

# Revision of *Irvingella tropica* Öpik 1963 from Australia and related species from North America: implications for correlation of the base of the Jiangshanian Stage (Cambrian, Furongian)

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*Irvingella angustilimbata* Kobayashi 1938 from Laurentian North America has been proposed as an auxiliary index species for the base of the Upper Cambrian global Jiangshanian stage, and also has been recorded from North China, South China and Siberia. *Irvingella tropica* Öpik 1963 from Queensland, Australia has been treated as a junior synonym of *I. angustilimbata*. However, study of types and new material shows that *I. angustilimbata* and *I. tropica* are distinct species that are discriminated by both cranidial and pygidial characters; reports of *I. angustilimbata* outside of Laurentia are at best doubtful. Restudy of poorly preserved, sandstone internal molds that constitute the type material of *I. major* Ulrich & Resser leads us to consider the species to be a *nomen dubium*; reports of this species outside of Laurentia are also doubtful. *Irvingella media* Resser 1942 and *I. deckeri* Resser 1942, formerly considered to be synonyms of *I. major*, are readily diagnosable, valid species. *Irvingella orrensis* from the Orr Formation of Utah is new.

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*Irvingella* Ulrich & Resser in Walcott 1924 was first described from Laurentian North America but has since been reported from most Cambrian continents (see Torsvik & Cocks 2013 for paleogeographic maps), including Gondwana (Öpik 1963; Henderson 1976; Shergold 1982), Avalonia (Rushton 1967), Baltica (Westergård 1947; Rushton & Weidner 2010), Siberia (Černyševa in Datsenko *et al.* 1968; Lazarenko 1968; Varlamov *et al.* 2006a; Lazarenko *et al.* 2008), the Altai-Sayan (Ivshin in Halfina 1960), North China (Kobayashi 1935, 1962; Lee & Choi 1995; Hong *et al.* 2003), South China (Peng 1992; Peng *et al.* 2012) and the Karatau-Naryn terrane of Kazakhstan (Ivshin 1962; Ergaliev 1980). Most of these occurrences apparently lie in the Jiangshanian global stage (see Hong *et al.* 2003 for species appearing in Paibian strata), and in the upper Steptoean to basal Sunwaptan (*Elvinia*–*Irvingella major* zones) stages of the Laurentian regional nomenclature (e.g., Palmer 1965; Westrop 1986). Fortey (1985) listed *Irvingella* among trilobites that were possibly pelagic; the wide distribution and marked homeomorphy with the Ordovician telephinid *Carolinites* Kobayashi 1940 is consistent with this hypothesis (see also Žylińska *et al.* 2015), but we note that it is equally compatible with dispersal through a long-lived planktonic larval stage.

*Irvingella angustilimbata* Kobayashi 1938 was proposed as an auxiliary index for the base of the Jiangshanian at the stratotype in Zhejiang, South China, by Peng *et al.* (2012), who regarded it as the senior synonym of *I. tropica* Öpik 1963 (Peng *et al.* 2012, p. 473). However, this claim is based largely upon an interpretation of the published literature, some of which is now 50 years old

(e.g. Palmer 1965; Öpik 1963). In this paper, we revise both *I. angustilimbata* and *I. tropica* using type and new material, and demonstrate that they are distinct species. We also make some preliminary observations on *Irvingella major* Ulrich & Resser in Walcott 1924, another species to which material from several Cambrian continents has been assigned (Pegel, 2000; Hong *et al.* 2003; Lazarenko *et al.* 2008; Rushton & Weidner 2010; Peng *et al.* 2012). We show that none of these assignments can be accepted with any confidence, and that even within Laurentia, material assigned to *I. major* belongs to multiple distinct species. Our revisions have major implications for intercontinental correlation, and also demonstrate the pitfalls of basing species identifications on a single sclerite type.

## SOURCES OF STUDY MATERIAL

This study is based on new material and primary types (Hall & Whitfield 1877; Walcott 1884; Resser 1942) from Nevada and Utah, as well as type and other archival sclerites from various parts of the United States (Walcott 1924, 1925; Resser 1942) and from Australia (Öpik 1963; Shergold 1982).

### Nevada and Utah

New material of *Irvingella angustilimbata* comes from the Corset Spring Shale Member of the Orr Formation (Hintze & Palmer 1976) at Shingle Pass, Nevada, and Orr Ridge, Utah, and from the upper Dunderberg Formation at McGill, Nevada. Silicified sclerites of a new species of *Irvingella* were obtained from the Corset Spring Shale at Orr Ridge. Rare specimens of a species identified below as *I. cf. I. tropica* Öpik are from the Hales Limestone at Tybo

Canyon, Hot Creek Range, Nye County, Nevada (Palmer 1965; Taylor 1976, fig. 1) and the Corset Spring Shale, Patterson Pass, Schell Creek Range, Lincoln County, Nevada (Westrop *et al.* 2007, fig. 2).

**Shingle Pass.** The Shingle Pass locality lies in the South Egan Range, Lincoln County, Nevada, and is described briefly by Palmer (1965, p. 95) and Westrop *et al.* (2007, p. 358, fig. 2). Sclerites of *Irvingella angustilimbata* Kobayashi 1938 were recovered from two closely spaced collections that were made 18.25 m and 18.60 m above the base of the Corset Spring Shale Member. The associated fauna indicates a position in the lower part of the *Elvinia* Zone (Westrop *et al.* 2007, 2008).

**McGill.** Palmer (1965, p. 94) provided an overview of the McGill locality, which is in the Duck Creek Range, about 4 km north-east of the town of McGill, White Pine County, Nevada. The succession is faulted, and we used airphotos to locate intact panels within which to measure a section. *Irvingella angustilimbata* occurs in sample MG2 69–70, which was collected from the uppermost Dunderberg Formation, 1.5 m below the base of the Barton Canyon Limestone. The assemblage also includes *Pseudokingstonia exotica* Palmer 1965 and several other taxa indicative of the *Elvinia* Zone (Westrop & Adrain 2009).

**Orr Ridge.** Our section at Orr Ridge was measured on the south side of Big Horse Canyon, northern House Range, Millard County, Utah (Westrop & Adrain 2007, fig. 1a). *Irvingella angustilimbata* is present in a sample collected at 14.8–15.0 m above the base of the Corset Spring Shale Member, as part of a fauna that also includes *Pseudokingstonia exotica*, *Kindbladina cf. affinis* (Walcott 1884), *Bynumina globosa* (Walcott 1884), *Housia cf. ovata* Palmer 1960, and undescribed species of *Dellea* Wilson 1949 and *Pulchricapitus* Kurtz 1975. Most of these species are shared with the lower *Elvinia* Zone fauna at Shingle Pass. Talus samples of silicified material collected 19 and 25 metres above the base of the member yielded *I. orrensis* n. sp., and this species also occurs *in situ* at 26.2 m.

The youngest sample with *Irvingella* occurs in the lowest Sunwaptan *I. major* Zone in the Sneakover Member of the Orr Formation, 60.2 m above the base of the section (Westrop & Adrain 2007). *Irvingella* “major” is relatively rare in the sample, which is dominated by *Bartonaspis palmeri* Westrop & Adrain 2007 and *B. wilsoni* Westrop & Adrain 2007; *Comanchia* Frederickson in Wilson & Frederickson 1950 and *Stenambon* Palmer 1965 are also present, as are the agnostoid arthropods *Kormagnostella advena* Westrop & Adrain 2013 and *K. insolita* Westrop & Adrain 2013. It is one of several species of *Irvingella* that we will describe elsewhere.

**Eureka District.** *Irvingella angustilimbata* was named (Kobayashi 1938) for sclerites that Walcott (1884) identified as *I. tumifrons* (Hall & Whitfield 1877). According to Walcott (1884), they were collected on the north side of the canyon, opposite Ruby Hill, which places the locality somewhere on the south side of Adams Hill (rather than on the north side, as suggested by Resser 1942, p. 26), about 3 km west of Eureka, Eureka County, Nevada. Palmer (1960) showed that this species occurred in the upper part of the Dunderberg Formation, in strata that he later (Palmer 1965, p. 12) assigned to the lower part of the *Elvinia* Zone. Types of *I. intermedia* (Resser 1942), considered by Palmer (1965) to be a synonym of *I. angustilimbata*, are from the

Hamberg Mine area, which is about 5.5 km south of Adams Hill.

Resser (1942) named *I. flohri* and its synonym, *I. adamsensis* (see Palmer 1965, p. 47), for sclerites that were collected near the Richmond Mine (USNM loc. 60). This mine is not marked on modern USGS topographic maps, but Walcott (1884) indicated that it was located on Ruby Hill, which is about 1 km south of Adams Hill. We also restudied specimens attributed to *I. flohri* by Palmer (1965), which were collected from Windfall Canyon (USGS loc 2579–CO), about 6.5 km southeast of Adams Hill.

The type material of *I. tumifrons* was collected by Arnold Hague from the “lowest limestone beds on the west side of Pogonip Mountain [Pogonip Ridge of modern USGS topographic maps], White Pine District, Nevada” (Hall & Whitfield 1877, p. 225), which is about 48 km southeast of Eureka. The associated fauna includes *Pterocephalia sanctisabae* (Roemer 1849) [= *P. laticeps* (Hall & Whitfield 1977); Palmer 1960, p. 89], and supports an assignment to the *Elvinia* Zone.

### Other areas of the United States

The type species of *Irvingella*, *I. major* Ulrich & Resser in Walcott 1924, was initially described from the Lone Rock Formation in Wisconsin, but has since been reported throughout North America (e.g., Palmer 1965; Wilson 1949; Stitt 1971; Westrop 1986), and from some other Cambrian continents (e.g., Hong *et al.* 2003; Lazarenko *et al.* 2008; Peng *et al.* 2012). However, as discussed below, this species is best considered a *nomen dubium*, and should be restricted to Walcott’s poorly preserved types.

Resser (1942) named eight species of *Irvingella* from the Honey Creek Formation of the Arbuckle and Wichita mountains of south-central Oklahoma, most of which likely come from the *Irvingella major* Zone (see Westrop & Adrain 2007 for a brief overview of this interval in Oklahoma). In addition to some of Resser’s types, we illustrate new cranidia of *I. media* Resser from a collection (DR 12.2) at the base of the *I. major* Zone at the Dotson Ranch section in the Arbuckle Mountains (Westrop & Adrain 2007, fig. 1C). Resser (1942) also described eight additional species from a correlative interval in the Morgan Creek Member of the Wilberns Formation of central Texas (see Wilson 1949 and Bell & Ellinwood 1962 for an outline of the succession and faunas); we illustrate the types of *I. media*. Initial assessments concluded that most, if not all, of Resser’s species were synonyms of *I. major* (Frederickson 1949; Gaines 1951; Palmer 1965), and this was followed in subsequent studies (e.g., Stitt 1971; Westrop 1986; Hong *et al.* 2003). However, preliminary study of Resser’s types shows that this is an extreme view and, as discussed later in the text, at least some record distinct, readily diagnosable species; contrary to the interpretation of Rushton & Weidner (2010), we consider Resser’s names to be available from the initial date of proposal (see Systematic Paleontology, below).

Although not restudied as part of this work, sclerites of *I. angustilimbata* reported from the Rabbitkettle Formation of the Mackenzie Mountains of northern Canada by Pratt (1992) are significant because the species enters the succession (collection N178, in Pratt’s section N, South Nahanni River area) with a strongly furrowed species of the agnostoid arthropod *Agnostotes* Öpik 1963 that is similar to those that have been used to define the base of the Jiangshanian Stage elsewhere (e.g., Peng *et al.* 2012).

## Australia

*Irvingella tropica* Öpik 1963 is known with certainty only from western Queensland. Type and other material revised in this paper are from the Burke River Structural Belt, and were collected from the Pomegranate Creek area at locality D120b, and from Mt. Murray sections 301 and 302, respectively (see Shergold 1982, figs 1, 2 for locality information). All of these occurrences lie within the Pomegranate Limestone (*Irvingella tropica* Zone at the base of the Australian Iverian Stage). Henderson (1976) reported *I. tropica* from the correlative strata of the Georgina Limestone at Brown's Creek in the Glenormiston region, about 185 km southwest of Mt. Murray.

## SPECIES CONCEPTS AND BIOSTRATIGRAPHY

Recent discussions of *Irvingella angustilimbata*, *I. tropica*, and other species with distinct preglabellar fields (e.g., Hong *et al.* 2003; Varlamov *et al.* 2006a) focused by necessity upon cranidial characters given the limited information on other parts of the exoskeleton. Varlamov *et al.* (2006a) suggested that many of these species might prove to be synonyms, including *I. angustilimbata*, *I. tropica*, and *I. typa* (Kobayashi, 1935), and Peng *et al.* (2012) went a step farther in proposing that *I. angustilimbata* was a cosmopolitan species that could be used as an auxiliary index for the base of the Jiangshanian.

Use of *I. angustilimbata* to help define the base of the Jiangshanian apparently relies upon a simple diagnosis as a “preglabellar field-bearing species” (Peng *et al.*, 2012, p. 471). However, Chatterton & Ludvigsen (1998) showed that co-occurring species of *Irvingella* with similar cranidia could be discriminated on librigenal, thoracic and pygidial characters, and this serves as a caution against broad diagnoses based on a single sclerite type. Peng *et al.* (2012, p. 467) also took a process-based approach to species recognition that incorporates evolutionary narratives (e.g., Palmer 1965; Hong *et al.* 2003) that are also used as guides to biostratigraphic correlation through the identification of supposedly “primitive” (e.g., *I. angustilimbata*) and “advanced” species (e.g., *I. major*). The process-based nature of their species concept is even more explicit in their definition (Peng & Babcock 2005) of the agnostoid arthropod *Agnostotes “orientalis”* (Kobayashi 1935; in our view, this name is a *nomen dubium* [Westrop & Adrain 2013]), which defines the base of the Jiangshanian. Peng *et al.* (2012) regarded cephalic morphs separated by differences in the morphology of the anterior glabella (e.g., Peng *et al.* 2012, figs 9A, 9C) as recording microevolutionary changes between “primitive” and “advanced” forms of a single species. Moreover, they claimed that these changes could be observed worldwide. Although many paleontologists remain entirely ignorant of the subject, a lack of any operational bases for process-based species concepts has long been understood in modern biological systematics (e.g., Wheeler & Meier 2000). Evolutionary processes such as ancestry and descent are not empirically discoverable (see, e.g., Smith 1994, p. 9; Norell 2006, p. 454). Their invocation in the fossil record is purely conjectural. In any case, while the notion of a globally distributed species transforming anagenetically in unison throughout its geographic range is pure storytelling, the presence of multiple stratigraphically successive morphologies (which would be properly recognised as a series of separate phylogenetic species) is testable. However, it is an hypothesis that demands support from

detailed stratigraphic sampling and quantitative analysis of variability; images of a few representative specimens with objectively different morphology (and which certainly represent different species) from the top and bottom of the stratigraphic range (Peng *et al.*, 2012, fig. 9A–G) will not suffice.

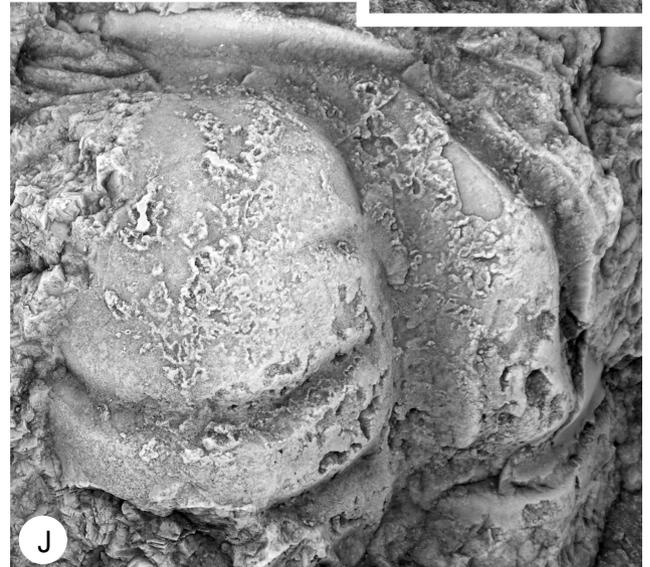
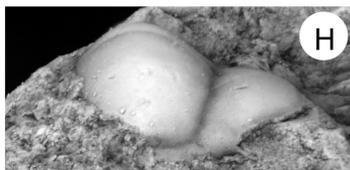
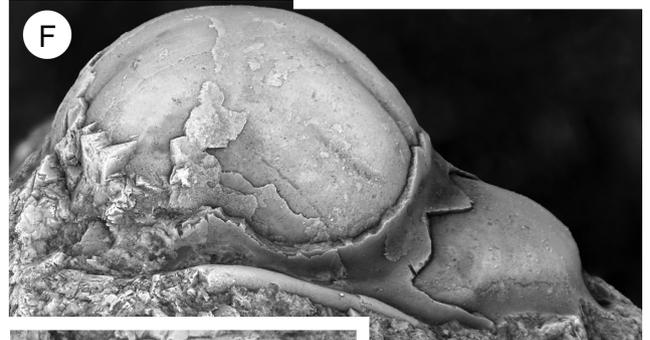
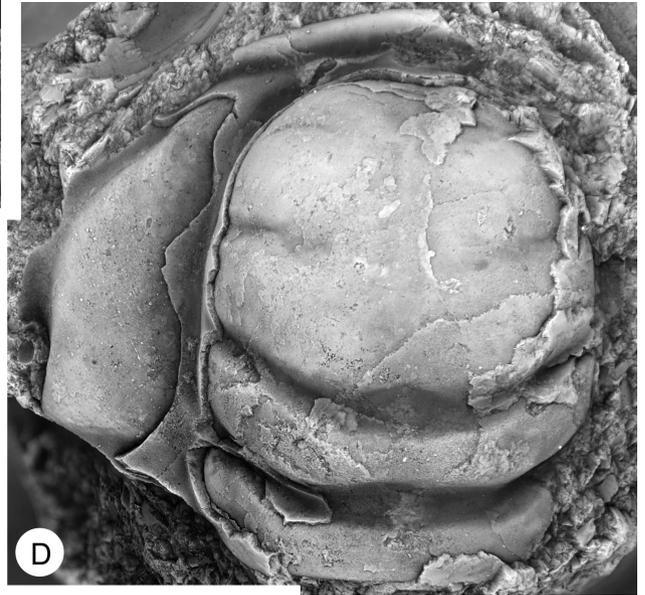
In this paper (and all others), we take a pattern-based approach to species recognition using a phylogenetic species concept (Wheeler & Platnick 2000). Our knowledge of the exoskeletons of *I. angustilimbata* and *I. tropica* is far from complete, but new information presented here shows that they are distinct species based on both cranidial and pygidial differences. As revised, they are restricted to Laurentian North America and the Australian sector of Gondwana, respectively. Use of a single species name in many Cambrian continents may create the illusion of high-resolution, global correlation, particularly when each lowest occurrence is designated as a “datum”. The allure of global “index species” is powerful, but we cannot allow our desire to make long-distance correlations to influence our taxonomic decisions. When “index species” are poorly founded, they imply an accuracy in correlation that is unsupported by the data.

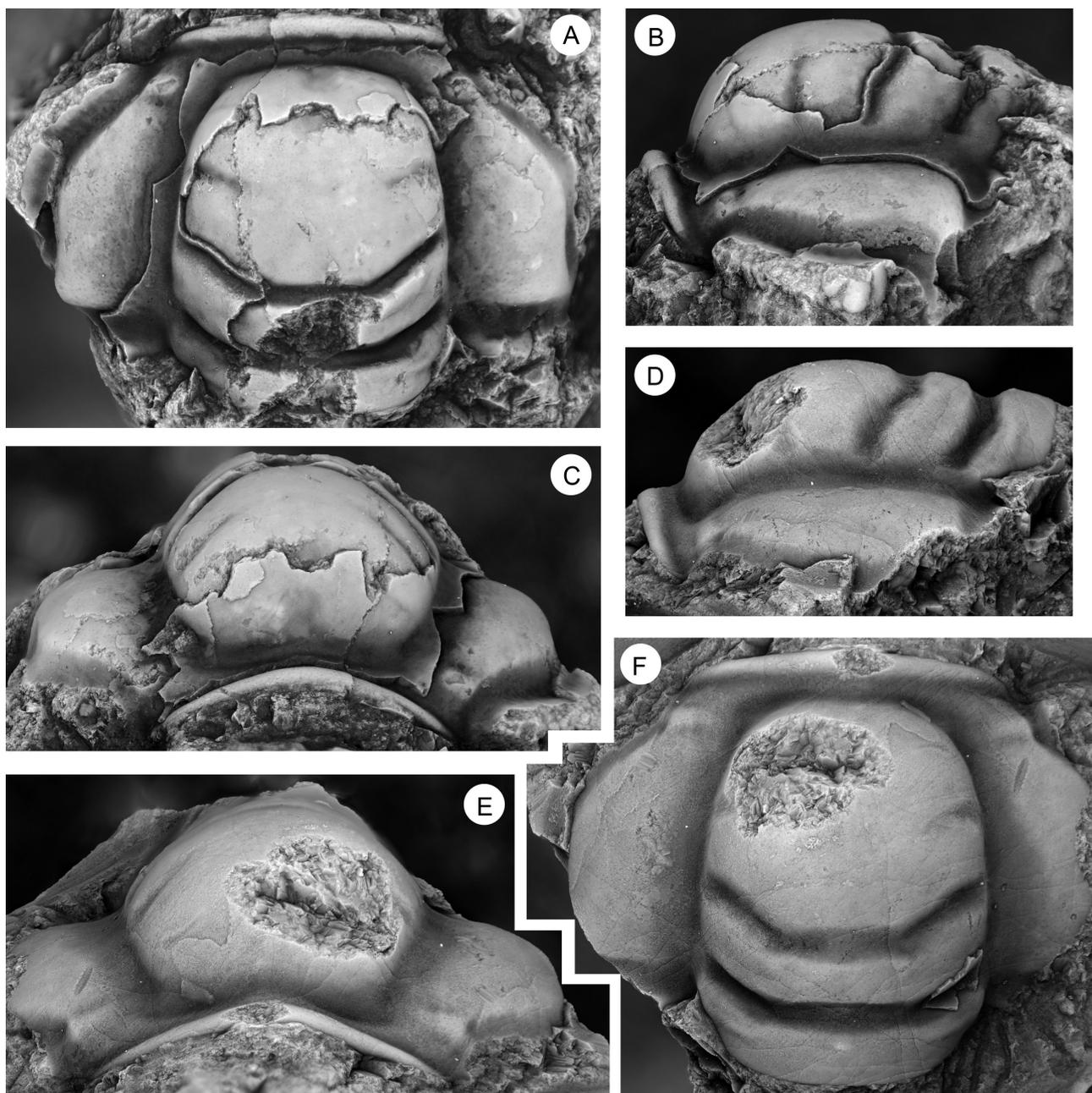
A more measured approach to species concepts need not lead to reduced biostratigraphic accuracy; even where identified globally, first appearances of species will inevitably be diachronous (see also Landing *et al.* 2013). In many regions, the first appearances of species of *Agnostotes* and *Irvingella* are coincident (e.g. Pratt 1992; Peng *et al.* 2012) or at least within metres of each other (e.g., Hong *et al.* 2003). Use of this interval of species overlap to roughly correlate the base of the Jiangshanian may be all that is available to us and, while less than ideal, it is surely more realistic than the false precision of supposedly global species concocted from many inadequately documented occurrences that cannot be evaluated with any confidence (see following discussions of *I. angustilimbata* and *I. major*).

