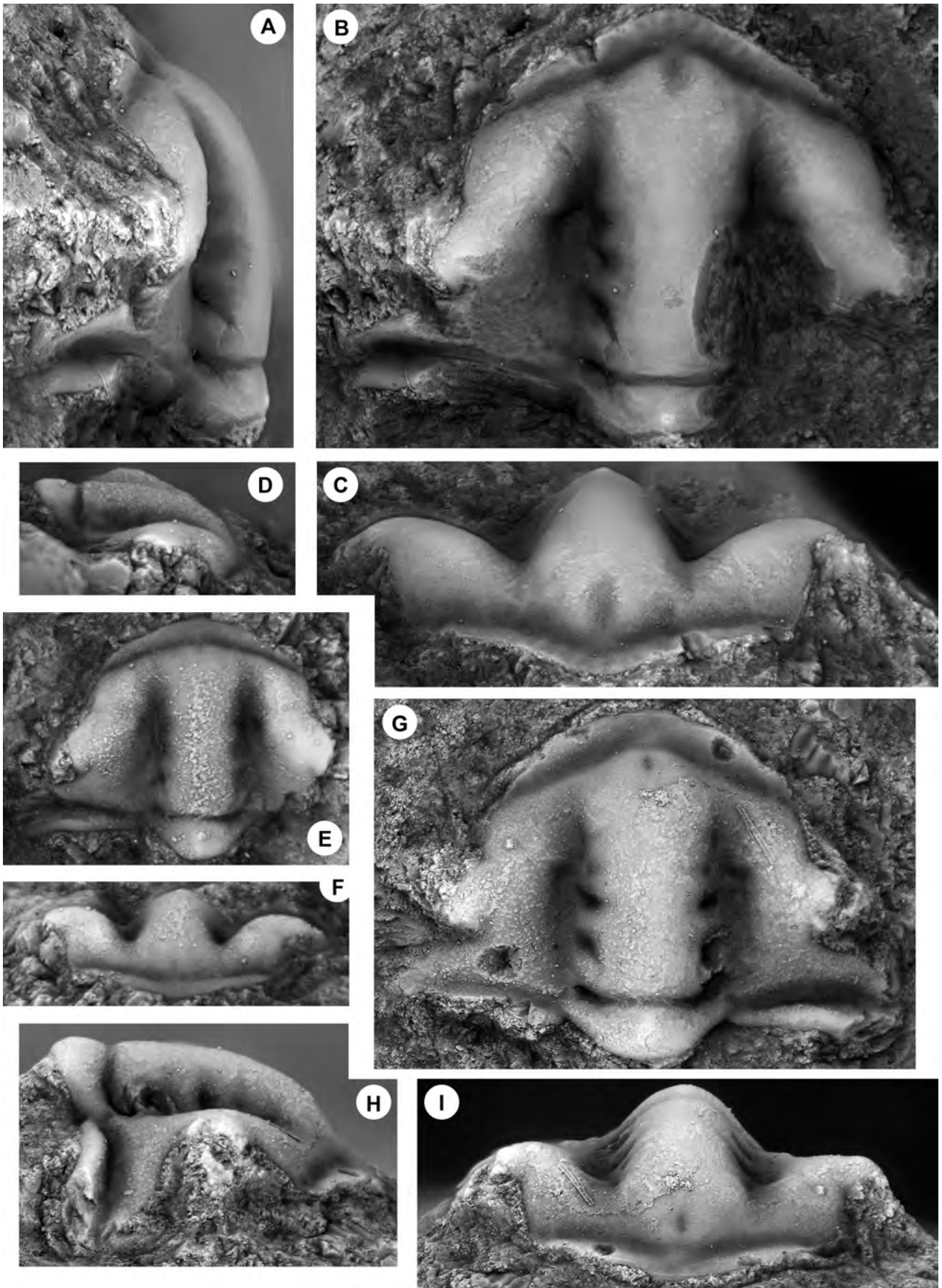
*Discussion.* The long triangular border and larger palpebral lobes separate this species from *L. trisecta* and *L. cf. L. trisecta*; border length is similar to the holotype of *Lunacrania enigmatica* but this specimen (Fig. 22A–C) is too poorly preserved to allow a more detailed comparison.

