



The Marjuman trilobite *Cedarina* Lochman: thoracic morphology, systematics, and new species from western Utah and eastern Nevada, USA

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Abstract

Cedarina schachtii n. sp. from the Marjuman (*Cedaria* Zone) Weeks Formation of western Utah, USA, provides the first information on thoracic morphology within the genus. Its thorax is radically different from those of species of *Cedaria* Walcott, with which *Cedarina* Lochman has been classified in Cedariidae Raymond, but strikingly similar to those of plesiomorphic remopleuridoideans grouped in the paraphyletic Richardsonellinae Raymond. If *Cedarina* and the remopleuridoideans are genuinely related it follows that 1) Cedariidae as traditionally conceived is paraphyletic; 2) *Cedarina* is a plesiomorphic sister taxon of the remopleuridoideans; and 3) the remopleuridoideans are not a component of the Order Asaphida. Silicified material of a second new species, *C. clevensis* from the Marjuman (*Crepiccephalus* Zone) Lincoln Peak Formation of eastern Nevada, confirms the presence of a long thoracic axial spine and provides the first information on ontogenetic development and ventral morphology within the genus.

Key words: Trilobita, Cedariidae, Remopleuridoidea, *Cedarina*, taxonomy, Cambrian

Introduction

Cedariidae Raymond, 1937, has been understood as a mainly Laurentian clade which is common in rocks of the upper Marjuman Stage. The main morphological feature used to define the group has been a "cedariform" facial suture, in which the posterior section of the facial suture curves forward toward the librigenal field, giving the posterior fixigenal projection a lobe-like appearance and with the librigenal field concomitantly reduced in length and separated from the base of the genal spine. This is an unusual morphology in trilobites, seen elsewhere only in the unrelated Ordovician-Devonian family Scharyiidae Osmólska, 1957, and there is every reason to suspect that it is a synapomorphy of a clade including the "cedariids."

New information presented herein, however, challenges the monophyly of Cedariidae. A new species of *Cedarina* Lochman, 1940, from the Weeks Formation of western Utah, reveals the first known thorax for the genus. *Cedarina* has universally been considered a cedariid, but its thoracic morphology is strikingly different from other members of the group, and very similar to that of plesiomorphic members of Remopleurididae Hawle and Corda, 1847. The goals of the present work are the description of *C. schachtii* and discussion of its potential implications for trilobite systematics. Additional morphological information is provided by rare but well preserved silicified sclerites from the Lincoln Peak Formation of eastern Nevada, described below as *C. clevensis* n. sp.

Localities and Stratigraphy

Weeks Formation. The material described herein as *Cedarina schachti* n. sp. was collected from the Weeks Formation in the central House Range, Millard County, western Utah (Figs. 1B, 2). The Weeks Formation and other Cambrian units in the House Range (especially the Wheeler Formation) are famous for their articulated trilobite specimens. The fauna of the Weeks Formation has received little modern study, and the only extensive published systematic descriptions of its species remain those of Walcott (1916a, 1916b). Material from the Weeks Formation is potentially very important, as specimens are typically preserved partially or completely articulated, revealing information on thoracic morphology and exoskeletal dimensions that has rarely been documented for many clades of Cambrian trilobites.