## SYSTEMATIC PALAEOLOGY

Illustrated material is housed at Geoscience Australia, Canberra (CPC), the University of Iowa Paleontology Repository (SUI), the Oklahoma Museum of Natural History (OU), and the US National Museum (USNM). Locations of stratigraphic sections are identified by the abbreviations MG, McGill; ORR, Orr Ridge; PP, Patterson Pass; SHP, Shingle Pass; sample numbers indicate the position in metres above the base of the section.

Rushton & Weidner (2010) noted Frederickson's (1949, p. 354) complaint that, in his view, Resser's (1942) descriptions of new species of *Irvingella* from Oklahoma were “incomplete and inaccurate”, and they concluded that most of the species names introduced by Resser are unavailable because they fail to meet Article 13.1 of the International Code of Zoological Nomenclature (I.C.Z.N 1999). We disagree with their interpretation of Article 13.1, which states that, “to be available, every new name published after 1930 .....must be accompanied by a description or definition that states in words characters that are purported to differentiate the taxon”. The critical word is “purported”. Resser (1942) presented a description of each of the new species that he named, and clearly intended them to differentiate those species (1942, p. 13). That is all that is required by Article 13.1. If availability depended on the subjective judgement of subsequent workers as to





**Figure 2.** *Irvingella angustilimbata* Kobayashi 1938 from Nevada. A–C, cranidium, USNM 108672, Dunderberg Formation, south side of Adams Hill, Eureka District, Eureka County (USNM loc. 62) dorsal, lateral and anterior views, x7 (illustrated previously by Resser 1942, pl. 4, figs 18–20 and by Palmer 1960, pl. 6, fig. 2); D–F, cranidium, USNM 141950, Hales Limestone, Tybo, Nye County, USGS collection 1471–CO, lateral, anterior and dorsal views, x5 (illustrated previously by Palmer 1965, pl. 6, fig. 22).

the quality of diagnoses or descriptions, nomenclatural chaos would ensue. The Code requires that a description or definition intended to differentiate the taxon exists, not that it meets some threshold of quality. All of Resser's species are plainly available according to Article 13.1. Furthermore, we have restudied the types of all species of Resser's species of *Irvingella* from Oklahoma and, unlike Frederickson, we had little difficulty in finding diagnostic

features within his descriptions. By way of example, Resser (1942, p. 19), described the cranidium of *I. deckeri* (Fig. 15) as having “a more ovate shape”, which reflects the curved anterior border (see discussion below); he also described the glabella as “large”, which in our view captures the relative proportions of the glabella and the fixigenae. In other words, Resser's descriptions do in fact refer to characters that are diagnostic, even though we have

**Figure 1** (opposite). *Irvingella angustilimbata* Kobayashi 1938, Dunderberg Formation, just north of Adams Hill, Eureka District, Eureka County (USNM loc. 63); all cranidia and all x5 except G–I (x16). A–C, USNM 24643 (lectotype), dorsal, anterior and lateral views (illustrated previously by Palmer 1960, pl. 6, fig. 3, and 1965, pl. 6, fig. 21); D–F, USNM 619730, dorsal, lateral and anterior views; G–I, USNM 619731, dorsal, anterior and lateral views; J, USNM 619732, dorsal view (illustrated previously by Resser 1942, pl. 4, figs 21–22).

chosen to describe them in different ways and, of course, with modern terminology (Whittington & Kelly 1997).

Family ELVINIIDAE Kobayashi 1935

**Irvingella** Ulrich & Resser, in Walcott 1924

=*Komaspis* Kobayashi 1935

=*Irvingellina* Kobayashi 1938

=*Parairvingella* Kobayashi 1938

**Type species.** *Irvingella major* Ulrich & Resser in Walcott 1924 from the Lone Rock Formation, Wisconsin (by original designation).

**Irvingella angustilimbata** Kobayashi 1938 (Figs 1–8)

1884 *Chariocephalus* (?) *tumifrons* Hall & Whitfield; Walcott, p. 61, pl. 10, fig. 16.

1938 *Irvingella* (*Parairvingella*) *angustilimbatus*; Kobayashi p. 175.

1942 *Irvingella angustilimbata* Kobayashi; Resser, p. 26, pl. 4, figs 18–22.

1942 *Irvingella intermedia*; Resser, p. 27, pl. 4, figs 25–31.

1942 *Irvingella eurekaensis*; Resser, p. 26, pl. 4, figs 15–17.

1960 *Irvingella* (*Parairvingella*) *angustilimbatus* Kobayashi; Palmer, p. 73, pl. 6, figs 2, 3.

1960 *Irvingella* (*Parairvingella*) *eurekaensis* (Resser); Palmer, p. 74, pl. 6, fig. 1.

1962 *Irvingella* (*Parairvingella*) *angustilimbatus* Kobayashi; Ivshin, p. 58.

1963 *Irvingella angustilimbata* Kobayashi; Öpik, p. 96.

1965 *Irvingella* (*Parairvingella*) *angustilimbatus* Kobayashi; Grant, p. 127.

1965 *Irvingella angustilimbatus* Kobayashi; Palmer, p. 46, pl. 6, figs 17, 18, 21–23.

?1965 *Irvingella* (*Parairvingella*) *eurekaensis*; Grant, p. 127, pl. 8, fig. 8.

1976 *Irvingella angustilimbatus* Kobayashi; Taylor, p. 673.

1986 *Irvingella angustilimbatus* Kobayashi; McNamara, p. 148, fig. 15.

non 1990 *Irvingella angustilimbata* Kobayashi; Peng, pl. 1, fig. 21 [= *I. sp. indet.*].

1992 *Irvingella angustilimbata* Kobayashi; Pratt, p. 49, pl. 11, figs 7–13, 16 [only].

non 1992 *Irvingella angustilimbata* Kobayashi; Peng, p. 56, fig. 23F–J [= *I. sp. indet.*].

1995 *Irvingella angustilimbata* Kobayashi; Lee & Choi, p. 11.

1998 *Irvingella angustilimbata* Kobayashi; Chatterton & Ludvigsen, p. 31.

2000 *Irvingella angustilimbata* Kobayashi; Saltzman *et al.*, p. 218.

2003 *Irvingella angustilimbata* Kobayashi; Hong *et al.*, p. 175.

non 2003 *Irvingella angustilimbata* Kobayashi; Peng, p. 141, fig. 2J [= *I. sp. indet.*].

non 2004 *Irvingella angustilimbata* Kobayashi; Peng *et al.*, p. 257.

non 2006a *Irvingella angustilimbatus* Kobayashi; Varlamov *et al.*, p. S35, pl. 7, figs 5, 5a, 5b, 6, 6a, 6b [= *I. sp. indet.*].

2006b *Irvingella angustilimbatus* Kobayashi; Varlamov *et al.*, p. S81.

non 2006 *Irvingella angustilimbata* Kobayashi; Duan, p. 117, pl. 8, fig. 5 [= *I. sp. indet.*].

non 2006 *Irvingella angustilimbata* Kobayashi; Choi & Kim, p. 349.

2007 *Irvingella angustilimbata* Kobayashi; Sundberg, p. 219.

2010 *Irvingella angustilimbata* Kobayashi; Rushton & Weidner, p. 194.

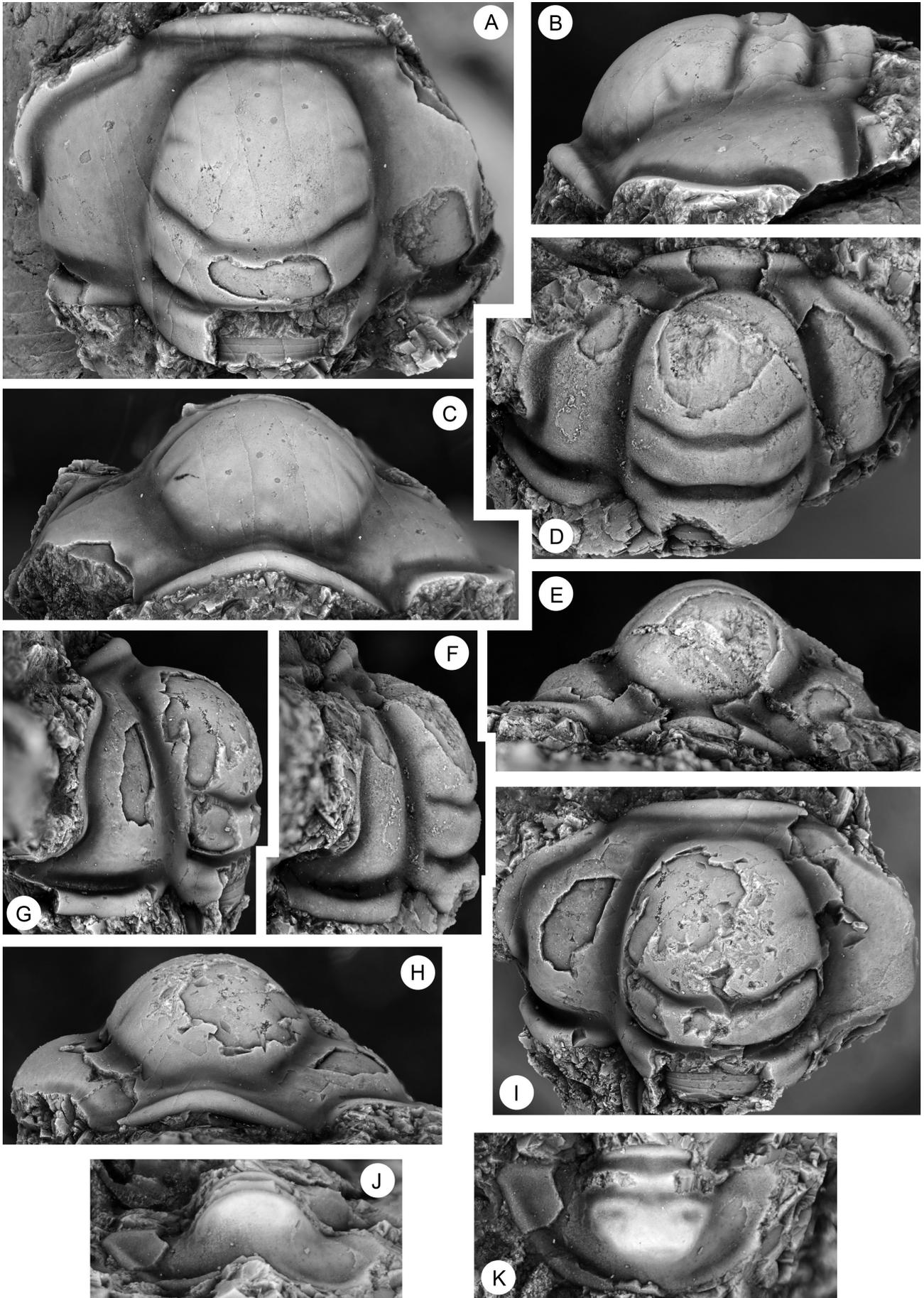
non 2012 *Irvingella angustilimbata* Kobayashi; Peng *et al.*, fig. 9H–J [= *I. sp. indet.*].

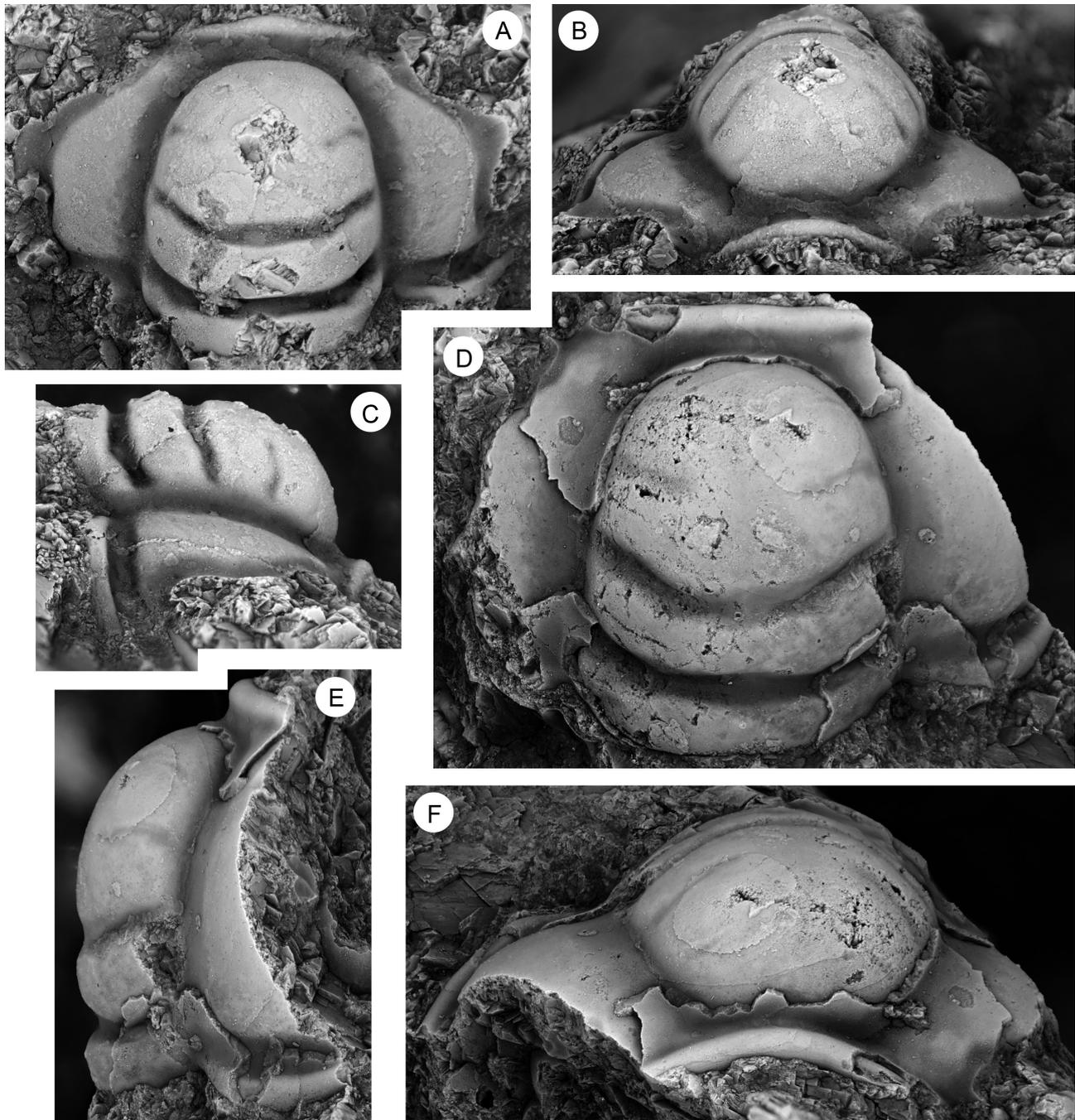
**Diagnosis.** Preglabellar field short, equal to about 5% (3–6) of cranial length, and shorter than anterior border on testate specimens (e.g., Figs 3A, I, 5A, 6G). Glabella tapered beyond S1 with well rounded anterior margin. Palpebral furrow firmly impressed arcuate groove of nearly even width (tr.). Pygidium transversely semielliptical, length equal to about 40% of maximum width, with broad axis accounting for 45% of maximum pygidial width; lateral margins converge strongly posteriorly.

**Lectotype.** A cranidium (USNM 24643) from the Dunderberg Formation, on Adams Hill, to the north of Ruby Hill, Eureka district, central Nevada (Fig. 1A–C). Resser (1942) and Palmer (1960, 1965) illustrated different cranidia (Fig. 1J and 1A–C, respectively) from the type lot (Fig. 1) of Walcott's (1884) material as the holotype. Walcott (1884, p. 61) mentions "a series of individuals", but illustrated only one of them (1884, pl. 10, fig. 16). This is clearly the specimen figured by Palmer, and it is selected as the lectotype.

**Description.** Cranidium strongly arched, roughly trapezoidal in outline, with length equal to about 81% (78–84) of maximum width between palpebral furrows. Anterior arch variably expressed, from strong (e.g., Fig. 3C) to weak (e.g., Fig. 5A, F). Axial and preglabellar furrows shallow. Glabella conspicuous, strongly convex, with lateral profile nearly flat between LO and posterior end of L2, then curved increasingly downward towards preglabellar furrow; occupies about 88% (85–92) of cranial length, and with width at SO equal to slightly more than half (53%; 50–57) of maximum cranial width between palpebral furrows; gently tapered in front of S1, becoming well rounded anteriorly, with width at S2 equal to about 89% (86–94) of width at SO. SO well incised on testate surfaces (e.g., Fig. 5A), and even more so on internal moulds (e.g., Fig. 1D); nearly transverse medially, but curved forward abaxially. LO occupies 15% (10–19) of glabellar length (sag.). S1 roughly parallel to SO, also more firmly impressed and slightly longer (sag.) on internal mould (compare Fig. 1A and 1D). L1 slightly longer (exsag.) than LO, equal to a about 18% (15–22) of glabella length (sag.). S2 gently curved, nearly transverse, shallow and expressed only abaxially. L2 shortest (exsag.) near axial furrow, length equal to about 21% (17–25) of glabellar length (sag.), but expands appreciably abaxially. Distinct preglabellar field on frontal area, accounting for about 5% (3–6) of cranial

**Figure 3.** *Irvingella angustilimbata* Kobayashi 1938 from the Corset Spring Shale, Shingle Pass, South Egan Range, Lincoln County, Nevada. All cranidia except J, K (pygidium). A–C, OU 237895, dorsal, lateral and anterior views, collection SHP 18.6, x7; D–F, OU 237896, dorsal, anterior and lateral views, collection SHP 18.6, x8; G–I, OU 237897, lateral, anterior and dorsal views, collection SHP 18.25, x12; J, K, OU 237898, posterior and dorsal views, collection SHP 18.25, x16,



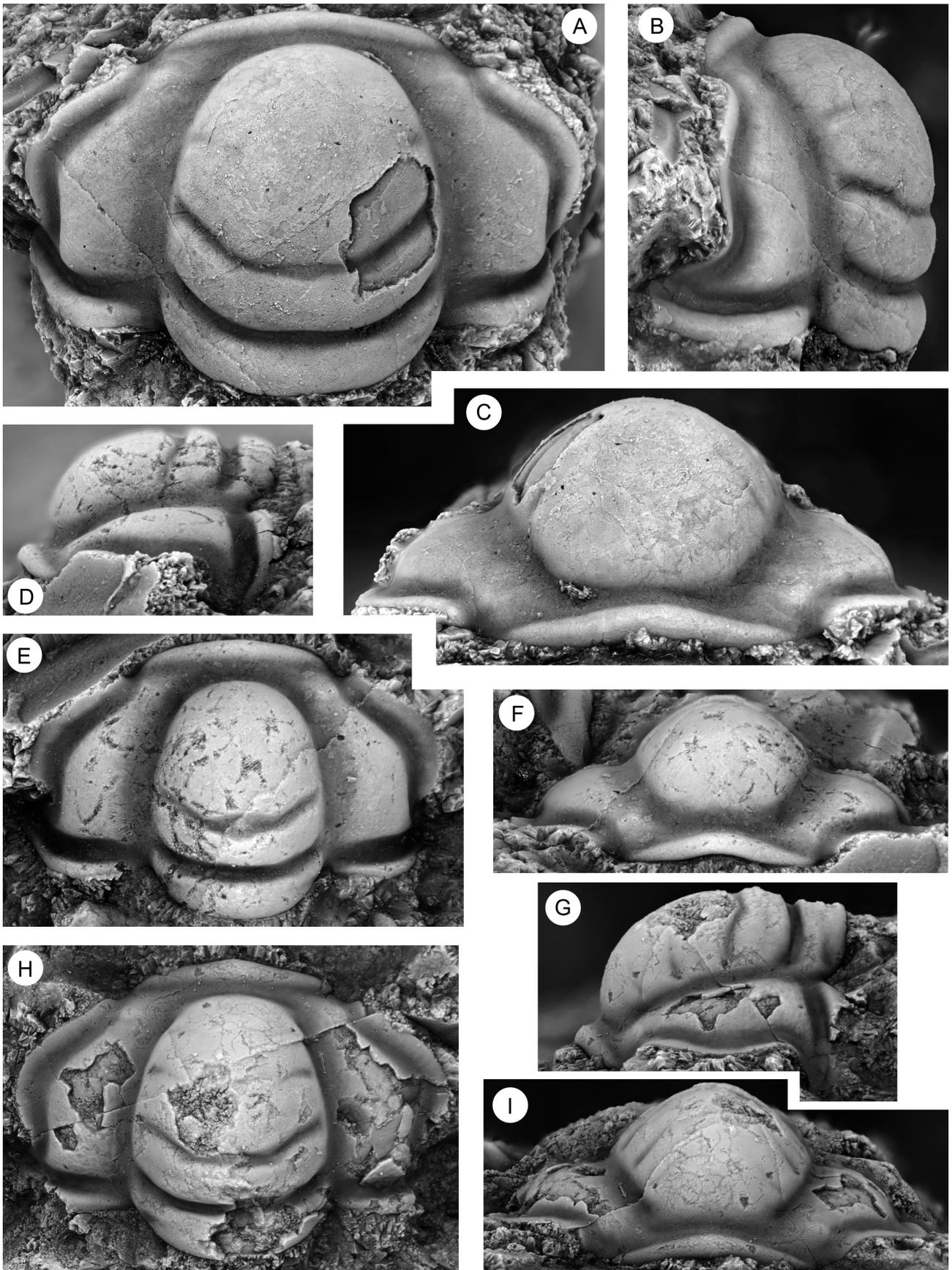


**Figure 4.** *Irvingella angustilimbata* Kobayashi 1938 from the Corset Spring Shale, Shingle Pass, South Egan Range, Lincoln County, Nevada. All cranidia. **A–C**, OU 237899, dorsal, anterior and lateral views, collection SHP 18.25, x9; **D–F**, OU 237900, dorsal, lateral and anterior views, collection SHP 18.6, x7.