***Lunacrania* sp. indet.** (Fig. 23H–M)

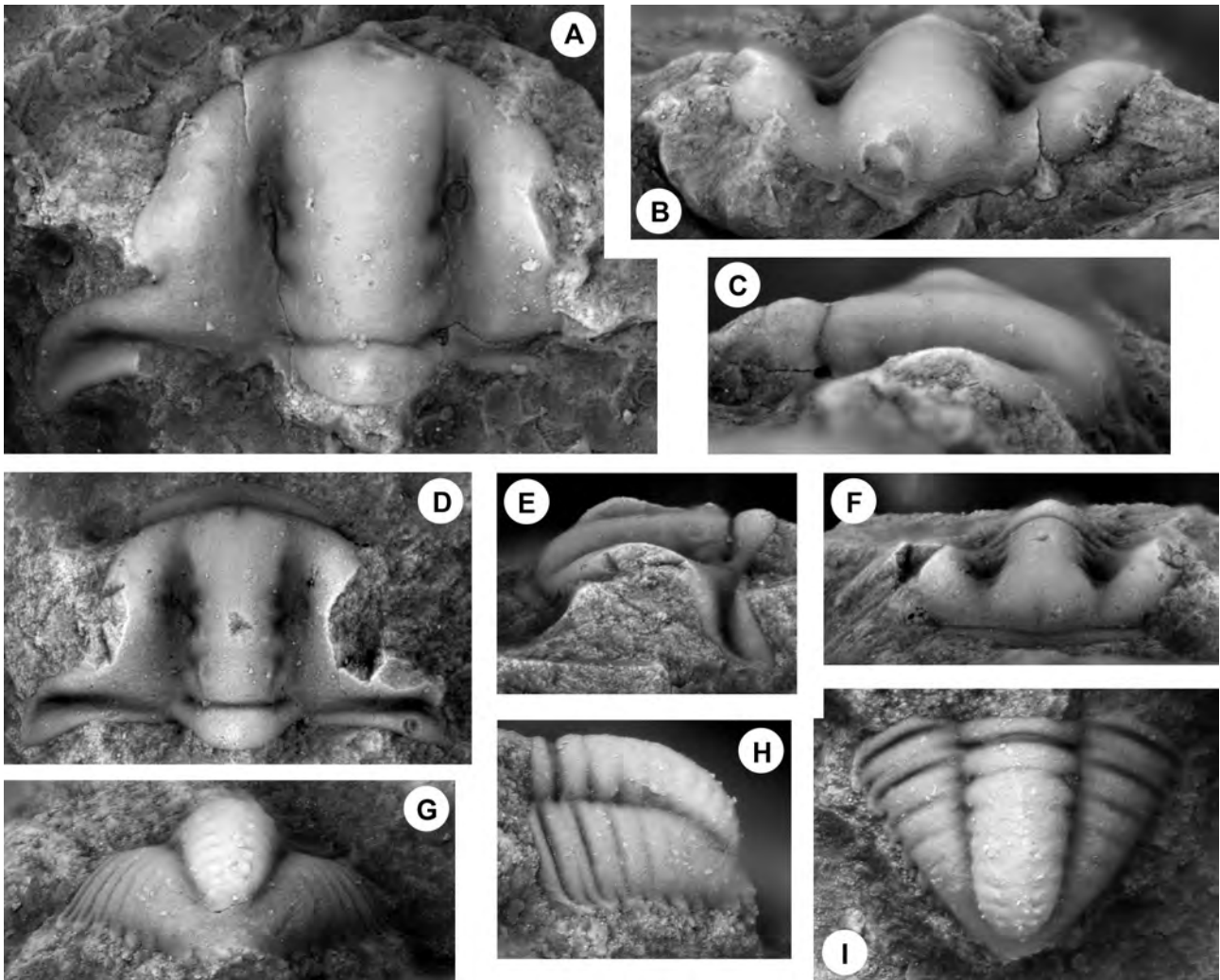
1977 *Missisquoia typicalis*; Dean, p. 4, pl. 1, figs 4, 7 [only].  
1986 *Missisquoia enigmatica*; Westrop, p. 67 [cum syn.].

**Figure 24** (opposite). *Lunacrania nasuta* (Winston & Nicholls 1967) from the San Saba Member, Wilberns Formation, Mason County, central Texas. All cranidia and all from Calf Creek section, except A–C (Threadgill Creek section) A–C, USNM 185921 (paratype), lateral, dorsal and anterior views, x16, collection TC–1421; **D–F,** cranidium, USNM 560660 (previously unfigured, *continued opposite*)





associated with USNM 185924), lateral, dorsal and anterior views, collection CC-93 x20; **G-I**, USMN 185922 (holotype), dorsal, lateral and anterior views, collection CC-93, x18.