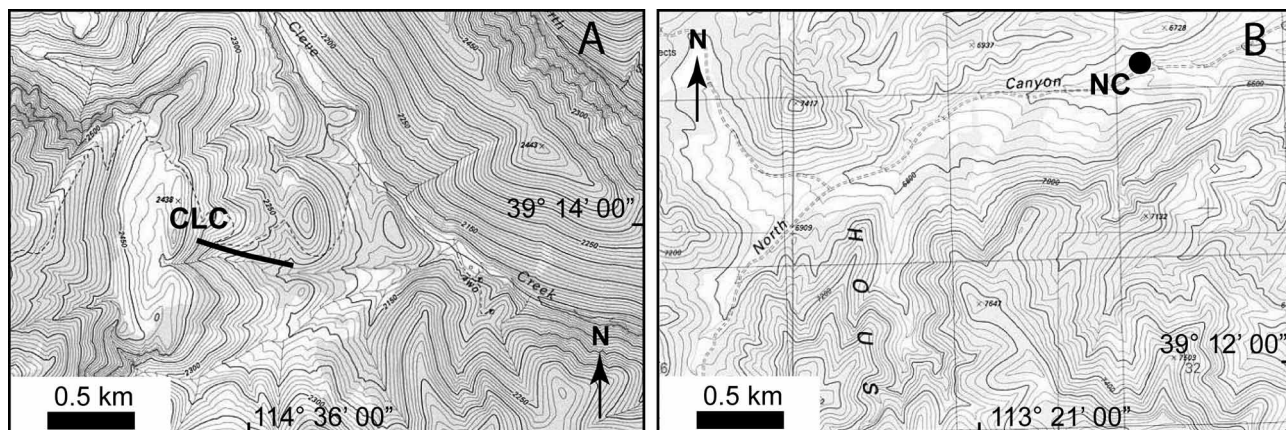


FIGURE 1. A. Line of Section CLC, near Cleve Creek, northern Schell Creek Range, White Pine County, eastern Nevada, USA. See Figure 2 for stratigraphic units and index map and Figure 3 for stratigraphic log of collecting interval in the Lincoln Peak Formation. B. Position of Weeks Formation collecting locality in North Canyon, central House Range, Millard County, western Utah. See Figure 2 for stratigraphy and index map.

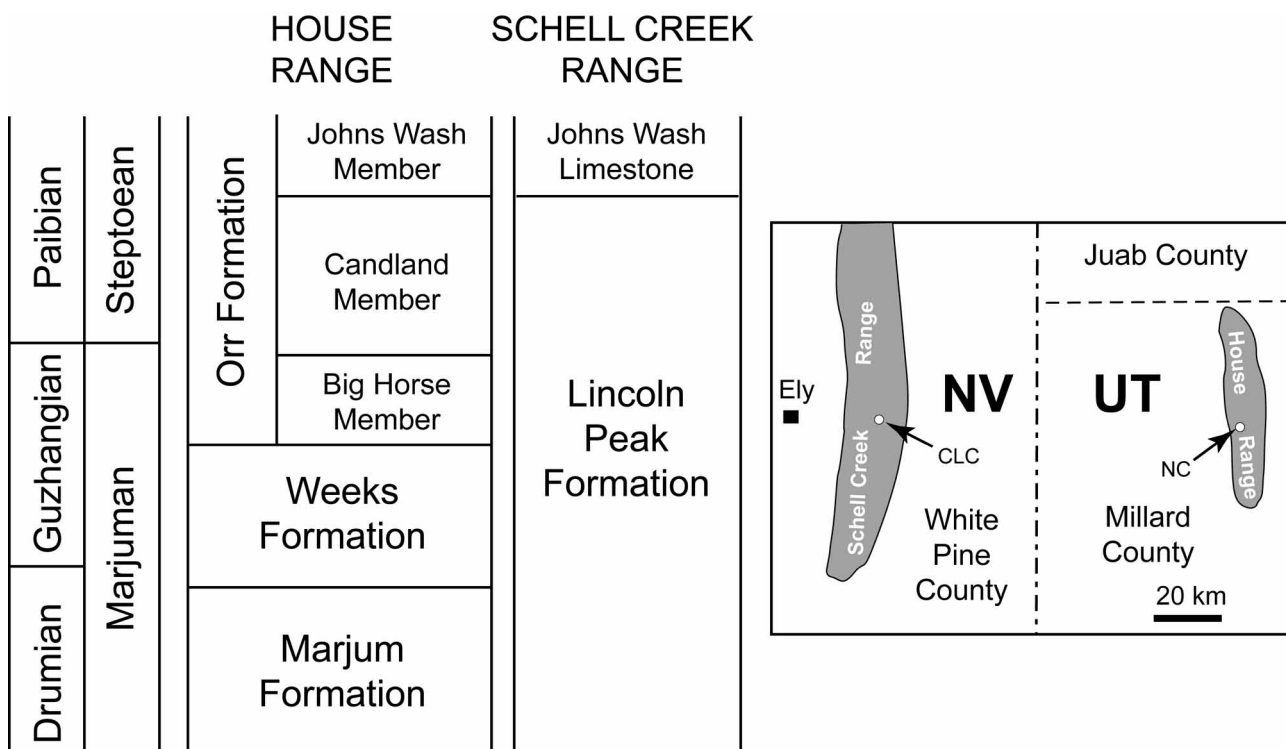


FIGURE 2. Stratigraphy and geographic position of localities from which material is described.