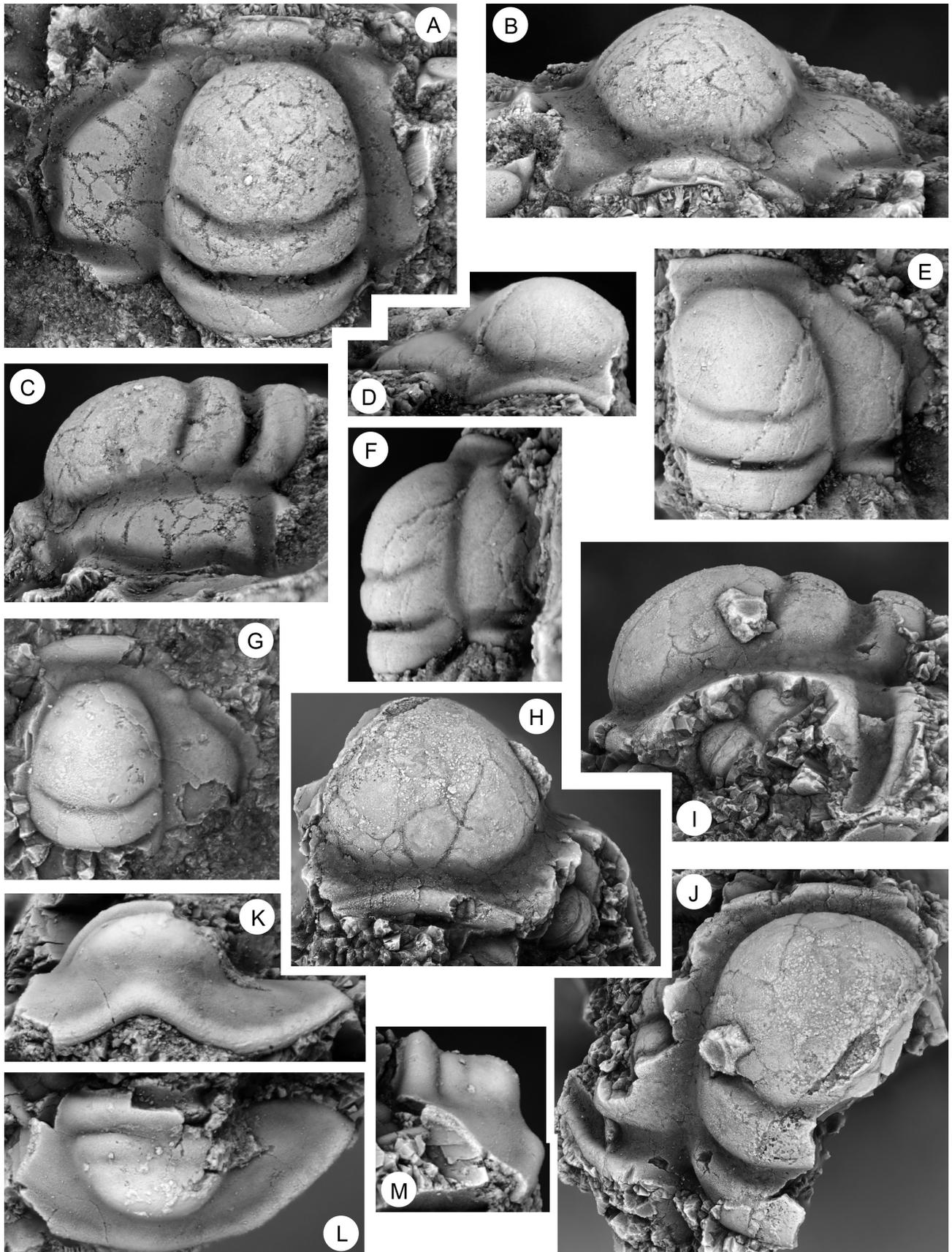
length and shorter than convex anterior border on testate specimens; anterior border furrow shallow and expressed largely by change in slope between border and preglabellar field. Palpebral lobe flat, arcuate band depressed below level of palpebral area of fixigena, extending from midpoint of L1 to apex, or just in front of apex, of glabella; anterior and posterior tips flexed sharply downward. Palpebral furrow firmly impressed arcuate groove of nearly even width (tr.). Palpebral area of fixigena broad, equal to about half (51%; 38–61; lower values in larger cranidia: Fig. 1A, D) of glabellar width at SO. Anterior branches of facial sutures, short and converge gently forward before turning sharply inward along anterior cranial margin; posterior branches

divergent before swinging backward towards posterior margin. Posterolateral projection short (exsag; tr.) and directed steeply downward. Posterior border furrow deeply incised and roughly equal in length to convex posterior border. External surface of cranium smooth.

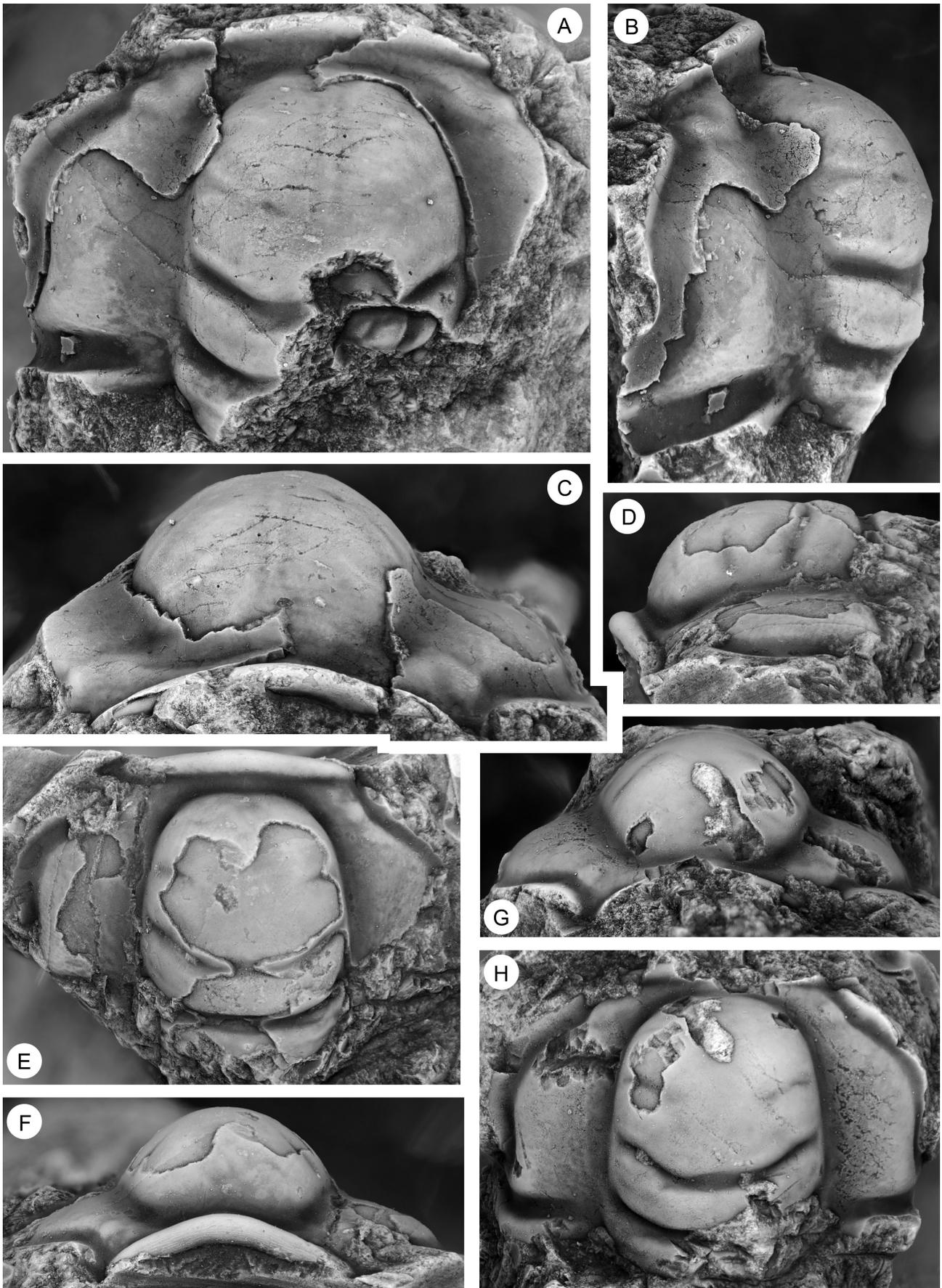
Pygidium transversely semielliptical, length equal to about 40% of maximum width; lateral margins converge strongly posteriorly, and with distinct medial arch in posterior view. Axis strongly convex and broad, width at first axial ring equal to about 45% of pygidial width; occupies about 80% of pygidial length. Axis with one well defined transverse ring furrow separating axial ring from terminal piece comprising at least two segments,



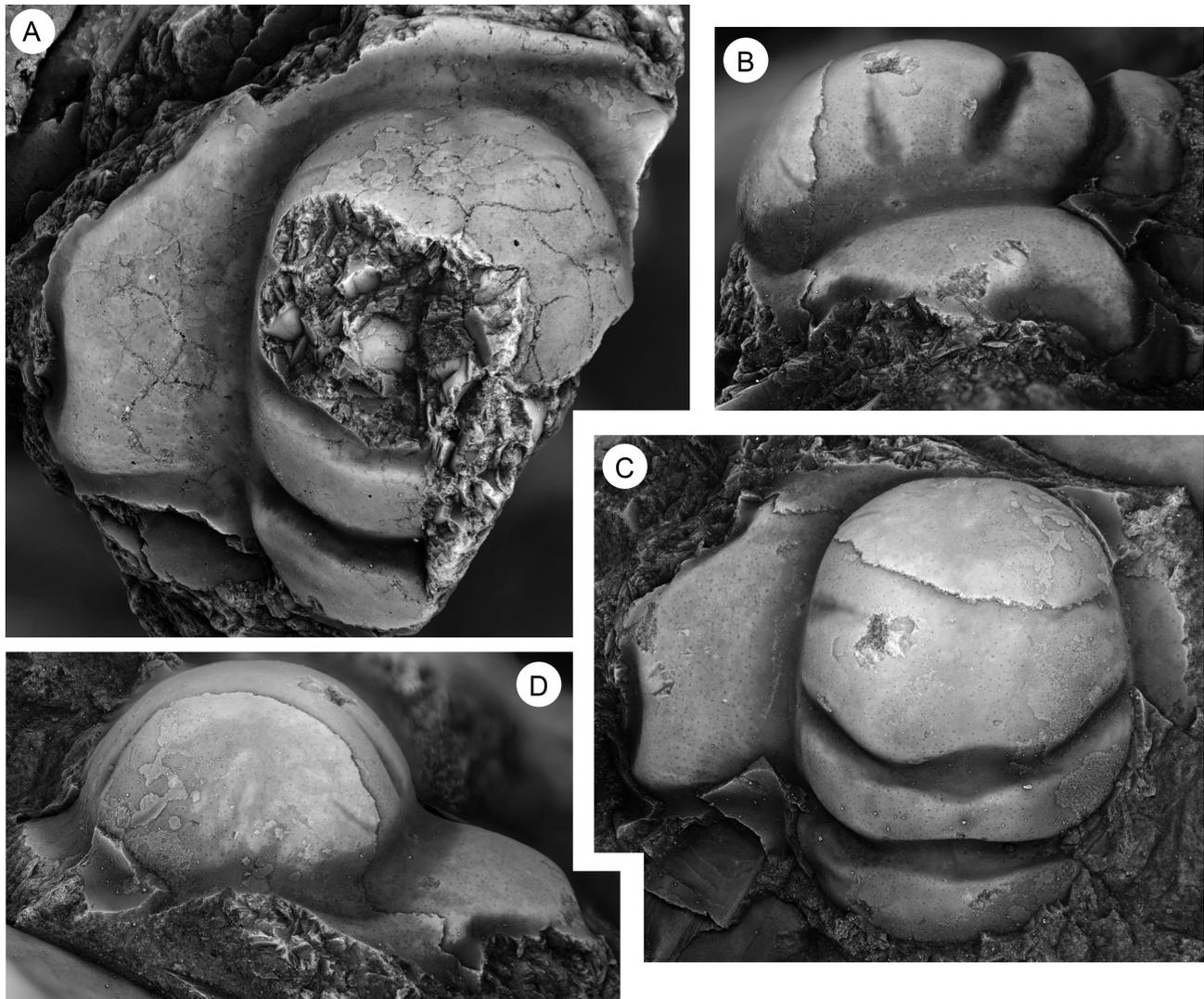
**Figure 5.** *Irvingella angustilimbata* Kobayashi 1938 from the Dunderberg Formation, McGill, Duck Creek Range, White Pine County, Nevada, collection MG2 69–70.5. All cranidia. A–C, OU 237901, dorsal, lateral and anterior views, x7; D–F, OU 237902, lateral, dorsal and anterior views, x12; G–I, OU 237903, lateral, dorsal and anterior views, x11.



**Figure 6.** *Irvingella angustilimbata* Kobayashi 1938 from the Dunderberg Formation, McGill, Duck Creek Range, White Pine County, Nevada, collection MG2 69–70.5. All cranidia except K–M (pygidium). **A–C**, OU 237904, dorsal, anterior and lateral views, x11; **D–F**, OU 237905, anterior, dorsal and lateral views, x16; **G**, OU 237906, dorsal view, x18; **H–J**, OU 237907, anterior, lateral and dorsal views, x7; **K–M**, OU 237908, posterior, dorsal and lateral views, x18.



**Figure 7.** *Irvingella angustilimbata* Kobayashi 1938 from the Dunderberg Formation, south of Hamberg Mine, Eureka District, Eureka County, Nevada, USNM loc. 61. All cranidia. A–C, USNM 619733, dorsal, lateral and anterior views, x5 (*continued overleaf*)



**Figure 8.** *Irvingella angustilimbata* Kobayashi 1938 from the Dunderberg Formation, south of Hamberg Mine, Eureka District, Eureka County, Nevada, USNM loc. 61. All cranidia. **A**, USNM 619735, dorsal view, x8 (paratype of of *I. intermedia* Resser 1942; not illustrated previously); **B–D**, USNM 619736, lateral, dorsal and anterior views, x8 (paratype of of *I. intermedia* Resser 1942; not illustrated previously).

as suggested by indistinct transverse (Fig. 6L) to pit-like (Fig. 3K) furrow. Pleural field unfurrowed and flexed down towards narrow border and shallow border furrow.

**Occurrence.** Corset Spring Shale Member, Orr Formation, and upper Dunderberg Formation, western Utah and eastern Nevada; Rabbitkettle Formation, Mackenzie Mountains, northern Canada (Pratt 1992).

**Discussion.** Cranidia in new collections from the Corset Spring Shale Member at Shingle Pass and coeval intervals of the upper Dunderberg Formation at McGill share a preglabellar field that is shorter than the anterior border on testate specimens (e.g., Figs 3A, 4D, 5A; the border may appear to be relatively shorter, and the preglabellar field longer, on exfoliated individuals such as Fig. 4A; see also Fig. 2A), and a glabella that tapers beyond S1, with a well rounded anterior margin; the palpebral furrow is a firmly

impressed arcuate groove of nearly even width (tr.) (e.g., Figs 3A, I, 5A). These shared characters are also evident in the types of *I. angustilimbata* (Fig. 1) and also its probable synonyms (Palmer 1965), *I. intermedia* (Resser 1942; Figs 7, 8) and *I. eurekaensis* (Resser 1942; Palmer 1960, pl. 6, fig. 1).

Cranidia from collection MG2 69–70 at McGill (Figs 5, 6) show variability in the extent of the anterior arch. Some have an evenly curved, well developed arch (e.g., Fig. 6B) whereas this feature is subdued in other specimens (e.g., Fig. 5C, F). The anterior border furrow is curved gently forward (Fig. 5A) to more transverse (Fig. 5E). There is also some evidence for a modest decrease in the length of the preglabellar field and frontal area during holaspid ontogeny (compare testate cranidia shown in Figs 6G and 5A), although large cranidia in the type lot of *I. angustilimbata* (Fig. 1) still retain a distinct preglabellar field.

(continued from previous page) (illustrated previously as a paratype of *I. intermedia* Resser 1942, pl. 4, figs 30–31); **D–F**, USNM 619734, lateral, dorsal and anterior views, x6 (illustrated previously as a paratype of *I. intermedia* Resser 1942 pl. 4, figs 28, 29); **G**, **H**, USNM 27018, anterior and dorsal views, x18 (illustrated previously as the holotype of *I. intermedia* Resser 1942, pl. 4, figs 25–27).

Testate cranidia from Shingle Pass have nearly transverse borders, (e.g., Figs 3A, 4D), although exfoliated specimens may have more curved anterior cranial margins (e.g., Fig. 4A); in all cranidia, the anterior arch is well developed (e.g., Figs 3C, E, 4B, F). Conspicuous arches also characterise the type lot of *I. intermedia* (Figs 7, 8), with anterior borders varying from nearly transverse (e.g., Fig. 7E) to more noticeably curved (e.g. Fig. 7A).

Elsewhere in Laurentia, Pratt (1992, pl. 11, figs 7–16) reported *I. angustilimbata* from Rabbitkettle Formation in the South Nahanni River area of the Mackenzie Mountains, northern Canada. The larger of the two figured cranidia (pl. 11, fig. 7) shares the short preglabellar field and anteriorly tapered, well rounded glabella with sclerites from the Great Basin. The associated pygidium (pl. 11, figs 14, 15) is coarsely silicified and incomplete, but appears to be relatively longer and more rounded posteriorly than the specimens associated with *I. angustilimbata* in our collections (e.g., Fig. 6K–M). The axis seems to have more segments than is typical for *Irvingella*, and the posterior-oblique view (pl. 6, fig. 15) indicates that it lacks the posterior arch that characterises the genus (e.g., Figs 6K, 9J); it may be misidentified. Palmer (1965) included a cranidium from the Snowy Range Formation of Montana (Grant 1965, pl. 8, fig. 8) in his synonymy of *I. angustilimbata*, but this specimen is too poorly preserved and illustrated for a confident identification.

Despite some variability in shape of border and expression of the anterior arch, all cranidia of *I. angustilimbata* are distinct from *I. tropica* Öpik. The glabella of the latter is more strongly tapered and conical in outline, and less well rounded anteriorly (e.g., Fig. 11). This contrast in glabellar outline is expressed even in small specimens (e.g., compare Figs 13B and 6G). Moreover, the preglabellar field is particularly long in the smallest cranidium of *I. tropica* (Fig. 13B), in which it is roughly equal in length to the L1 glabellar lobe, and about twice as long as the preglabellar field of the similarly sized cranidium of *I. angustilimbata* (Fig. 6G). Comparison of similarly sized cranidia shows that the preglabellar field of *I. tropica* remains longer than that of *I. angustilimbata* during holaspid ontogeny, although the differences are less striking than between small specimens (e.g., compare Figs 3A and 12E; Figs 6A and 11H; Figs 3D and 11D).

There are few pygidia available for study, but they add support for the separation of *I. angustilimbata* and *I. tropica* as distinct species. A pygidium of *I. angustilimbata* from MG2 69–70 (Fig. 6K–M) is transversely semi-elliptical, with a relatively broad axis that occupies about half of pygidial width at the first axial ring. A smaller pygidium from SHP 18.25 (Fig. 3J, K) is similar in outline and in the width of the axis, differing in having a slightly narrower

pleural field. The only known pygidium of *I. tropica*, from the type area in Queensland, is similar in size to our pygidia of *I. angustilimbata*, but is relatively longer and subtrapezoidal in outline; it has a proportionately narrower axis (accounting for no more than 40% of pygidial width at the first axial ring), and is relatively shorter (sag.).