**Figure 25.** *Lunacrania nasuta* (Winston & Nicholls 1967) from the Signal Mountain Formation, Joins Ranch section, Murray County, Oklahoma, collection JoR-1153 (Stitt 1971, p. 59). **A–C**, cranium, OU 13253, dorsal, anterior and lateral views, x20; **D–F**, cranium, OU 13254, dorsal, lateral and anterior views, x20; **G–I**, pygidium, OU 13255, posterior, lateral and dorsal views.

**Occurrence.** Basal Silty Member, Survey Peak Formation, Wilcox Pass, Jasper National Park, Alberta, GSC loc. 92223 (Dean 1977, 1989).

**Discussion.** The larger of two pygidia (Fig. 23K–L) from Wilcox Pass is relatively longer and narrower than those of *Lunacrania* cf. *L. trisecta*, and has a gently downsloping border behind an anterior region with very short marginal spines (Fig. 23M). The border is broad medially but narrows rapidly forward. The convex axis tapers rapidly along its posterior half to terminate at a blunt point. The anteriormost ring furrow is firmly impressed, but the rest are mostly effaced to barely perceptible. Four pairs of oblique pleural furrows are evident, although the two posterior pairs are very faint. The smaller pygidium (Fig. 23H–J) has not been illustrated previously, and differs from the larger specimen in having somewhat deeper furrows and a shorter border.

Dean (1977) considered the larger specimen to be a juvenile of *Missisquoia typicalis*, but Westrop (1986) transferred it to *Missisquoia enigmatica*. It may prove to belong to the species illustrated here as *Lunacrania* cf. *L. enigmatica*, but until an association of these sclerites can be demonstrated, we prefer to leave both pygidia unassigned at the species level.

***Lunacrania nasuta*** (Winston & Nicholls 1967) (Figs 24–25)

- 1967 *Missisquoia nasuta*; Winston & Nicholls, p. 89, pl. 13, figs 1, 2 [only; fig. 9 = *Parakoldinioidia* sp. nov. A]  
 1971 *Missisquoia nasuta* Winston & Nicholls; Hu, p. 108.  
 1975 *Missisquoia nasuta* Winston & Nicholls; Shergold, p. 195.  
 1977 *Missisquoia nasuta* Winston & Nicholls; Dean, p. 3.  
 1977 *Missisquoia nasuta* Winston & Nicholls; Stitt, fig. 10.  
 1982 *Missisquoia nasuta* Winston & Nicholls; Fortey in Fortey *et al.*, p. 101.  
 1985 *Missisquoia nasuta* Winston & Nicholls; Zhou & Zhang, p. 95.  
 1993 *Missisquoia nasuta* Winston & Nicholls; Loch *et al.*, p. 499.  
 2008 *Lunacrania? nasuta* (Winston & Nicholls); Lee *et al.*, p. 332, appendix 1.

**Diagnosis.** Relatively long palpebral lobe centred near cranial midlength. Short (tr.) but firmly impressed S1 and S2, and faint S3, furrows. Vestigial median anterior furrow isolated from anterior border furrow. Palpebral area of fixigena inflated well above axial furrow. Pygidium with small spines along lateral margin at least as far back as level

of tip of axis.

*Holotype.* A cranidium (USMN 185922; Fig. 24G–I) from San Saba Member, Wilberns Formation, Mason County, central Texas.

*Occurrence.* San Saba Member, Wilberns Formation, Calf Creek and Threadgill Creek sections, Mason County, central Texas (Winston & Nicholls 1967), collections CC–93 and TC–1421; Signal Mountain Formation, Joins Ranch section, Murray County, Oklahoma (Stitt 1971, p. 59), collection JoR–1153.

*Discussion.* Dean (1977) argued that *Lunacrania nasuta* was a synonym of *L. enigmatica*, a position that was followed by Westrop (1986). In contrast, Lee *et al.* (2008) listed them as separate species, albeit without discussion. From restudy of the types, it is clear that *L. nasuta* is distinct from all of the various *Lunacrania* species present in western Canada (see discussion of genus, above). One of the paratypes of *L. nasuta* (Fig. 18A–C) is transferred to *Parakoldinioidia* (see *Parakoldinioidia* sp. nov. A, above).

The larger of two cranidia from Oklahoma that are assigned to *P. nasuta* is incomplete anteriorly (Fig. 25A–C), but is otherwise closely similar to the paratype of Winston & Nicholls (1967; Fig. 24A–C). The smaller cranidium (Fig. 25D–F) compares favorably with a similarly sized, previously unillustrated specimen (Fig. 24D–F) from collection CC–93 at Calf Creek.

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