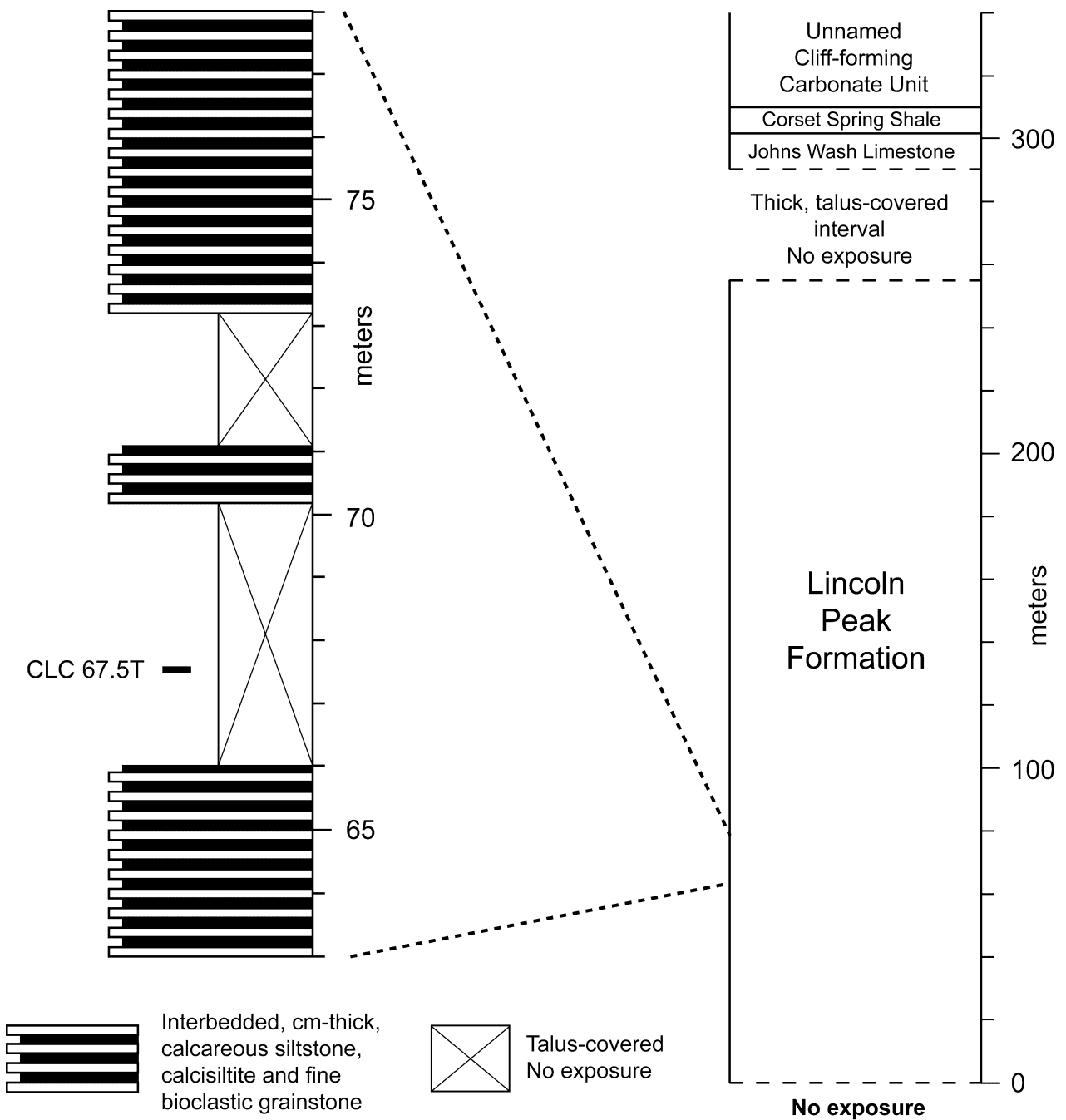


FIGURE 3. General stratigraphic succession (right) and detail of collecting interval (left) in the Lincoln Peak Formation near Cleve Creek (see Figure 1 for line of section and Figure 2 for index map).

The history of study and stratigraphy of the Weeks Formation has been summarized by Hintze (in Hintze and Davis, 2003). The unit is restricted to the limited geographic area of the House Range embayment (Rees, 1986), characterized by Hintze and Davis (2003, pp. 58–59) as "a paleotrough of Middle and Late Cambrian time where the seaway was slightly deeper than on adjacent shallow shelves." The formation is over 300 m thick and is entirely Marjuman in age (*sensu* Ludvigsen and Westrop, 1985, and Sundberg, 2005, not the greatly expanded concept of Palmer, 1998). The lower part of the formation contains faunas of the *Eldoradia* Zone, whereas the upper part, which yielded the articulated specimens described herein, contains *Cedaria* Zone assemblages. The Weeks Formation overlies the Marjum Formation and is itself overlain by the Orr Formation, the basal Big Horse Member of which also contains *Cedaria* Zone faunas as well as uppermost Marjuman *Crepicephalus* Zone trilobites.