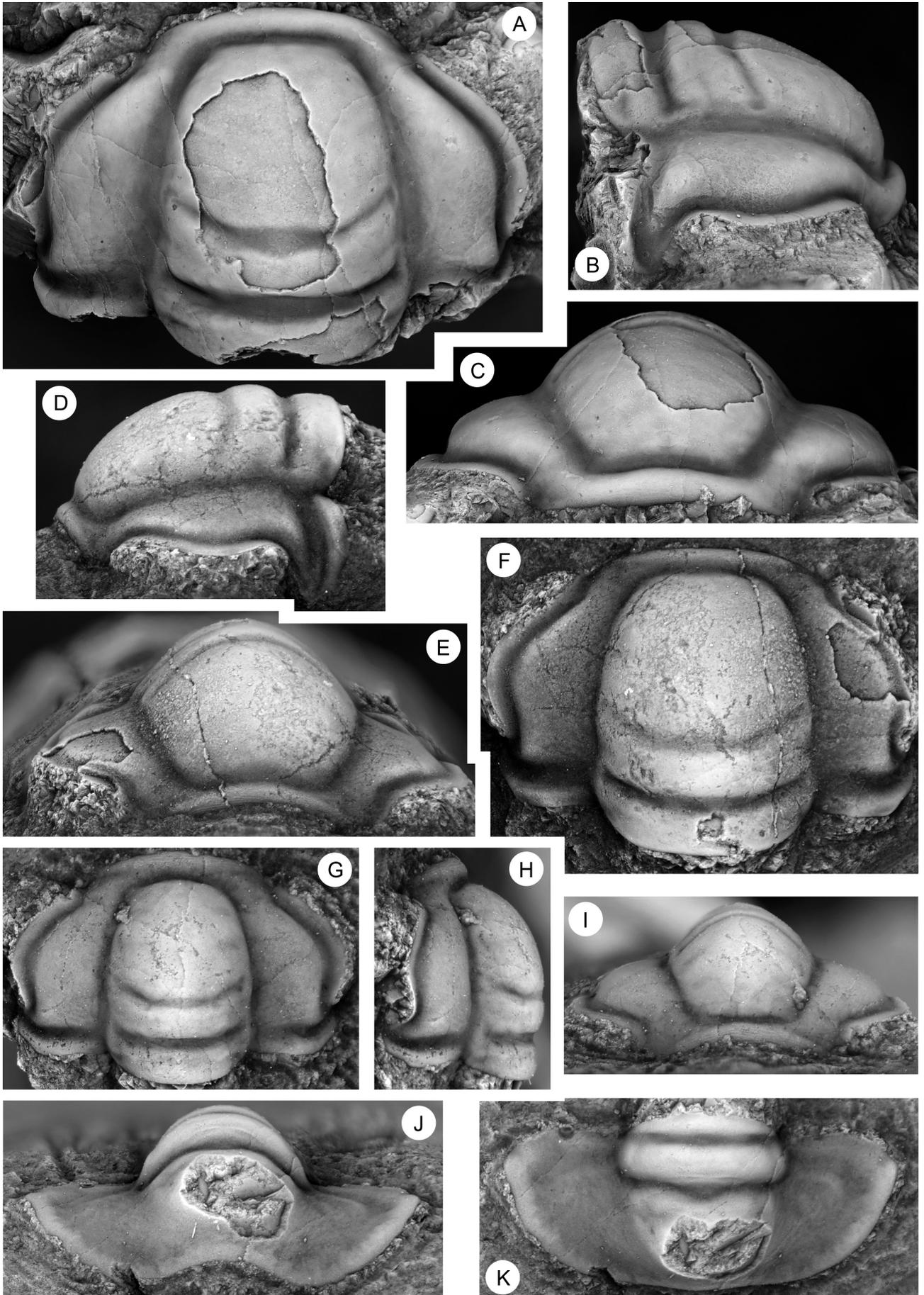
Outside of Laurentia, *I. angustilimbata* has been reported from Hunan (Peng 1992; Duan 2006) and Zhejiang (Peng *et al.* 2012), South China, and from Siberia (Varlamov *et al.* 2006a). All of these occurrence are supported by images of cranidia only and cannot be evaluated fully. The most complete of the cranidia from Hunan (Peng 1992, fig. 23H) is an internal mould illustrated in dorsal view, and appears to have a very short (sag.), upturned border that contrasts with the longer borders of similarly sized, exfoliated specimens of *I. angustilimbata* (e.g., Fig. 6A–C). Small cranidia (e.g., Peng 1992, fig. 23G) differ from small *I. angustilimbata* (e.g., Figs 1G–I, 6G) in having unusually narrow, nearly parallel-sided glabellae. Cranidia from the Jiangshanian stratotype in Zhejiang (Peng *et al.*, 2012, fig. 9H–J) have long preglabellar fields but are too poorly preserved for a species-level identification.

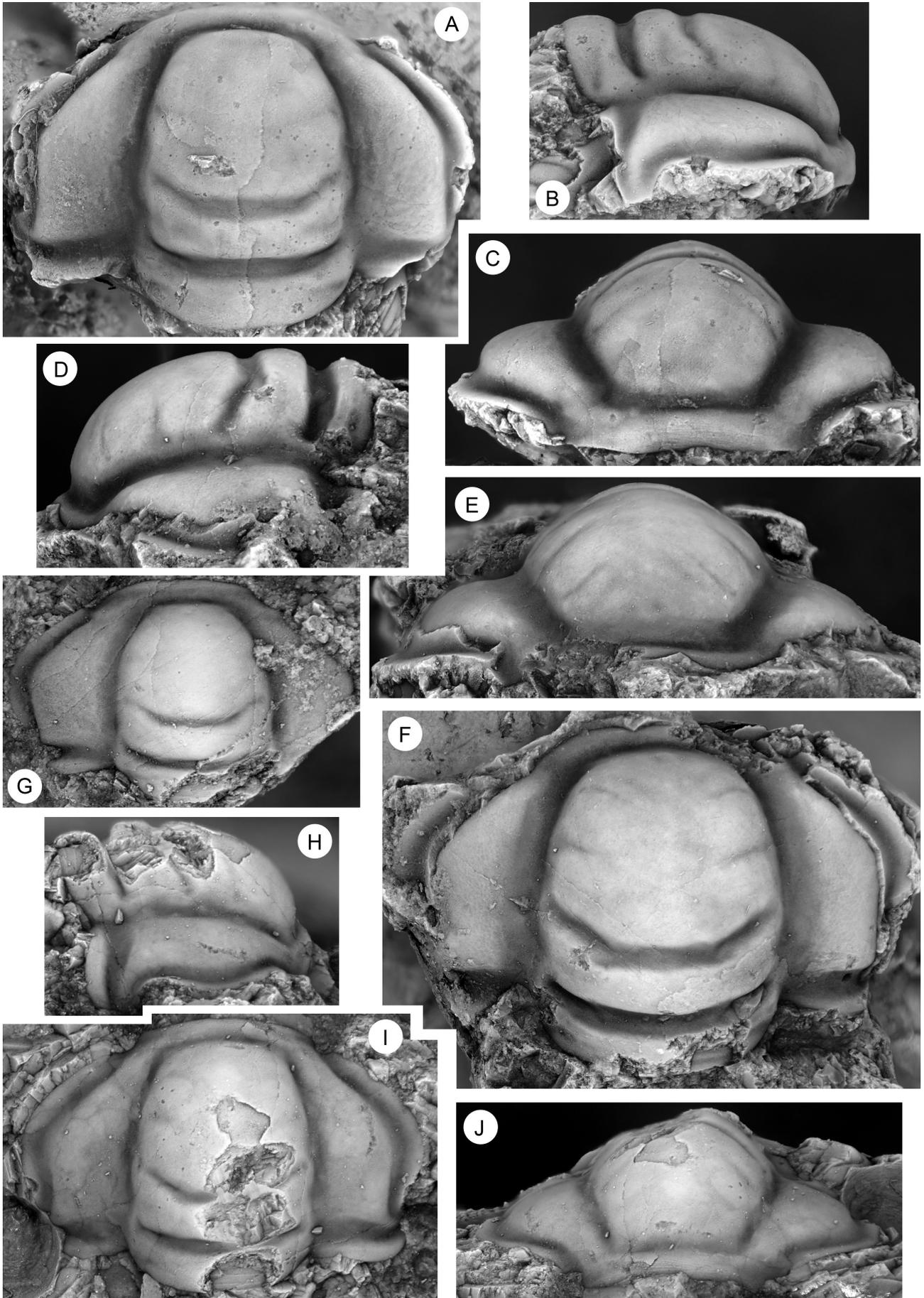
Varlamov *et al.* (2006a, pl. 7, figs 5–5b, 6–6b) illustrated two similarly sized cranidia (6.5 and 6.7 mm in length; Varlamov *et al.* 2006a, p. S35) from Jiangshanian (*Agnostotes clavatus*–*I. perfecta* Zone) strata of Member 3 of the Chopko Formation, Chopko River, northwest Siberia, that they identified as *I. angustilimbata*. These specimens are from talus piles (fauna Ch-10d) at 99 m above the base of the member (Varlamov *et al.*, 2006a, p. S5) and, although both have distinct preglabellar fields, they are sufficiently different in other respects that it is far from clear that they represent a single taxon given the limitations of the sample size. One cranidium (pl. 7, fig. 5) has a relatively long glabella with S1 furrows that are isolated medially, whereas the other (pl. 7, fig. 6) has a relatively short glabella with transglabellar S1 furrows. Cranidia of comparable sizes from the Great Basin (e.g., Figs 3D–F, 4A–C) have relatively shorter preglabellar fields. For these reasons, together with the absence of an associated pygidium, we regard the material of Varlamov *et al.* as belonging to an indeterminate species of *Irvingella*.

*Irvingella typa* (Kobayashi 1935) and *I. megalops* (Kobayashi 1962), from the Korean sector of North China (Hong *et al.* 2003), retain distinct preglabellar fields, but comparisons with *I. angustilimbata* are difficult because almost all figured material is partly to completely flattened (e.g., Hong *et al.* 2003, pl. 1, figs 1–23). Pygidia of *I. megalops* differ from those of the latter in having much narrower pleural fields (e.g., compare Hong *et al.* 2003, pl. 1, fig. 23 with Fig. 6L); as far as can be determined from flattened specimens, the preglabellar field of *I. megalops*

**Figure 9** (overleaf). *Irvingella flohri* Resser 1942 from the Eureka District, Eureka County, Nevada; all from Windfall Canyon (USGS loc. 2579–CO, except A–C (near Richmond Mine; USNM loc. 60). A–C, cranidium, USNM 108667 (holotype), dorsal, lateral and anterior views, x9 (illustrated previously by Resser 1942, pl. 4, figs 12–14 and by Palmer, 1965, pl. 6, fig. 16); D–F, cranidium, USNM 141587, lateral, anterior and dorsal views, x12 (illustrated previously by Palmer 1965, pl. 6, fig. 20); G–I, cranidium, USNM 141586, dorsal, lateral and anterior views, x14 (illustrated previously by Palmer 1965, pl. 6, fig. 19); J, K, pygidium, USNM 141588, posterior and dorsal views, x14 (illustrated previously by Palmer 1965, pl. 6, fig. 24).

**Figure 10** (page 409). *Irvingella* spp. from the Dunderberg Formation, near Richmond Mine, Eureka District (USNM loc. 60), Eureka County, Nevada. All cranidia. A–C, H–J, *Irvingella flohri* Resser 1942. A–C, USNM 108666a (holotype of *I. adamsensis* Resser 1942), dorsal, lateral and anterior views, x11 (illustrated previously by Resser 1942, pl. 4, figs 7–9); H–J, USNM 619738, lateral, dorsal and anterior views, x14 (previously unillustrated specimen from the type lot of *I. adamsensis*); D–G, *Irvingella* sp. indet. D–F, USNM 108666b (paratype of *I. adamsensis*), lateral, anterior and dorsal views, x9 (illustrated previously by Resser 1942, pl. 4, figs 10, 11); G, USNM 619737, dorsal view, x14 (previously unillustrated specimen from the type lot of *I. adamsensis*).





(Hong *et al.* 2003, pl. 1, figs 12–18) is proportionately longer than in *I. angustilimbata*, and the glabella is evenly tapered forward and anteriorly truncate. *Irvingella typa* appears to have a less tapered, anteriorly rounded glabella that is closer to *I. angustilimbata* but, as in *I. megalops*, the preglabellar field is relatively longer.

**Irvingella flohri** Resser 1942 (Figs 9, 10A–C, H–J)

- 1942 *Irvingella flohri*; Resser, p. 24, pl. 4, figs 12–14.  
 1942 *Irvingella adamsensis*; Resser, p. 24, pl. 4, figs 7–9 [only; 10–11 = *I. sp. indet.*]  
 1956 *Irvingella flohri* Resser; Deland & Shaw, p. 556.  
 1965 *Irvingella flohri* Resser; Palmer, p. 47, pl. 6, figs 16, 19, 20, 24.  
 1967 *Irvingella flohri* Resser; Rushton, p. 347.  
 1971 *Irvingella flohri* Resser; Stitt, p. 21.  
 non 1975 *Irvingella flohri* Resser; Kurtz, p. 1031, pl. 4, fig. 36 [= *I. sp. indet.*].  
 non 1976 *Irvingella flohri?* Resser; Hintze & Palmer, p. G21 [= *Irvingella orrensis sp. nov.*].  
 1982 *Irvingella flohri* Resser; Shergold, p. 33.  
 1986 *Irvingella flohri* Resser; McNamara, p. 148, fig. 15.  
 non 1994 *Irvingella flohri* Resser; Qian, p. 92, pl. 12, figs 4–11, pl. 16, fig. 8.  
 non 1999 *Irvingella flohri* Resser; Zhang, p. 107.  
 2003 *Irvingella flohri* Resser; Hong *et al.*, p. 175.  
 2006 *Irvingella flohri* Resser; Duan, p. 117.  
 non 2006 *Irvingella flohri* Resser; Choi & Kim, p. 349.  
 2006a *Irvingella flohri* Resser; Varlamov *et al.*, p. S36.  
 2007 *Irvingella flohri* Resser; Sundberg, p. 219.  
 2008 *Irvingella flohri* Resser; Choi *et al.*, p. 184.  
 non 2009 *Irvingella flohri* Resser; Luo *et al.*, p. 144, pl. 38, figs 10–12.  
 2010 *Irvingella flohri* Palmer *ex* Resser; Rushton & Weidner, p. 198.

**Diagnosis.** Frontal area without anterior border or border furrow in larger holaspids; anterior cranial margin nearly transverse. Glabella weakly tapered, with gently rounded, nearly transverse anterior margin. Palpebral area accounts for about 25% of cranial width between palpebral furrows. Pygidium transversely semielliptical, with lateral margins gently curved and weakly convergent posteriorly; pleural field narrows slightly posteriorly, and axis terminates just short of posterior margin.

**Holotype.** A cranidium (USMN ; Fig. 9A–C) from the Dunderberg Formation, Richmond Mine (USNM loc. 60), 1 km south of Adams Hill and 3 km west of Eureka, Eureka County, Nevada.

**Occurrence.** Dunderberg Formation, Eureka Mining District, Eureka County, Nevada, at Rickmond Mine and Windfall Canyon (USGS loc 2579–CO), 1 km south, and 6.5 km southeast, respectively, from Adams Hill.

**Discussion.** Contrary to the recent interpretation of Rushton & Weidner (2010), we regard the name *Irvingella flohri* Resser 1942, as being available from the date of publication. The respective holotypes of *I. flohri* (Fig. 9A–C) and *I. adamsensis* Resser 1942 (Fig. 10A–C) are closely comparable in glabellar outline, expression of glabellar furrows, fixigenal width, size of palpebral lobes and the undivided frontal area, supporting Palmer's (1965) decision to treat them as synonyms. A smaller, previously unfigured cranidium from the type lot of *I. adamsensis* (Fig. 10H–J) appears to be conspecific with

both holotypes, but the paratype of *I. adamsensis* (Fig. 10 D–F) and a second, previously unfigured, small cranidium from the type lot (Fig. 10G) may be misassigned. Both of these cranidia differ in having barrel-shaped glabellae with strongly convergent margins in front of S1, relatively wide fixigenae, and more strongly curved palpebral lobes. Until more material becomes available, they are best treated as an indeterminate species of *Irvingella*. The single incomplete cranidium from the Davis Formation, Missouri, that Kurtz (1975, pl. 4, fig. 36) assigned to *I. flohri* also represents an indeterminate species.

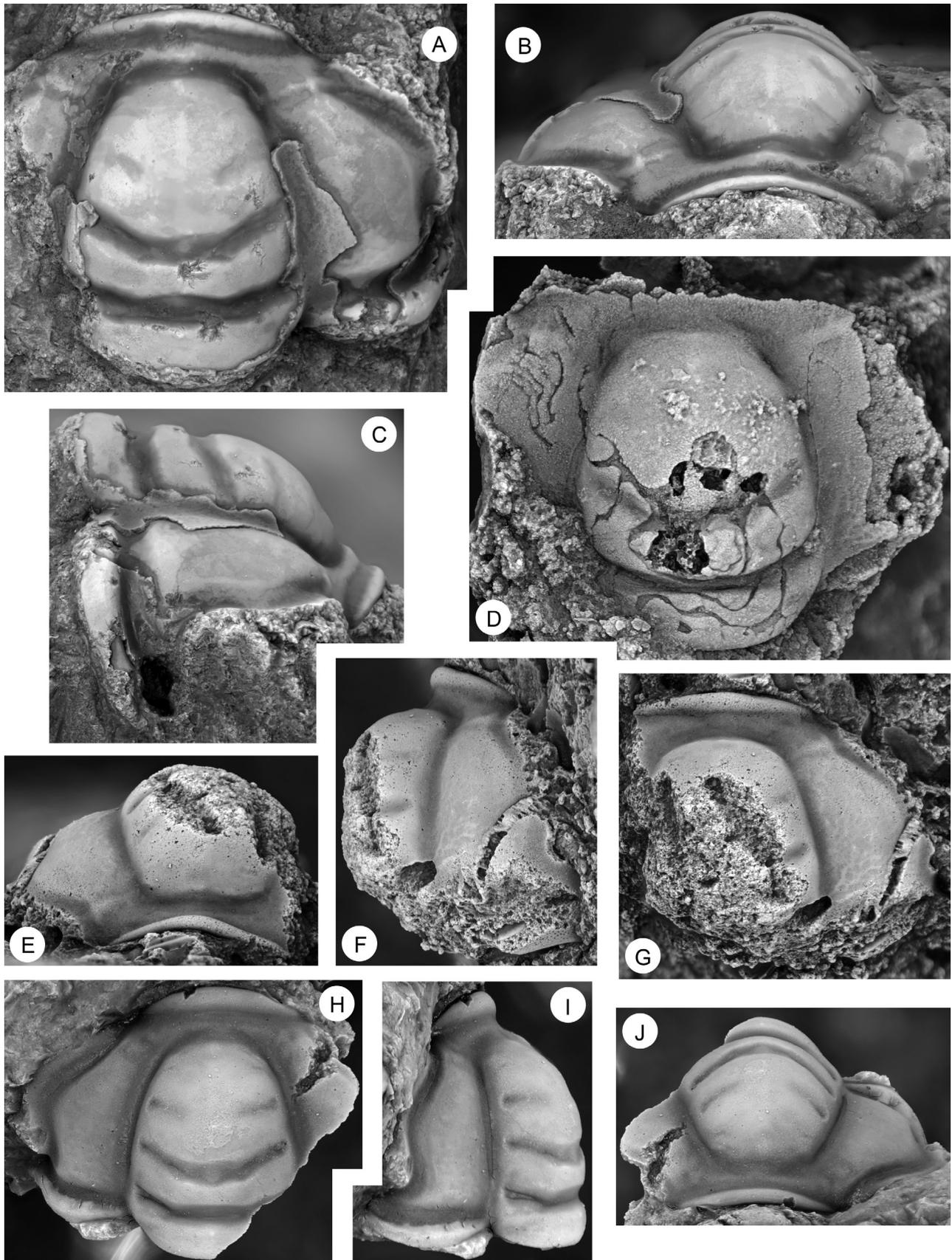
Reports of *I. flohri* beyond Laurentia are poorly documented and cannot be evaluated properly. By way of example, cranidia from the Changshan Formation, North China (Qian 1994, pl. 12, figs. 6–10), are illustrated only in dorsal view and, while they have comparable frontal areas, they also appear to have narrower fixigenae than *I. flohri* (Fig. 9). In the absence of an associated pygidium, little more can be said.

*Irvingella flohri* differs from *I. angustilimbata* most clearly in the undifferentiated frontal area in larger holaspids (e.g., Fig. 9A–C), and is also distinguished from *I. tropica*, *I. typa* and *I. megalops* in this regard. In smaller cranidia, the anterior border of *I. flohri* is expressed as a weakly convex band (e.g., Fig. 9D–I), but the preglabellar field is at best an exceedingly narrow sliver. The glabella of *I. flohri* is gently tapered, with a weakly rounded, anterior margin, whereas *I. angustilimbata* is well rounded anteriorly (e.g., Figs 1, 5). The only pygidium assigned to *I. flohri* (Fig. 9J, K) is about 25% longer (sag.) than the largest known pygidium of *I. angustilimbata* (Fig. 6K–M). The lateral margins converge less strongly posteriorly than in the latter, so that the pleural field maintains a more even width (tr.). The only known pygidium of *I. tropica* (Fig. 13C, D) is also small and, in addition to being relatively longer than *I. angustilimbata*, is subtrapezoidal in outline with strongly convergent lateral margins.

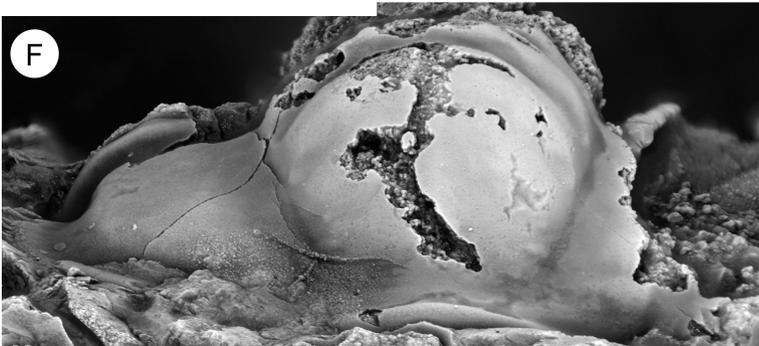
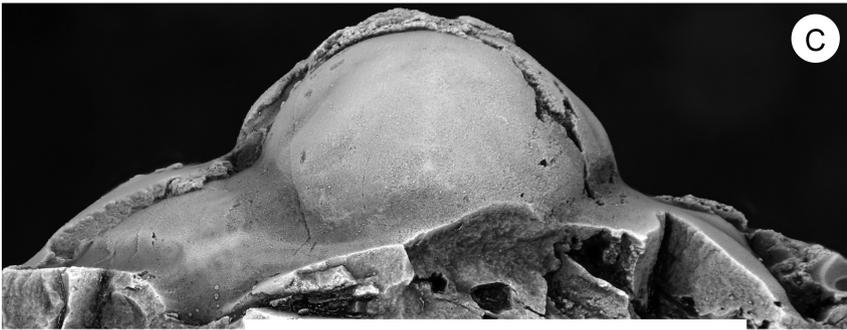
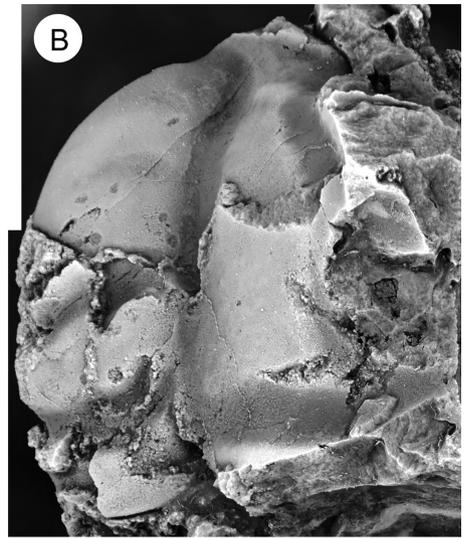
*Irvingella major* Ulrich & Resser (Fig. 14) and related species, such as *I. deckeri* Resser 1942 (Fig. 15) and *I. media* Resser 1942 (Figs. 16, 17), all possess glabellae with well rounded anterior margins that contrast with the more transverse margin of *I. flohri*. *Irvingella deckeri* is also separated from *I. flohri* on the basis of its narrower fixigenae and shorter, curved anterior margin, whereas *I. media* has wider fixigenae, and retains a distinct border on the frontal area later into the holaspis stage (compare Figs 9A–C and 17A–C, G–I)

**Irvingella tropica** Öpik 1963 (Figs 11, 12, 13A–D)

- 1963 *Irvingella tropica*; Öpik, p. 96, pl. 4, figs 5–8; text-fig. 36.  
 1965 *Irvingella tropica* Öpik; Palmer, p. 46.  
 1967 *Irvingella tropica* Öpik; Öpik, p. 57.  
 1967 *Irvingella tropica* Öpik; Rushton, p. 339.  
 1976 *Irvingella tropica* Öpik; Shergold *et al.*, p. 271.  
 1977 *Irvingella tropica* Öpik; Henderson, fig. 9.  
 1980 *Irvingella tropica* Öpik; Shergold, p. 18.  
 1982 *Irvingella tropica* Öpik; Shergold, p. 34, pl. 7, figs 4–7, pl. 8, fig. 10.  
 non 1980 *Irvingella tropica* Öpik; Ergaliev, p. 143, pl. 12, figs 12, 13 [= *Irvingella sp. indet.*].  
 1985 *Irvingella tropica* Öpik; Xiang & Zhang in Wang *et al.*, p. 45, 232.  
 1992 *Irvingella tropica* Öpik; Peng, p. 57.  
 1992 *Irvingella tropica* Öpik; Pratt, p. 49.



**Figure 11.** *Irvingella tropica* Öpik 1963 from the Pomegranate Limestone, western Queensland, Australia. All from Mt. Murray (Shergold 1982) except A–C (from Pomegranate Creek; Öpik 1963). All cranidia. A–C, CPC 4279 (holotype), dorsal, anterior and lateral views, x8 (illustrated previously by Öpik 1963, pl. 4, figs 5–7); D, CPC 19242, dorsal view, x9 (not illustrated previously); E–G, CPC 19240, anterior, lateral and dorsal views, x9 (not illustrated previously); H–J, CPC 15161, dorsal, lateral and anterior views, x9 (illustrated previously by Shergold 1982, pl. 7, fig. 8 [additional preparation to expose the left anterior corner]).



- 1993 *Irvingella tropica* Öpik; Shergold, p. 345.  
 1994 *Irvingella tropica* Öpik; Qian, p. 93.  
 2000 *Irvingella tropica* Öpik; Geyer & Shergold, p. 194.  
 2003 *Irvingella tropica* Öpik; Hong *et al.*, p. 175.  
 2006 *Irvingella tropica* Öpik; Duan, p. 117.  
 2006a *Irvingella tropica* Öpik; Varlamov *et al.*, p. S36.  
 non 2009 *Irvingella tropica* Öpik; Ergaliev *et al.*, p. 43, fig. 11.5, 11.8–11.11 [= *I. sp. indet.*].  
 2013 *Irvingella tropica* Öpik; Westrop & Adrain, p. 806.

**Diagnosis.** Glabella strongly tapered and conical in outline, with gently rounded anterior margin. Long frontal area with well developed preglabellar field that is equal to slightly more than 10% of cranial length. Palpebral furrow well incised arcuate groove of even width. Pygidium subtrapezoidal in outline, with axis occupying about 40% of pygidial width at the first axial ring and about 75% of pygidial length.

**Holotype.** A cranidium (CPC 4279) from the Pomegranate Limestone, Pomegranate Creek, western Queensland, Australia (Fig. 11A–C).

**Occurrence.** Pomegranate Limestone and Georgina Limestone western Queensland, Australia (Öpik 1963; Henderson 1976; Shergold 1982).

**Discussion.** *Irvingella tropica* was compared to *I. angustilimbata* earlier in the text, and a full description is unnecessary. Flattened sclerites (Hong *et al.* 2003) of *I. typa* (Kobayashi) and *I. megalops* (Kobayashi) from the Machari Formation of Korea suggest the presence of long preglabellar fields comparable to *I. tropica*, although both species have relatively shorter pygidia, with narrower pleural fields (compare Hong *et al.* 2003, pl. 1, figs 6, 22, 23 with Fig. 13C, D). Unlike *I. tropica*, the glabella of *I. megalops* appears to have been strongly truncate anteriorly (e.g. Hong *et al.* 2003, pl. 1, figs 12–14; Lazarenko *et al.* 2008, pl. 17, fig. 7 assign similar cranidia from latest Paibian strata from eastern Siberia to this species); *I. typa* is closer to *I. tropica* in having a tapered, more rounded glabella, but has conspicuous S2 furrows (Hong *et al.* 2003, pl. 1, fig. 11). Further comparisons are prevented by the poor quality of the Korean material.

Cranidia from Kazakhstan attributed to *I. tropica* by Ergaliev (1980, pl. 12, figs 12, 13) are poorly preserved and may be compacted; subsequent better material (Ergaliev *et al.* 2009, fig. 11.5, 11.8–11.11) includes a pygidium. The glabellae are not as strongly tapered as in sclerites from Australia, and the pygidium appears to be relatively broader and more rounded posteriorly. The Kazakh cranidia are also similar to *I. typa* and *I. megalops* from Korea (Hong *et al.* 2003, pl. 1), and they are best viewed as an indeterminate species of *Irvingella*. *Irvingella specioza* (Ivshin 1962), from strata of the Seletinian horizon of the Kuyandian Stage exposed along the Seleta River, Bestube District, central Kazakhstan, appears to have a tapered glabella that is comparable to *I. tropica*, and Ivshin's (1962, text-fig. 14) line drawing shows a distinct preglabellar field, albeit shorter than in *I. tropica* (e.g., Fig. 11). Unfortunately, the accompanying very small, cropped photographs (Ivshin

1962, pl. 4, figs. 3, 4) provide no details of the structure of the frontal area, although if completely preserved, it is much shorter than the frontal area of *I. tropica*.

**Irvingella cf. I. tropica** Öpik, 1963 (Fig. 13E–J)

cf. 1963 *Irvingella tropica*; Öpik, p. 96, pl. 4, figs 5–8; text-fig. 36.

1965 *Irvingella angustilimbatus*; Palmer, p. 46, pl. 6, fig. 23 [only].

**Occurrence.** Hales Limestone, Tybo, Nye County Nevada (USGS loc. 1471–CO); Corset Spring Shale Member, Orr Formation, Patterson Pass, collection PP 280.4.

**Discussion.** Palmer (1965, pl. 6, fig. 23) illustrated a cranidium that he felt (1965, p. 47) could not be “objectively distinguished” from the types of *I. tropica*. He entertained the possibility that this specimen recorded the occurrence of that species in Laurentia, but ultimately treated it as a “variant” of *I. angustilimbata* (although he hedged his identification in the caption to plate 6 by adding parenthetically “= *Irvingella tropica* Öpik?”). Our new images of this (Fig. 13E–G) and a smaller individual (Fig. 13H–J) show that, while they are certainly similar to *I. tropica*, there is also at least one character that sets them apart. They share a relatively long preglabellar field and tapered, bluntly rounded glabella with *I. tropica* (e.g., Figs 11, 12), but both differ in possessing palpebral furrows that are very wide (tr.), deeply incised and crescentic in outline; the expression of these furrows is particularly striking as both specimens are testate. As the pygidium is unknown, we place these cranidia in open nomenclature.

Fifty years ago, there was limited information on variability of *I. angustilimbata*, so that Palmer's (1965) decision to include all cranidia from the Great Basin with a distinct preglabellar field in that species was defensible. However, the cranidia in the type lot of *I. angustilimbata* have narrow, arcuate palpebral furrows even on exfoliated surfaces (e.g., Fig. 1A, D, J), and our new collections from the lower Corset Spring Shale at Shingle Pass and the upper Dunderberg Formation at McGill demonstrate the same morphology on testate surfaces in both early (Fig. 6G) and later holaspids (Figs 3A, I, 5A). This is clearly different from the palpebral furrow morphology of *I. cf. I. tropica*, which also has a longer preglabellar field than in similarly sized cranidia of *I. angustilimbata* (compare Fig. 13E–G with Figs 3A–C, 5A–C).

**Irvingella major** Ulrich & Resser 1924 (Fig. 14)

1924 *Irvingella major*; Ulrich & Resser in Walcott, p. 58, pl. 10, fig. 3.

1925 *Irvingella major* Ulrich & Resser; Ulrich & Resser in Walcott, p. 98, pl. 15, figs 26–29.

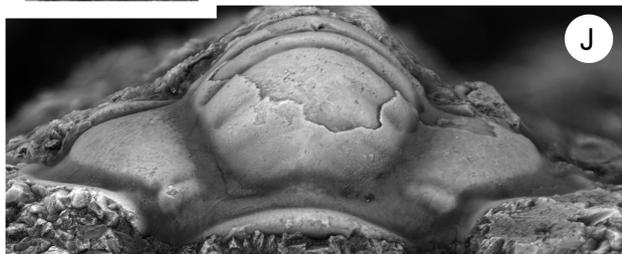
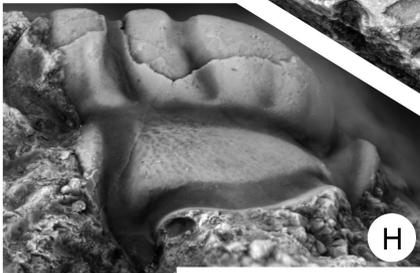
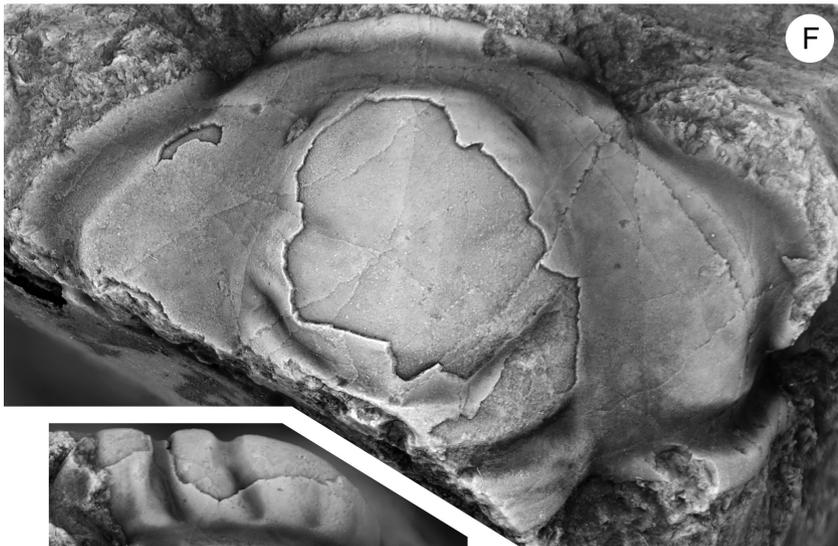
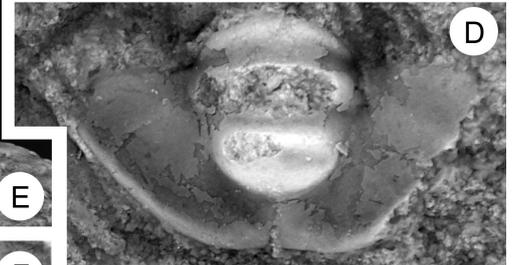
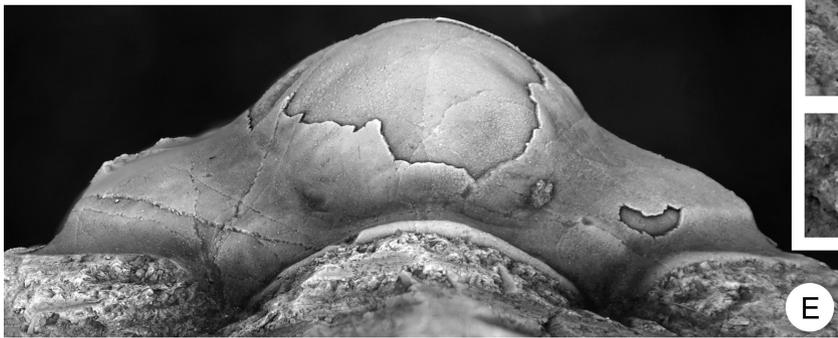
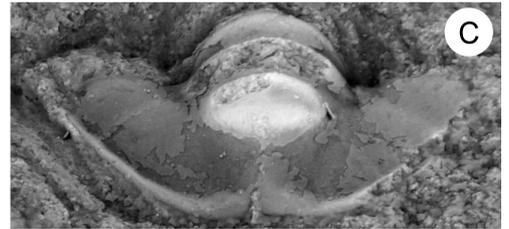
1944 *Irvingella major* Ulrich & Resser; Shimer & Shrock, p. 627, pl. 265, fig. 25.

non 1951 *Irvingella major* Ulrich & Resser; Wilson, p. 644, pl. 93, figs. 14, 21–23.

non 1962 *Irvingella major* Ulrich & Resser; Ivshin, p. 49, text-fig. 10, pl. 3, figs 7–15.

non 1965 *Irvingella major* Ulrich & Resser; Palmer, p. 48,

**Figure 12.** *Irvingella tropica* Öpik 1963, Pomegranate Limestone, Mount Murray, western Queensland, Australia. All cranidia. **A–C**, CPC 15163, dorsal, lateral and anterior views, x6.5 (illustrated previously by Shergold 1982, pl. 7, fig. 5); **D–F**, CPC 15162, lateral, dorsal and anterior views, x8 (illustrated previously by Shergold 1982, pl. 7, fig. 4); **G**, CPC 19241, dorsal view, x9 (not illustrated previously).



- pl. 6, figs 15–19.  
*non* 1965 *Irvingella major* Ulrich & Resser; Grant, p. 126, pl. 10, figs 8, 9, 11.  
*non* 1971 *Irvingella major* Ulrich & Resser; Stitt, p. 21, pl. 1, fig. 12.  
*non* 1975 *Irvingella major* Ulrich & Resser; Kurtz, p. 1030, pl. 4, fig. 35.  
*non* 1979 *Irvingella major* Ulrich & Resser; Hu, p. 53, text-fig. 2, pl. 8, figs 29–36.  
*non* 1980 *Irvingella major* Ulrich & Resser; Ergaliev, p. 46, pl. 13, fig. 9.  
*non* 1985 *Irvingella major* Ulrich & Resser; Xiang & Zhang, pp. 45, 232.  
*non* 1986 *Irvingella major* Ulrich & Resser; Westrop, p. 63, pl. 30, figs 8–13.  
*non* 1986 *Irvingella major* Ulrich & Resser; McNamara, p. 148, fig. 15.  
*non* 1992 *Irvingella major* Ulrich & Resser; Pratt, p. 48, pl. 11, figs 1, 2.  
*non* 2003 *Irvingella major* Ulrich & Resser; Hong *et al.*, p. 186, pl. 2, figs 21–27.  
*non* 2008 *Irvingella major* Ulrich & Resser; Lazarenko *et al.*, p. 91, pl. 17, figs. 9–12, 12a.  
*non* 2010 *Irvingella major* Ulrich & Resser; Rushton & Weidner, p. 195, fig. 3A–D.  
*non* 2012 *Irvingella major* Ulrich & Resser; Peng *et al.* p. 467, fig. 9O–R.

**Diagnosis.** Convex, gently tapered glabella well rounded anteriorly. Conspicuous, apparently undivided frontal area with transverse anterior margin. Fixigena relatively broad, with maximum width of palpebral area equal to slightly more than 20% of maximum cranial width.

**Lectotype.** A cranidium (USNM 70238; selected by Pratt 1992) from the Lone Rock Formation, Ableman, Wisconsin (USNM loc. 80n) (Fig. 14B, C; located on far right of slab illustrated in Fig. 14A). This specimen was illustrated previously by Walcott (1925, pl. 15, fig 27, upper cranidium), and was also the specimen on which his restoration (Walcott 1925, pl. 15, fig. 26) was based.

**Occurrence.** Lone Rock Formation, Wisconsin.

**Discussion.** The type lot of *I. major* consists of five partly weathered, sandstone internal moulds of cranidia, two of which are largely buried in the matrix, and two others are incomplete; the most complete sclerite (lectotype; Fig. 14B, C) seems to be slightly distorted anteriorly. The close packing of the sclerites suggests that they are from one of the bioclastic rudstone horizons (“*Irvingella major* coquina”) that are typical of the basal Sunwaptan *Irvingella major* Zone across much of Laurentian North America (Wilson & Frederickson 1950).

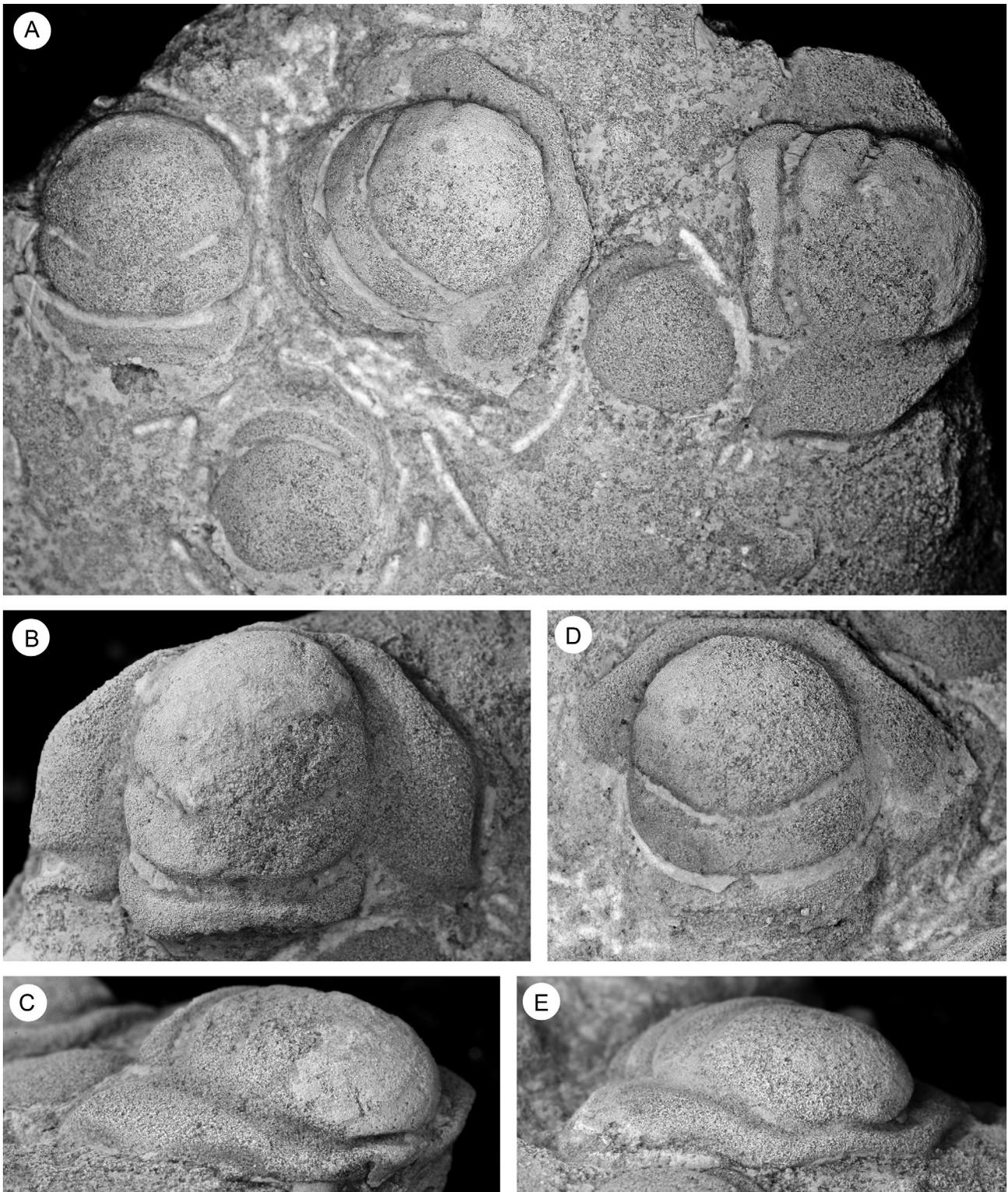
Cranidia of *Irvingella major* are similar to smaller sclerites of *I. media* Resser 1942 in the type lot (Fig. 16) and from new collections in Oklahoma (Fig. 17) in possessing relatively broad fixigena and a well defined frontal area. The strong anterior taper of glabellae of *I. media* (e.g.,

Fig. 17A, G) contrasts with the more parallel-sided, well rounded glabellae of *I. major* (Fig. 14A, D). The largest available cranidium of *I. media* (Fig. 17A–C) is about two-thirds of the sagittal length of the types of *I. major*, but we have no evidence to suggest that the two sets of sclerites record ontogenetic change in glabella outline of a single species. Moreover, there is an ontogenetic shortening of the frontal area in *I. media* (e.g., compare the series in Figs 17F, 16H, 16A, 17G and 17A), so that the relative length of this feature is already slightly shorter in our specimens (Fig. 17A–G) than in much larger, undistorted sclerites in the type lot of *I. major* (Fig. 14D). Subtle features, such as the weak anterior border, border furrow and preglabellar field that are present on all cranidia of *I. media* (e.g., Fig. 17A, G) are likely to be obscured by the poor preservational quality of the types of *I. major*. Indeed, this underscores the problematic nature of the types: they are sufficiently well preserved to demonstrate the general morphology of *Irvingella*, but are inadequate for detailed comparisons at the species level. In our view, the long synonymy lists that have been accepted by many authors in the past (e.g., Palmer 1965; Westrop 1986; Hong *et al.* 2003) can no longer be justified. Although the name has been used widely in the literature, we suggest that *I. major* is better considered a *nomen dubium*, and should be restricted to the types (see also Eoff 2008).