Upper Weeks Formation trilobites are typically preserved articulated on bedding planes. Trilobites are by far the most common faunal elements, but abundant phosphatic brachiopods also occur, along with rare aglaspidid arthropods, echinoderms, and other groups. The trilobites are partially to wholly silicified, but silicification tends to be weak and the specimens disintegrate when the limestone is digested in dilute acid. Because the specimens are considerably harder than the limestone matrix, however, preparation using air abrasive techniques is quite easy. The material tends to be moderately to strongly compacted, but otherwise preservation is very good, with excellent surface detail.

Lincoln Peak Formation. The Lincoln Peak Formation was established by Drewes and Palmer (1957) for a 630+ m succession of shales, siltstones, and thin-bedded limestones representing generally deep subtidal environments. The upper part of the formation includes upper Marjuman faunas of the traditional *Cedaria* and *Crepicephalus* zones, and the uppermost part contains Steptoean faunas up to and including the *Dunderbergia* Zone (Palmer, 1971). The type section is in Lincoln Canyon in the Snake Range. The unit is exposed in the northern Schell Creek Range near Cleve Creek (Figs. 1–3). At this locality, exposure is generally poor and the rocks have been subject to complex local faulting. Nevertheless, thin-bedded calcareous siltstone and calcisiltite yield a succession of exceptionally well preserved silicified trilobite faunas of late Marjuman and Steptoean age. *Cedarina* is a rare component of the upper Marjuman faunas. Several species appear to be present through the section. The material described herein as *C. clevensis* **n. sp.** was derived from two thin-bedded (1–2 cm) limestone float samples collected at 67.5 m and 70.5 m in our section CLC 1. Where exposed, this stratigraphic interval consists of plane laminated calcisiltite and calcareous siltstone with cm-thick interbeds of green shale. Two juvenile cranidia were collected from a third small float sample (CC1) in talus below the base of the exposed section.

Implications of *Cedarina schachtii*

Classification of Remopleurididae. The Superfamily Remopleuridoidea Hawle and Corda, 1847, includes taxa of late Cambrian and Ordovician age. It has traditionally been divided into a Cambrian-Ordovician Family Richardsonellidae Raymond, 1924 (=Kainellidae Ulrich and Resser, 1930; see Ludvigsen and Westrop in Ludvigsen *et al.*, 1989), and an exclusively Ordovician Remopleurididae. Shergold (1980) erected the small subfamily Atratebiinae for three genera, which he regarded as family *incertae sedis* but of dikelocephaloidean affinities. This was followed by Peng (1992), though Dean (2006) assigned *Taishania* Sun, 1935, which had been included in Atratebiinae by Shergold (1980), to Pterocephaliidae Kobayashi, 1935a. Jell (in Jell and Adrain, 2003) assigned the genera grouped as Atratebiinae by Shergold (1980) to Remopleurididae. Shergold (1980, p. 54) characterized the atratebiines as "dikelocephalacean trilobites whose morphology has remopleuridacean aspects."

Affinity of Atratebiinae aside, there has been general agreement on a Remopleuridoidea divided into two families. No modern phylogenetic analysis has been attempted for any component of the group (save for the inclusion of the superfamily itself as a terminal taxon in the early cladistic analysis of Fortey and Chatterton [1988]). The monophyly of the younger and more derived Remopleurididae seems highly likely as it is supported by a suite of characters such as large eyes, loss of the prelabellar field and fixigenal area, a distinctive librigena with a strong genal notch, a general streamlining of the body, and a distinctive pygidial morphology. These features are possibly associated with a nektobenthic life habit (Fortey, 1985, pp. 227–228). Richardsonellidae, however, is almost certainly rendered paraphyletic by traditional Remopleurididae and as such should not be recognized. It is possible that components of traditional Richardsonellidae may prove monophyletic, but this can only be assessed with careful, modern phylogenetic analysis. For these reasons, Jell and Adrain (2003) did not recognize separate families, referring all of the remopleuridoideans to a single Family Remopleurididae, and this course is followed herein.