Many of the sclerites attributed to *I. major* in Laurentian occurrences are too poorly documented to be evaluated properly. For example, Grant (1965, pl. 10, figs 8, 9, 11) illustrated two cranidia and a pygidium from the Snowy Range Formation at three different localities in Montana and Wyoming with postage stamp-sized images. The individual cranidia resemble *I. deckeri* and *I. media* (see below), and may record separate species, rather than ontogenetic variability as implied by Grant (1965, p. 161 [figure caption]); the pygidium may be better assigned to *Elvinia* (e.g., Westrop 1986, pl. 30, fig. 15). The larger of only two cranidia figured by Westrop (1986, pl. 30, figs 12, 13) from Alberta has narrower fixigenae and a shorter frontal area than Walcott’s types. Similar fixigenal proportions occur in holaspids from the Great Basin (Palmer 1965, pl. 6, fig. 10). However, associated pygidia are unlike those illustrated from Alberta (Westrop 1986, pl. 30, figs 10, 11), and include extremely narrow morphologies (Palmer, 1965, pl. 6, fig. 9). There is not enough information to make an informed interpretation of this variation. However, the notion of a single, pandemic species in the basal Sunwaptan of Laurentia no longer seems defensible (see following discussions of *I. deckeri* and *I. media*), and an entirely new study of the fauna of the *I. major* Zone is needed.

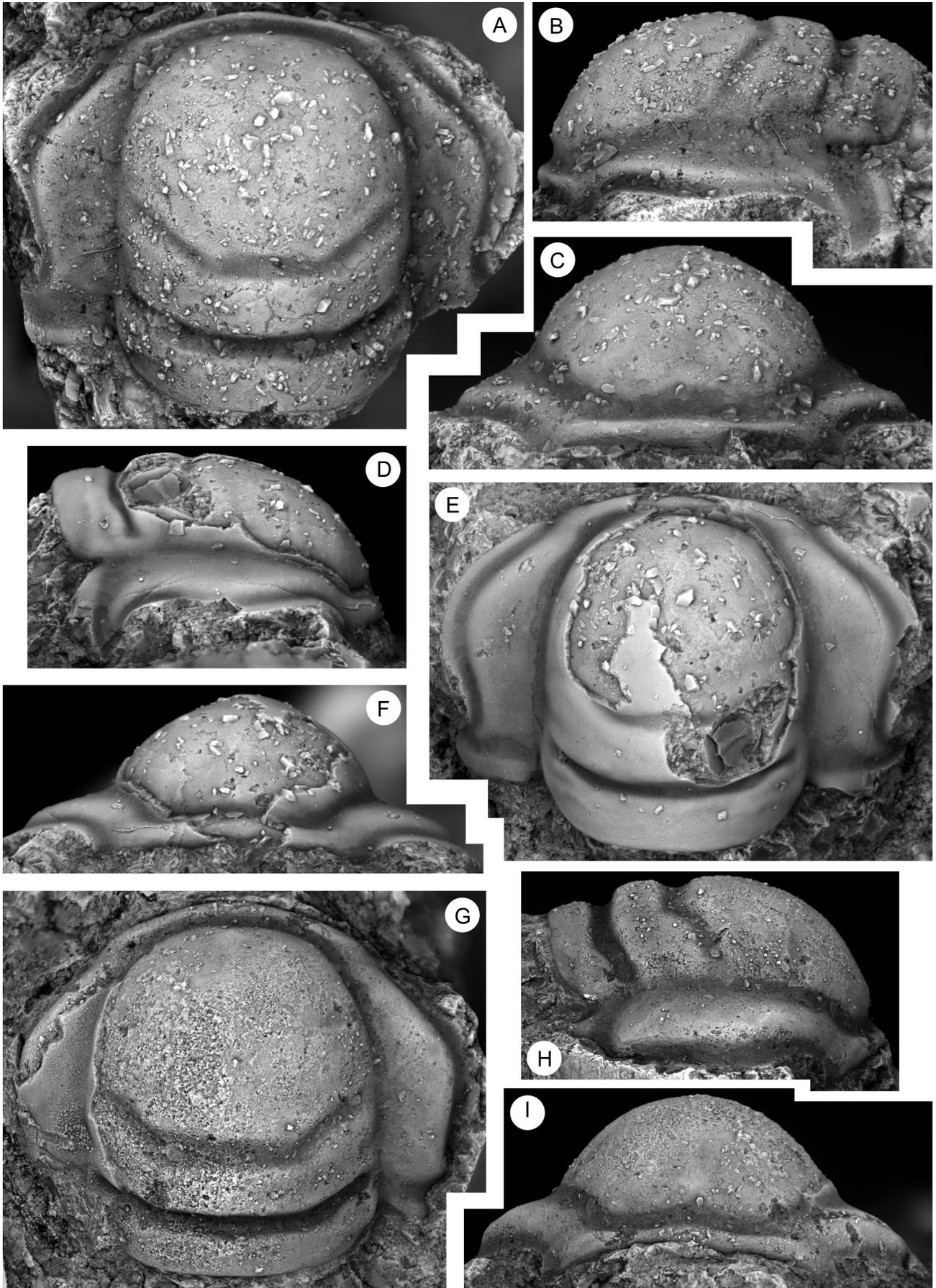
Of the material from other Cambrian continents assigned to *I. major*, sclerites from North China (Hong *et al.* 2003, pl. 2, figs 21–27) are so badly flattened that they cannot be compared to Laurentian specimens in any meaningful way. The most completely preserved cranidium illustrated by Peng *et al.* (2012, fig. 9Q) from the *Eolotagnostus* Zone in the Jiangshanian stratotype in South China is similar to

**Figure 13.** *Irvingella* from Australia and the United States. **A–D**, *Irvingella tropica* Öpik 1963, Pomegranate Limestone, western Queensland, Australia. A, cranidium, CPC 19243, dorsal view, Mt. Murray, x9 (not illustrated previously); B, Cranidium, CPC 15164, dorsal view, Mt. Murray, x18 (illustrated previously by Shergold 1982, pl. 8, fig. 10). C, D, pygidium, CPC 4283 (paratype), dorsal view, Pomegranate Creek (Öpik 1963) x20 (illustrated previously by Öpik 1963, pl. 4, fig. 8). **E–J**, *Irvingella cf. I. tropica* Öpik 1963. E–G, cranidium, USNM 141591 (Hales Limestone, Tybo, Nye County Nevada), anterior, dorsal and lateral views, USGS loc. 1471–CO, x8 (illustrated previous by Palmer 1965, pl. 6, fig. 23); H–J, cranidium, OU 237909, lateral, dorsal and anterior views, collection PP 280.4 (Corset Spring Shale, Patterson Pass, Lincoln County, Nevada), x8.



**Figure 14.** *Irvingella major* Ulrich & Resser in Walcott 1924, Lone Rock Formation, Ableman, Wisconsin (USNM loc. 80n). **A**, slab with several cranidia, USNM 70238, x3.5 (illustrated previously by Walcott, 1925, pl. 15, figs 27, 29); **B**, **C**, cranidium, lectotype, USNM 70238a (far right of slab in Fig. A), dorsal and anterior-oblique views (illustrated previously by Walcott, 1925, pl. 15, fig 27 [upper cranidium], and was also the specimen on which the restoration of pl. 15, fig. 26 was based); **D**, **E**, cranidium, paralectotype, USNM 70238b (centre of slab in Fig. A), dorsal and anterior-oblique views (illustrated previously by Walcott, 1925, pl. 15, fig 27 [lower cranidium]).

**Figure 15** (opposite). *Irvingella deckeri* Resser 1942, Honey Creek Limestone, West Timbered Hills, Murray County, southern Oklahoma (USNM loc. 89y). All cranidia. **A–C**, USNM 108657b (paratype), dorsal, lateral and anterior views, x12 (illustrated previously by Resser 1942, pl. 3, figs 19–21); **D–F**, USNM 108657a (holotype), lateral, dorsal and anterior views, x13 (illustrated previously by Resser 1942, pl. 3, figs 25–27); **G–I**, USNM 108657c (paratype), dorsal, lateral and anterior views, x7.5 (illustrated previously by Resser, 1942, pl. 3, figs 22–24).



*I. media* (Fig. 16) in having a relatively long frontal area that appears to possess a short anterior border, and has relatively wide fixigenae. The associated pygidium (Peng *et al.* 2012, fig. 9R) is relative narrow and, aside from the apparent effacement of the axial ring furrows, resembles a small pygidium from the Great Basin that was figured by Palmer (1965, pl. 6, fig. 9).

Lazarenko *et al.* (2008, pl. 17, figs. 9–12, 12a) assigned three cranidia and an incomplete pygidium from the Ogon'or Formation, Khos-Nelege River, northeast Siberian Platform to *I. major*. The cranidia are perhaps most similar to the large cranidium illustrated by Westrop (1986, pl. 30, figs 12, 13) in having relatively narrow fixigenae, a convex glabella that is well rounded anteriorly, and a short anterior border; the pygidium certainly belongs to *Irvingella* but little more can be said. Cranidia from upper Cambrian strata in central (Ivshin 1962) and southern (Ergaliev 1980) Kazakhstan have been illustrated as *I. major*, although in both cases documentation is inadequate. The single specimen figured by Ergaliev (1980, pl. 13, fig. 9) is poorly preserved, lacking the frontal area, and cannot be identified to the species level. *Irvingella major* of Ivshin (1962, pl. 3, figs. 7–15) has a convex, well rounded glabella but, if the closely cropped photographs convey the morphology correctly, the frontal area is very short, and unlike Walcott's types (Fig. 14).

A single cranidium from Baltica (Rushton & Weidner 2010, fig. 3) records a species that is related to *I. major*; Rushton & Weidner noted similarities with Palmer's (1965) cranidia from the Great Basin, but more material are needed for further assessment.

#### ***Irvingella deckeri* Resser 1942 (Fig. 15)**

1942 *Irvingella deckeri*; Resser, p. 19, pl. 3, figs 19–27.  
 1949 *Irvingella major* Ulrich & Resser; Frederickson, p. 354.  
 1962 *Irvingella major* Ulrich & Resser; Ivshin, p. 48.  
 1965 *Irvingella major* Ulrich & Resser; Palmer, p. 48.  
 2003 *Irvingella major* Ulrich & Resser; Hong *et al.*, p. 196.

**Diagnosis.** Short, gently curved anterior border; preglabellar field absent. Convex glabella gently tapered in front of S1, rounded anteriorly. Fixigenae narrow, with maximum width of palpebral area (excluding palpebral lobe) equal to slightly more than one-quarter of glabellar width at abaxial tip of S1.

**Holotype.** A cranidium (USNM 108657a) from the Honey Creek Formation, west Timbered Hills (USNM loc. 89y), Arbuckle Mountain region, Oklahoma (Fig. 15D–F).

**Occurrence.** Honey Creek Formation, central Oklahoma.

**Discussion.** Although Frederickson (1949) considered *I. deckeri* to be a junior synonym of *I. major*, the narrow (tr.) fixigenae and very short, forwardly curved anterior border indicate that is a distinct species. The largest cranidium among Resser's types (Fig. 15G–I) is about 70% of the size of Walcott's material. However, fixigenal width and border morphology of *I. deckeri* shows no appreciable change through size range of specimens in the type lot (Fig. 15), and it is highly unlikely that these are early ontogenetic morphs of a single species that also includes the larger *I. major* types.

#### ***Irvingella media* Resser 1942 (Figs 16, 17)**

1942 *Irvingella media*; Resser, p. 22, pl. 3, figs 46–54.

1944 *Irvingella media* Resser; Shimer & Schrock, p. 627, pl. 265, figs 26, 27.

1949 *Irvingella media* Resser; Wilson, p. 39, pl. 10, fig. 7, pl. 11, figs 16, 17, 19, 20.

1951 *Irvingella major* Ulrich & Resser; Wilson, p. 644.

1962 *Irvingella major* Ulrich & Resser; Ivshin, p. 49.

1965 *Irvingella major* Ulrich & Resser; Palmer, p. 48.

2003 *Irvingella major* Ulrich & Resser; Hong *et al.*, p. 196.

**Diagnosis.** Glabella tapered strongly forward beyond S1; rounded anteriorly. Distinct anterior border weakly inflated above very short preglabellar field. Fixigena broad, with maximum width of palpebral area equal to half of glabellar width at abaxial tip of S1.

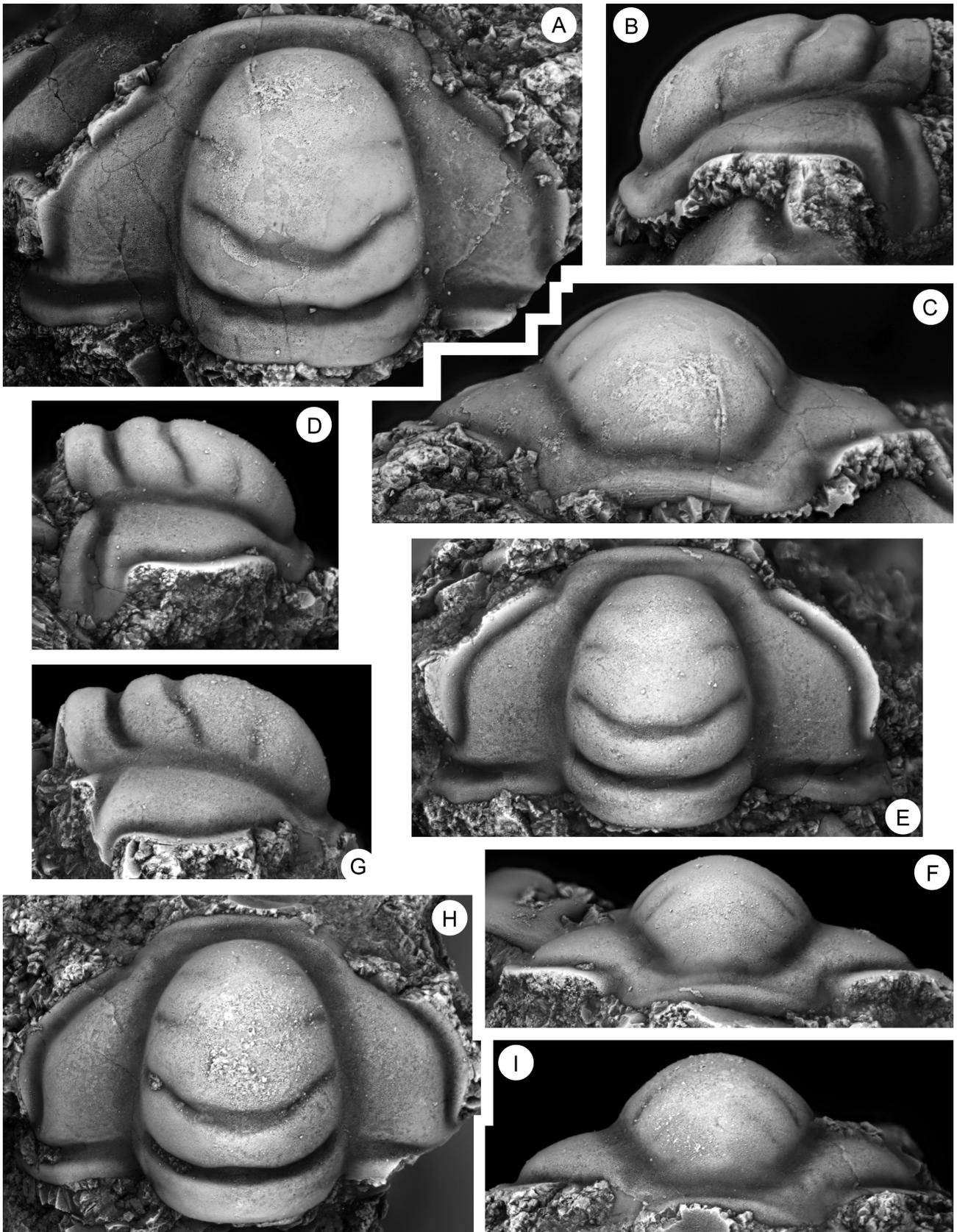
**Holotype.** A cranidium (USNM 108662a) from the Morgan Creek Member, Wilberns Formation, Baldy Mountain, Burnett County (USNM loc. 70), Texas (Fig. 16G–I).

**Occurrence.** Morgan Creek Member, Wilberns Formation, central Texas. Honey Creek Formation, Dotson Ranch section, collection DR 12.2 (*Irvingella major* Zone), Arbuckle Mountains, Oklahoma (see Westrop & Adrain 2007 for locality information).

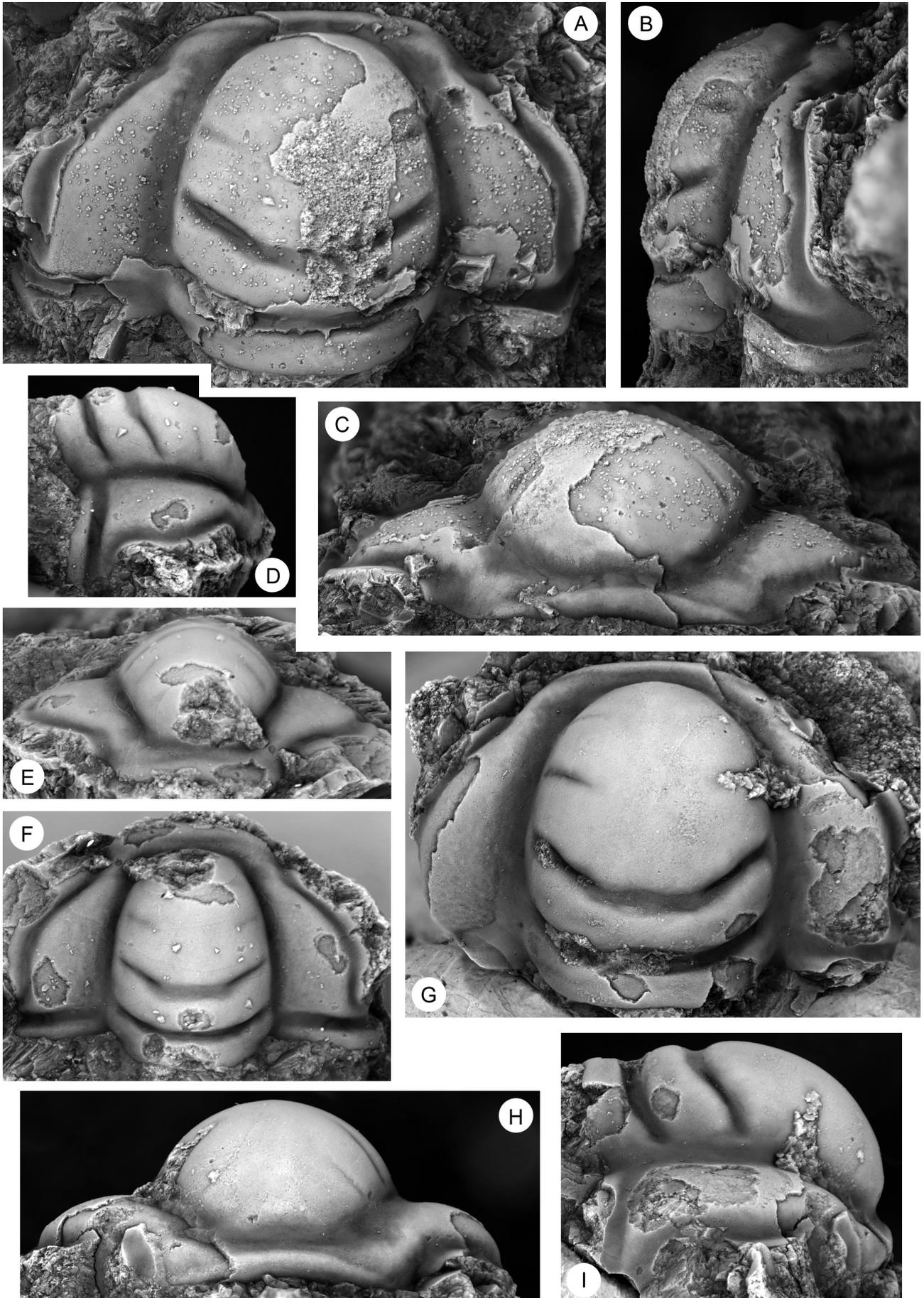
**Discussion.** Gaines (1951) used simple bivariate methods to conclude that several species from Texas named by Resser (1942), including *I. media*, were synonyms of *I. major*, although he apparently did not examine Walcott's types of the latter. We compared those types of *I. major* to *I. media* earlier in the text and, at the current state of knowledge, we can see no reason to suppose that they record a single species. Wilson (1951) independently suggested synonymy of *I. media* and *I. major*, although both of the cranidia from Pennsylvania that he (Wilson 1951, pl. 93, figs. 21–23) illustrated under the latter name possess very short frontal areas that lack the distinct borders evident in type and other material of the former. These cranidia record an indeterminate species of *Irvingella*, and the pygidium (Wilson 1951, pl. 93, fig. 14) is probably misassigned.

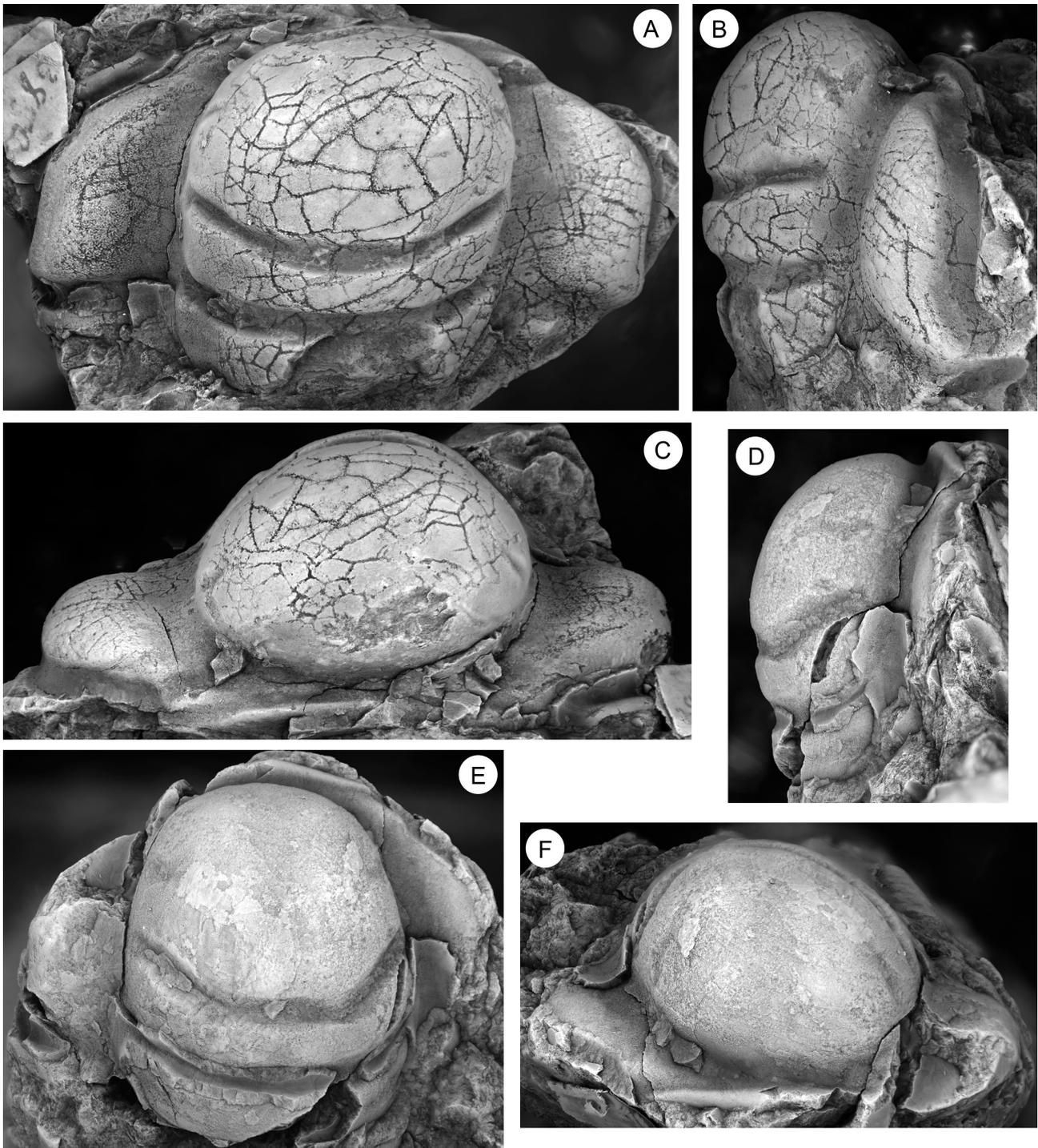
Palmer (1965, p. 48) listed both *I. media* and *I. deckeri* as synonyms of *I. major*. Available cranidia of the former two species overlap in size (compare Fig. 15 with Figs 16A, 17A, G), and differ clearly in the relative width of the fixigenae and in the morphology of the frontal area. *Irvingella media* has a wider fixigena (equal to slightly more than half of glabellar width at SO, versus about 30% in *I. deckeri*), a longer frontal area with a transverse rather than a gently curved margin, and a very short but distinct preglabellar field. In addition, *I. media* has a strongly tapered glabella, whereas *I. deckeri* is gently tapered. That they represent separate species is, in our view, unequivocal; in a preliminary morphometric analysis of sclerites from our collections, using both bivariate and landmark-based methods, Barker (2012) concluded that there were two cranidial morphotypes in the *I. major* Zone of Oklahoma, and assigned one of them to *I. media*. Pygidia assigned by Wilson (1949, pl. 10, fig. 7, pl. 11, fig. 17) to *I. media* are subtrapezoidal in outline with relatively narrow pleural fields and short axes.

Topotype cranidia of *I. suecica* Westergård 1947 from the Alum Shale Formation, Karbåken, Ångermanland, Sweden, illustrated by Rushton & Weidner (2010, fig. 8), resemble *I. media* in possessing a transverse anterior margin with a weak anterior border. Larger cranidia figured by Westergård (1947, pl. 3, figs 1–3, 5, 6) have more strongly rounded palpebral lobes that are also shorter



**Figure 16.** *Irvingella media* Resser 1942, Morgan Creek Member, Wilberns Formation, central Texas; A–C from Cold Creek, San Saba County (USNM loc. 14b), and D–I from Baldy Mountain, Burnet County (USNM loc. 70). All cranidia. A–C, USNM 108663 (paratype), dorsal, lateral and anterior view, x12 (illustrated previously by Resser 1942, pl. 3, figs 52–54); D–F, USNM 108662b (paratype), lateral, dorsal and anterior views, x14 (illustrated previously by Resser 1942, pl. 3, figs 49–51); G–I, USNM 108662a (holotype), lateral, dorsal and anterior views, x14 (illustrated previously by Resser 1942, pl. 3, figs 46–48).





**Figure 18.** *Irvingella tumifrons* (Hall & Whitfield 1877) from the Dunderberg Formation, Pogonip Ridge, White Pine County, Nevada. All cranidia. **A–C**, USNM 24561 (lectotype), dorsal, lateral and anterior views x3.5 (illustrated previously with Resser 1942, pl. 4, figs 42, 43); **D–F**, USNM 619739, lateral, dorsal and anterior views, x4 (not illustrated previously).

(exsag.), extending back only slightly beyond the level of S1. Unfortunately, other sclerites are unknown (we agree with Rushton & Weidner 2010, p. 198 [in synonymy] that the pygidium attributed to *I. suecica* by Westergård 1947, pl. 3, fig. 4 is misassigned) for both species, limiting further comparisons.

As revised by Rushton (1967), *I. nuneatonensis* (Sharman 1886) shares the transverse anterior cranial margin and tapered glabella of *I. media*. It differs from the latter in having well incised S2 furrows and relatively narrower fixigenae.

**Figure 17.** *Irvingella media* Resser 1942, Honey Creek Formation, Dotson Ranch, Murray County, Oklahoma, collection DR 12.2. All cranidia. **A–C**, OU 237910, dorsal, lateral and anterior views, x8; **D–F**, OU 237911, lateral, anterior and dorsal views, x15; **G–I**, OU 237912, dorsal, anterior and lateral views, x9.

**Irvingella tumifrons** (Hall & Whitfield 1877) (Fig. 18)

1877 *Chariocephalus tumifrons*; Hall & Whitfield, p. 224, pl. 2, figs 38, 39.

1938 *Irvingella* (*Irvingellina*) *tumifrons* (Hall & Whitfield); Kobayashi, p. 175.

1942 *Irvingella tumifrons* (Hall & Whitfield); Resser, p. 25, pl. 4, figs 42, 43 [see for synonymy].

1950 *Parairvingella angustifimbriata* Kobayashi; Stubblefield, p. 350.

1960 *Irvingella* (*Parairvingella*) *tumifrons* (Walcott); Černyševa, p. 129.

non 1962 *Irvingella tumifrons* (Hall & Whitfield); Ivshin, p. 52, pl. 3, figs 1–4., text-fig. 11 (= *I. sp. indet.*)

1965 *Irvingella* (*Parairvingella*) *tumifrons* (Walcott); Grant, p. 127.

1992 *Irvingella angustilimbata* Kobayashi; Peng, p. 56.

1992 *Irvingella angustilimbata* Kobayashi; Pratt, p. 49.

2003 probably *Irvingella major* Ulrich & Resser; Hong *et al.*, p. 196.

**Lectotype.** A cranium (USNM 24561; selected here) from the Dunderberg Formation, Pogonip Ridge, White Pine County, Nevada (Fig. 18A–C).

**Occurrence.** Dunderberg Formation, Pogonip Ridge, White Pine County, Nevada

**Discussion.** There are two cranidia in the type lot (Fig. 18) of *Irvingella tumifrons*, and the most complete specimen, which was figured by Hall & Whitfield (1877, pl. 2, figs 38, 39), is selected as the lectotype. Palmer (1965) suggested that *I. tumifrons* might be a synonym of *I. major*, but both cranidia have a distinct anterior border and very short preglabellar field, and more likely represent a distinct species; at the current state of knowledge it is, however, best treated as a *nomen dubium*. The glabella of the lectotype (Fig. 18A–C) overhangs the anterior border, but this is not the case in the other, slightly smaller specimen (Fig. 18D–F), and may be the product of minor deformation.

Ivshin (1962) identified *I. tumifrons* from Upper Cambrian of central Kazakhstan. The two cranidia that he illustrated (Ivshin 1962, pl. 3, figs. 1–4) have conspicuous, convex glabellae that resemble those of the types of Hall & Whitfield (Fig. 18), but they lack anterior borders on the frontal areas and represent an indeterminate species of *Irvingella*.

**Irvingella orrensis sp. nov.** (Figs 19–23, 24B, C, E, I–T)

1976 *Irvingella flohri?* Resser; Hintze & Palmer, p. G21.

**Diagnosis.** Cranium with curved anterior margin. Frontal area with faint anterior border furrow; longest on small cranidia (e.g., Fig. 21), but becomes much shorter on larger specimens (e.g., Fig. 19A, C, F). Glabella gently tapered, with truncate to bluntly rounded anterior margin; S1 firmly impressed, but faint S2 and S3 furrows seldom expressed (e.g., Figs 19B, G, 21B). Palpebral lobe long, equal to almost entire preoccipital glabellar length; anterior tips separated by distance roughly equal to glabellar width at SO. Palpebral area of fixigena broad in larger individuals (e.g. Fig. 19A, B), equal to half of glabellar width at SO (50%; 47–54), but is somewhat wider in smaller cranidia, about 59% (55–66) of glabellar width at SO (e.g., Fig. 21B, H, S); in anterior view, slopes evenly down from axial furrow to palpebral furrow, with little change in slope from flanks of glabella.

**Holotype.** A cranium (SUI 142056; Fig. 19A, C, F, H, K) from the Corset Spring Shale Member, Orr Formation, Orr Ridge, Eureka District, Millard County, Utah.

**Occurrence.** Corset Spring Shale Member, Orr Formation, Orr Ridge, Eureka District, Millard County, Utah, collections ORR 19T, ORR 25T, ORR 26.2.

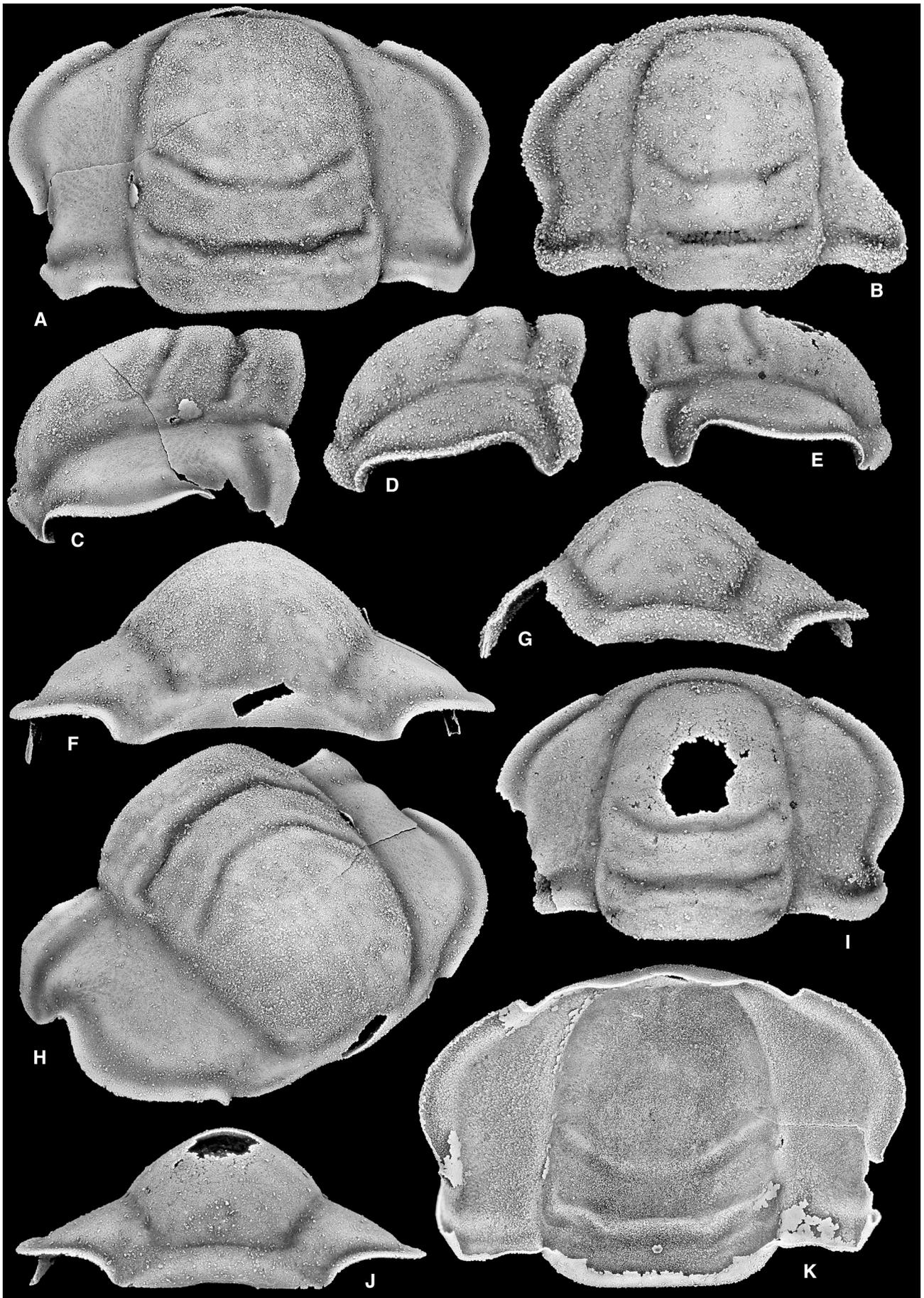
**Name.** From Orr Ridge.

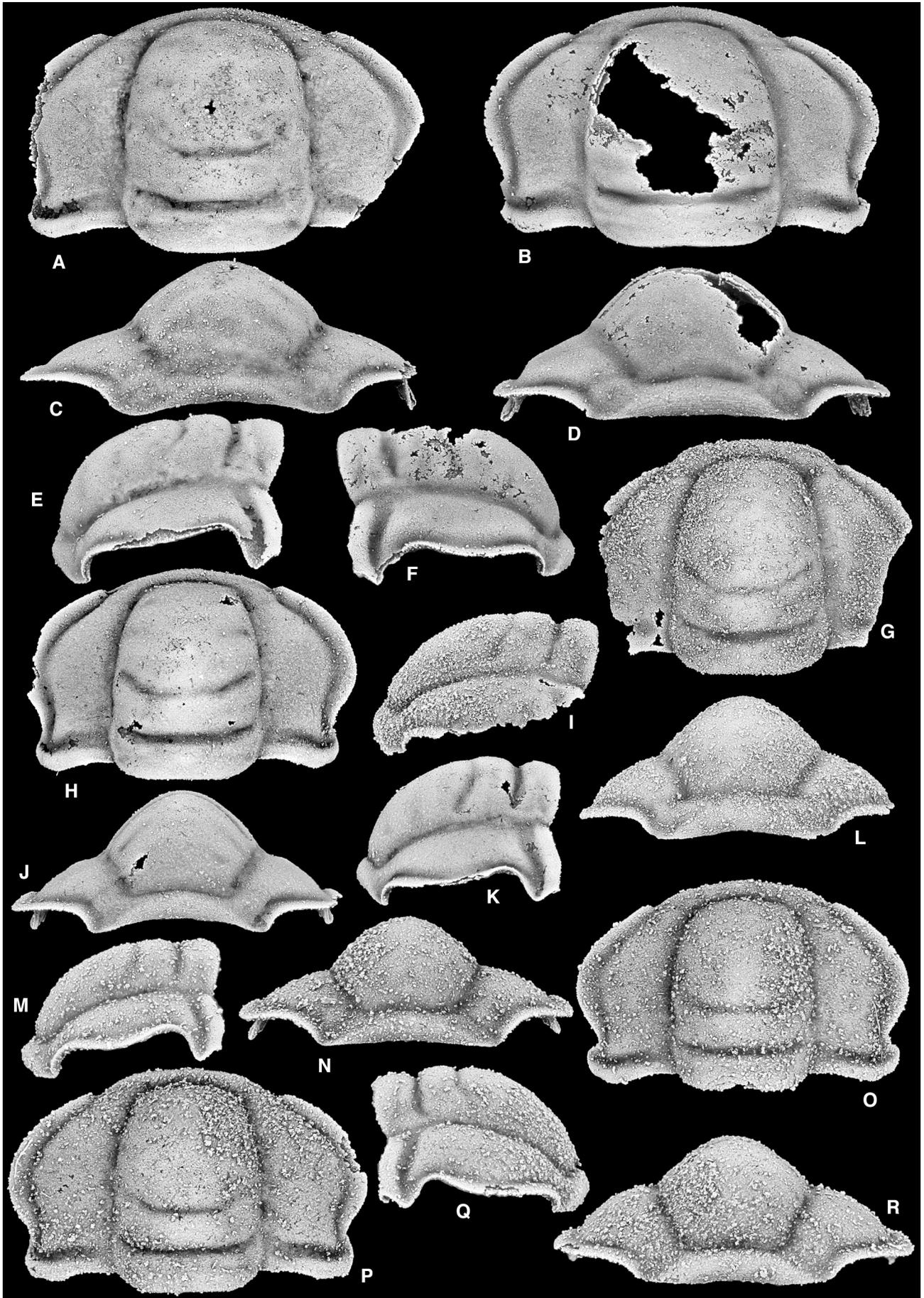
**Description.** Cranium subsemielliptical in outline, length equal to about 92% (89–98; highest values in largest specimens) of maximum width between palpebral furrows, with curved anterior margin; strongly convex with glabella standing well above fixigenae; anterior arch weak (Fig. 20C) to absent (Fig. 20D). Long, broad glabella outlined by shallow axial and preglabellar furrows, accounts for about 92% (89–98; highest values in largest specimens) of cranial length and about half (51%; 46–59; highest values in larger specimens) of maximum cranial width between palpebral furrows; gently tapered, with width at S2 equal to 90% (86–97; lowest values in largest specimens) width at SO; anterior margin truncate to bluntly rounded; lateral profile flexed downward in front of S1. SO deep, evenly curved backward on smaller cranidia (Fig. 21), becoming more transverse medially in larger individuals (Fig. 19); LO accounts for slightly less than one-fifth (18%; 16–20) of glabellar length. S1 well defined, parallel to SO, with neither furrow reaching axial furrow, changing from evenly

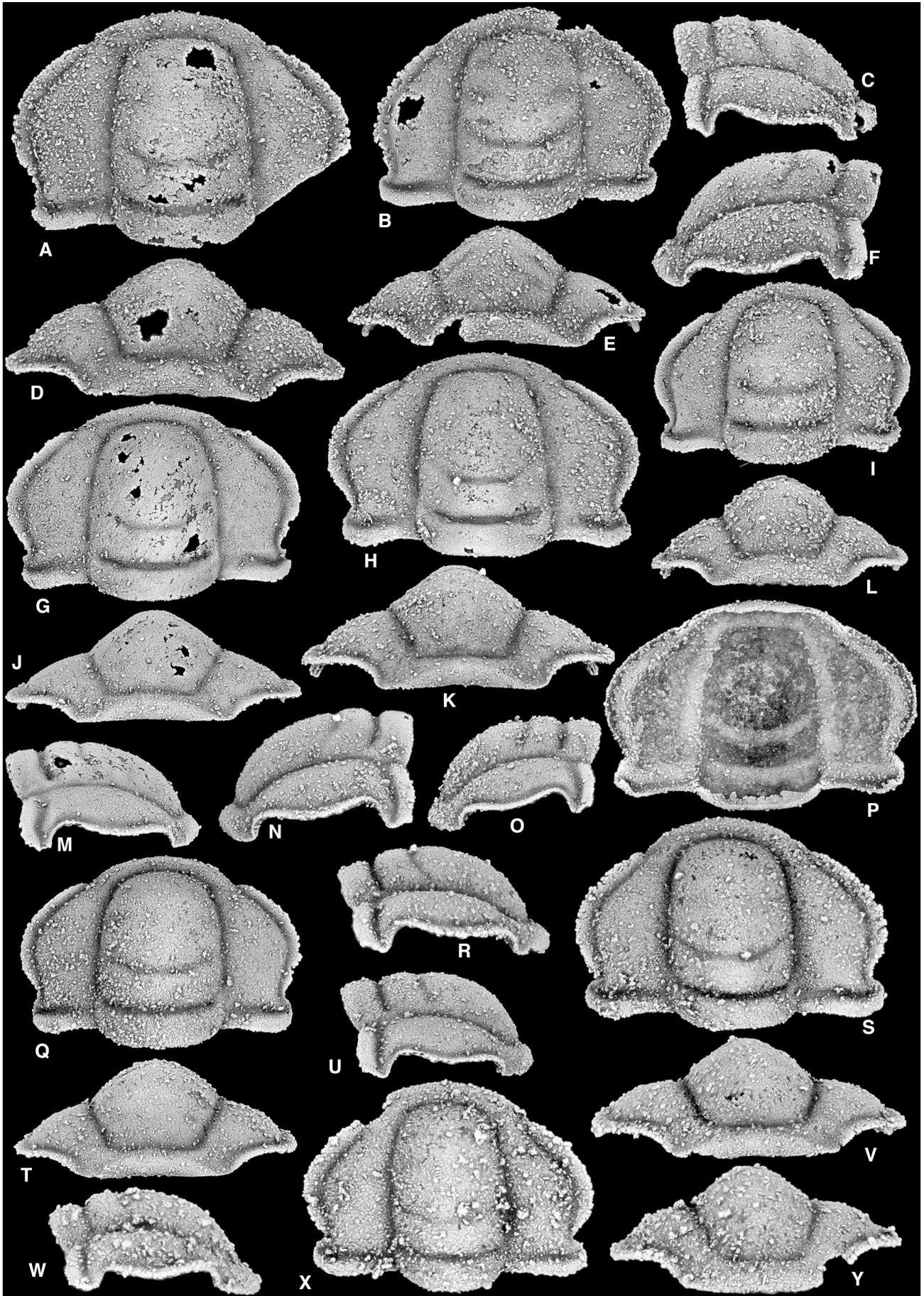
**Figure 19** (*opposite*). *Irvingella orrensis* sp. nov., Orr Formation, Orr Ridge, Eureka District, Millard County, Utah; all are from horizon ORR 25T. **A, C, F, H, K**, holotype cranium, SUI 142056, dorsal, left lateral, anterior, oblique, and ventral views, x7.5; **B, D, G**, cranium, SUI 142057, dorsal, left lateral, and anterior views, x12; **E, I, J**, cranium, SUI 142058, right lateral, dorsal, and anterior views, x12.

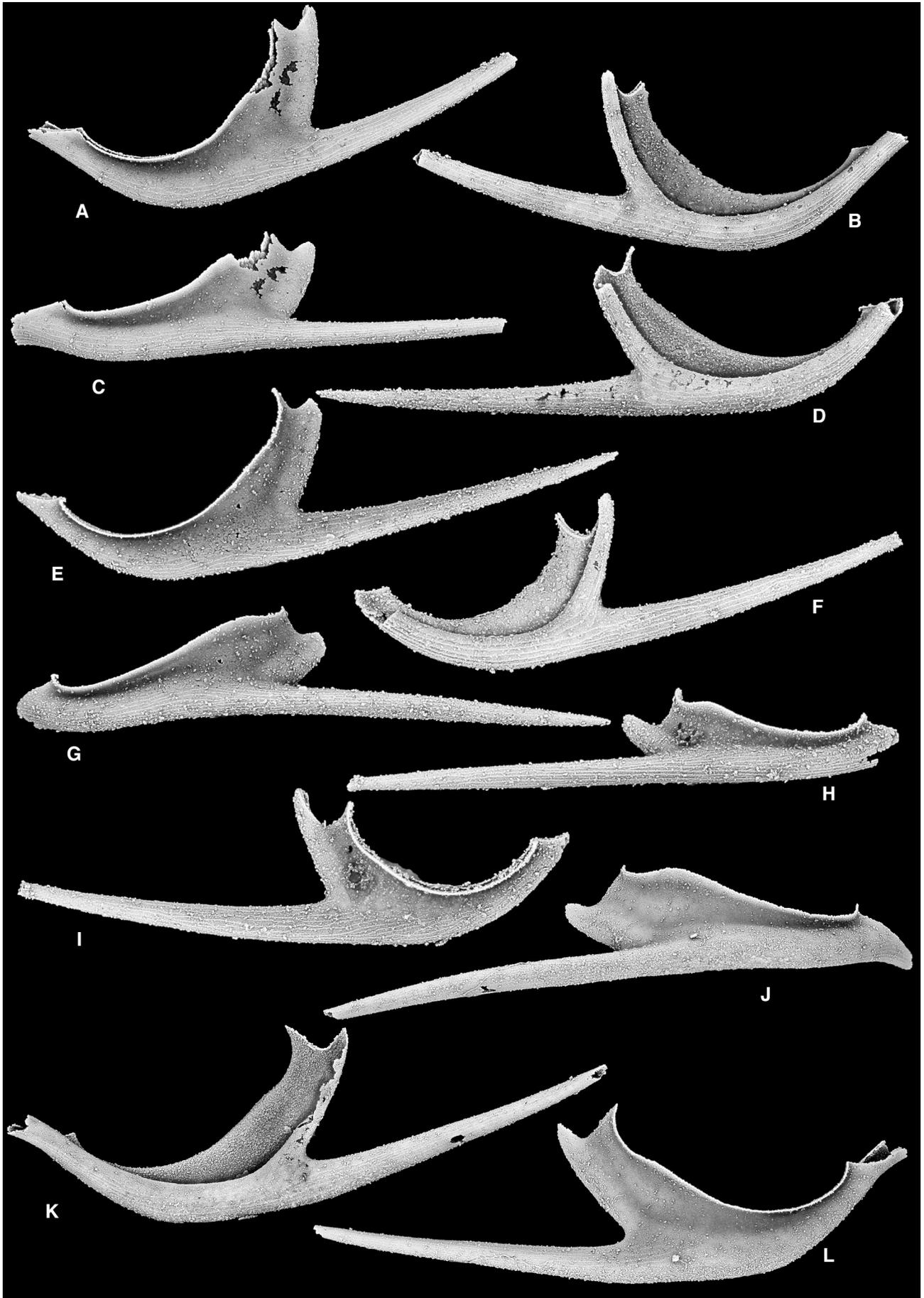
**Figure 20** (*overleaf*). *Irvingella orrensis* sp. nov., Orr Formation, Orr Ridge, Eureka District, Millard County, Utah. **A, C, E**, cranium, SUI 142059, dorsal, anterior, and left lateral views, x12 (ORR 25T); **B, D, F**, cranium, SUI 142060, dorsal, anterior, and right lateral views, x12 (ORR 25T); **G, I, L**, cranium, SUI 142061, dorsal, left lateral, and anterior views, x10 (ORR 19T); **H, J, K**, cranium, SUI 142062, dorsal, anterior, and left lateral views, x12 (ORR 25T); **M–O**, cranium, SUI 142063, left lateral, anterior, and dorsal views, x15 (ORR 25T); **P–R**, cranium, SUI 142064, dorsal, right lateral, and anterior views x15 (ORR 19T).

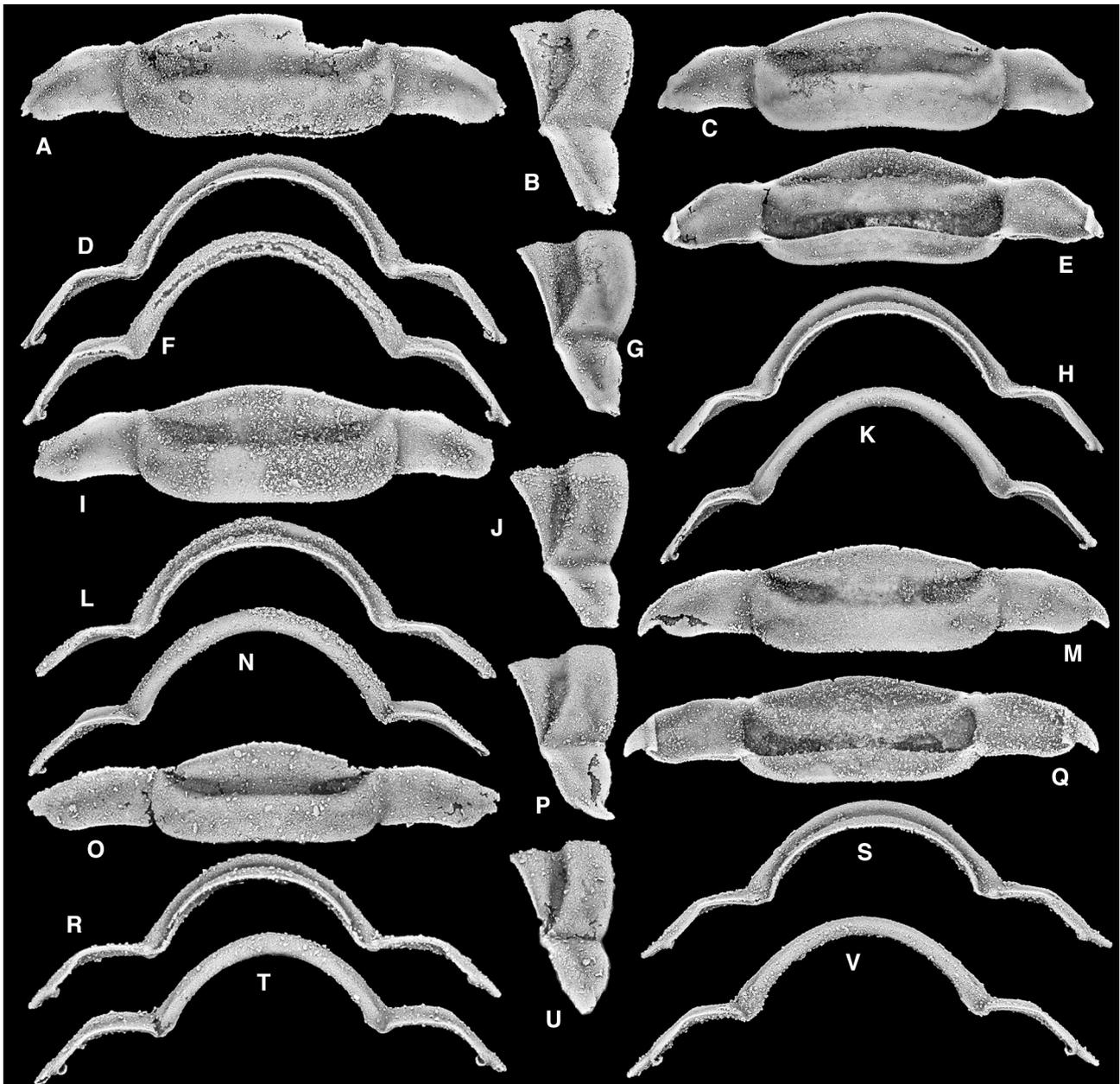
**Figure 21** (*page 425*). *Irvingella orrensis* sp. nov., Orr Formation, Orr Ridge, Eureka District, Millard County, Utah. **A, D, F**, cranium, SUI 142065, dorsal, anterior, and left lateral views, x15 (ORR 19T); **B, C, E**, cranium, SUI 142066, dorsal, right lateral, and anterior views, x15 (ORR 19T); **G, J, M**, cranium, SUI 142067, dorsal, anterior, and right lateral views, x15 (ORR 25T); **H, K, N, P**, cranium, SUI 142068, dorsal, anterior, left lateral, and ventral views, x15 (ORR 25T); **I, L, O**, cranium, SUI 142069, dorsal, anterior, and left lateral views, x15 (ORR 19T); **Q, T, U**, cranium, SUI 142070, dorsal, anterior, and right lateral views, x15 (ORR 25T); **R, S, V**, cranium, SUI 142071, right lateral, dorsal, and anterior views, x20 (ORR 25T); **W–Y**, cranium, SUI 142072, right lateral, dorsal, and anterior views, x30 (ORR 25T).











**Figure 23.** *Irvingella orrensis* sp. nov., Orr Formation, Orr Ridge, Eureka District, Millard County, Utah. All are from horizon ORR 19T. **A, B, D, F**, thoracic segment, SUI 142077, dorsal, left lateral, anterior, and posterior views, x7.5; **C, E, G, H, K**, thoracic segment, SUI 142078, dorsal, ventral, left lateral, anterior and posterior views, x7.5; **I, J, L, N**, thoracic segment, SUI 142079, dorsal, left lateral, anterior, and posterior views, x10; **M, P, Q, S, V**, thoracic segment, SUI 142080, dorsal, left lateral, ventral, anterior, and posterior views, x10; **O, R, T, U**, thoracic segment, SUI 142081, dorsal, anterior, posterior, and left lateral views, x15.

curved medially to more transverse during ontogeny; L1 occupies about 23% (19–25) of glabellar length (exsag.). S2 and S3 obsolete on all but a few small (e.g. Fig. 21B) and occasional larger (Fig. 19B, G) cranidia; where recognisable, L2 equal to about 20% (19–22) of glabellar length. Frontal area without preglabellar field, occupying about 10% of cranial length in smaller specimens (e.g., Fig. 20I, S, X), but decreases to less than 5% during ontogeny (e.g., Fig. 19A, B). Palpebral lobe long, evenly curved, flat band depressed below level of palpebral area

of fixigena; extends from mid-point of L1 to just short of anterior end of glabella and with anterior and posterior tips curved downward. Palpebral furrow well defined albeit shallow groove of even width (tr.). Palpebral area equal to 55% (47–66; values near 50% in larger specimens) of glabellar width at SO; flexed downward in lateral view from axial furrow to palpebral furrow, with little change in slope between it and glabella (e.g. Fig. 19F, G, J). Anterior branches of facial suture curve gently inward along anterior cranial margin; posterior branches initially divergent

**Figure 22** (opposite). *Irvingella orrensis* sp. nov., Orr Formation, Orr Ridge, Eureka District, Millard County, Utah. **A–C**, left librigena, SUI 142073, external, internal, and dorsolateral views, x10 (ORR 19T); **D, E, G**, left librigena, SUI 142074, internal, external, and dorsolateral views, x12 (ORR 19T); **F, H, I**, right librigena, SUI 142075, internal, dorsolateral, and external views, x15 (ORR 25T); **J–L**, right librigena, SUI 142076, dorsolateral, internal, and external views, x7.5 (ORR 25T).



before curving inward to posterior margin. Posterolateral projection short (exsag., tr.) and directed almost vertically downward. Posterior border furrow well incised groove; posterior border longer, convex band. External surface of cranidium smooth.

Librigena with weakly convex lateral border separated from librigenal field by faint border furrow and disappearance of terrace ridges; extended into long, evenly tapered genal spine. Posterior border also weakly convex; posterior border furrow shallow. Librigenal field barely expressed anteriorly, widens backward but remains narrower than lateral border; eye socle low; socle furrow barely perceptible. Doublure convex, extends inward as far as border furrows. Doublure, lateral border and genal spine with sculpture of terrace ridges; remainder of surface smooth.

Convex hypostome roughly oval in outline with stout triangular anterior wing and slender, pointed posterior wing. Median body with long, subelliptical anterior lobe and u-shaped posterior lobe; middle furrow well incised abaxially, but disappears abruptly medially. Lateral border furrows firmly impressed; posterior border furrow shallower. Lateral borders convex, maintaining nearly even width; posterior border narrows to very short rim. Doublure extends inward as far as lateral and posterior border furrows. Borders and wings with sculpture of terrace ridges; remainder of surface smooth.

Thoracic segments with narrow pleurae; likely from anterior part of thorax (e.g. Rushton 1967, pl. 52, figs 10a, 11). Axis strongly convex, occupies more than half of segment, with deeply incised articulating furrow and semielliptical articulating half-ring; some segments with low triangular inflations on axis at axial furrows (e.g., Fig. 23C). Axial doublure extends forward as far as level of posterior end of pleura. Pleura with short, flat inner portion, but flexed steeply downward at fulcrum. Shallow pleural furrow widest at axial furrow, narrows abaxially. Anterior and posterior pleural bands weakly convex, subequal in length; anterior band extended into short pleural spine floored by doublure.

Pygidium semielliptical in outline, length about 40% of maximum width, with distinct arch in posterior view. Axial furrows shallow. Axis raised well above pleural field, gently tapered posteriorly, and well rounded posteriorly; accounts for about 90 % of pygidial length and 40% of pygidial width at first axial ring. Axis with one well incised, transverse axial ring furrow and single axial ring in front of terminal piece of at least two segments. Terminal piece with weak, incomplete furrow, and occupies about half of axis length (including articulating half-ring). Articulating furrow deep, transverse; articulating half-ring transversely subelliptical in outline, accounts for about 15% of axis length. Pleural field narrows backward, gently inflated near axis but curves down distally, with diffuse border furrow so that narrow border separated largely by change in slope. Doublure narrow, convex, with inner edge coincident with border furrow.

**Discussion.** *Irvingella orrensis* sp. nov. is very similar

to *I. flohri* in glabellar outline, but differs clearly in the reduction of the frontal area during holaspide ontogeny. In the largest cranidium of the former (Fig. 19A–H), the frontal area is vestigial, but is well developed in similarly sized specimens of *I. flohri* (e.g., Fig. 9A–C). In anterior view, the palpebral area of the fixigena shows little change in slope from the flanks of the glabella and descends more or less evenly to the palpebral lobe (e.g., Figs 19F, G, J). In contrast, the palpebral area of *I. flohri* is more inflated and nearly flat at the axial furrow, but curves steeply downward abaxially; consequently, there is a sharp change in slope between the flanks of the glabella and the palpebral area in anterior view (e.g., Figs 9A–C, 10A–C).

In equivalently sized, large cranidia, *I. angustilimbata* (e.g., Figs 2A, 3A, 5A), *I. tropica* (e.g., Figs 11A, H) and *I. media* (Figs 17A, G) have longer frontal areas that retain distinct preglabellar fields. *Irvingella deckeri* has a frontal area that is equivalent in length to that of *I. orrensis* sp. nov. (e.g., Fig. 15A, G), but is separated by several character states, including a glabella that is well rounded anteriorly, and a much narrower palpebral area of the fixigena that is equal to only about 30% of glabellar width at SO.

Assignment of the hypostome is based on comparison with complete exoskeletons of *Irvingella* illustrated by Chatterton & Ludvigsen (1998, fig. 26.7, 26.8, 26.10). Although these specimens are flattened, they show that the hypostome has a short posterior lobe of the median body, and a border that narrows abruptly along the posterior margin; the same characters are present in our specimens (Fig. 24K–T).

Only two pygidia that are potentially assignable to *I. orrensis* were recovered from the silicified samples. The smaller of the two (Fig. 24B, C, E, I, J) is comparable to the pygidium assigned to *I. flohri* by Palmer (Fig. 9J–K), differing in having lateral margins that converge more abruptly backwards, and it is tentatively assigned to *I. orrensis*. The larger pygidium (Fig. 24A, D, F–H) is relatively longer and narrower than the smaller specimen, with length equal to about 60%, rather than about 40%, of maximum width, and is more rounded posteriorly with a less pronounced median arch. It also has a broader border and a distinct, albeit shallow border furrow; an additional segment may be incorporated into the terminal piece. This variation is beyond interpretation with the available sample. It could perhaps represent ontogenetic differences, but could equally well record the presence of a second species. We assign it here to *I. sp. indet.*

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**Figure 24.** *Irvingella* spp., Orr Formation, Orr Ridge, Eureka District, Millard County, Utah. **A, D, F–H, *Irvingella sp. indet.***, pygidium, SUI 142085, dorsal, ventral, left lateral, posterior, and anterior views x10 (ORR 25T). **B, C, E, I–T, *Irvingella orrensis* sp. nov.**, B, C, E, I, J, pygidium, SUI 142082, dorsal, right lateral, posterior, ventral, and anterior views, x20 (ORR 25T); K, L, N, P, R, hypostome, SUI 142083, ventral, dorsal, right lateral, posterior, and anterior views, x10 (ORR 19T); M, O, Q, S, T, hypostome, SUI 142084, ventral, right lateral, posterior, anterior, and dorsal views, x10 (ORR 19T).

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