The Cambrian "richardsonellids" have been further split by the proposal of several smaller family-group taxa which are (apparently) obvious components of the broader group and the recognition of which would

likely create paraphyly. These are: Apatokephalinae Kobayashi, 1953 (which Shergold [1975] advocated classifying with the traditional remopleuridids, as opposed to the richardsonellids/kainellids); Loshanellidae Lu, 1975; and Apatokephalopsidae Zhou and Zhang, 1978. All are regarded here as synonyms of Remopleurididae.

Fortey and Chatterton (1988) also assigned the families Bohemillidae Barrande, 1872, and Opipeuteridae Fortey, 1974, to Remopleuridoidea. Bohemillids have been interpreted as adapted for a pelagic life habit and their morphology is similar to that of other such groups, including derived remopleuridids. Fortey and Owens (1987, pp. 128–129) acknowledged the difficulties in inferring higher relationship of such derived forms, but nevertheless suggested that they were remopleuridoideans, based on the presence of a mid-glabellar lateral bulge, librigenal morphology, very narrow cranial anterior border, and spinose pygidium. The narrow border and librigenal morphology are not similar to plesiomorphic remopleuridids ("richardsonellids"), but rather to highly derived Ordovician forms. Remopleuridids have a thorax of either 12 or 11 segments, with a median axial spine on the eighth. This is true even of the most derived forms such as *Hypodicranotus* Whittington, 1952, (see Ludvigsen and Chatterton, 1991). The thorax of *Fenniops sabulon* (Fortey and Owens, 1987), the only bohemillid species for which thoracic information is available, apparently had only seven segments and lacked a spine (Fortey and Owens, 1987, fig. 23), though no specimens are known with the pygidium articulated, so the segment count remains provisional. If this morphology is confirmed, it is very unlikely that bohemillids are remopleuridoideans. They may be derived cyclopygoidean asaphides.

Opipeuteridae Fortey, 1974, was erected for *Opipeuterella* Fortey, 2005 (*pro Opipeuter* Fortey, 1974, preoccupied). Fortey argued repeatedly (1974, 1975, 1979, 1980) that the taxon is a remopleuridoidean, but Laurie and Shergold (1996) demonstrated that it is ingroup Telephinidae Marek, 1952.

The earliest Laurentian taxa which have been considered remopleuridoideans are of Sunwaptan age, and almost all of the global Cambrian diversity of the family is of Sunwaptan equivalent age. Jell (in Jell and Adrain, 2003) reported that the type species of *Tostonia* Walcott, 1924, *T. iole* (Walcott, 1884), was from the Hamburg Limestone which is of Marjuman age. Jell assigned the genus to Eurekaidae, an otherwise exclusively Sunwaptan taxon. Previous workers (e.g., Wilson, 1954; Shergold, 1972) had considered the genus to be a richardsonelline remopleuridoidean. The specimens assigned to *T. iole* by Walcott (1925, pl. 18, figs. 10–14) are actually from the Sunwaptan Windfall Formation in the Eureka district of Nevada. Walcott's cranidia, one of which is the holotype, are likely conspecific, but they are almost certainly misassociated with his assigned pygidia. The latter represent a species of the remopleuridoidean *Naustia* Ludvigsen, 1982. Abundant silicified material of what is likely the same species has been collected from the Bullwhacker Member of the Windfall Formation at Barton Canyon, Cherry Creek Range, Nevada (J.M.A. and S.R.W., unpublished data).

Morphology of *Cedarina schachtii*. The thoracic morphology of members of Remopleurididae is remarkably stable. Plesiomorphic taxa ("richardsonellines") have a thorax of 12 segments. The segments are of relatively simple morphology, with a prominent transverse pleural furrow. The pleural tips are free, and are turned posteriorly into tapering, blunt pleural spines. All species for which information is available have a single median axial spine located on the eighth segment. Examples include *Pseudokainella keideli* Harrington, 1938 (Harrington and Leanza, 1957, figs. 51, 52.6), *Parakainella lata* (Kobayashi, 1935b) (Harrington and Leanza, 1957, figs. 53, 54.3), *Parakainella pustulosa* Harrington and Leanza (1957, fig. 55), *Apatokephalus exiguus* Harrington and Leanza (1957, figs. 57, 58), *Apatokephalus diggerensis* (Jell, 1985, pl. 25, figs. 10, 11), and *Apatokephalus latilimbatus* Peng (1990, pl. 11, figs. 4, 6). Highly derived Ordovician taxa with an inferred pelagic life habit ("remopleuridines") reduced the number of segments to 11, but retained a median spine on the eighth (e.g., *Remopleurides eximius* Whittington, 1959, pl. 14, and other examples in the same work).

Cedarina has been regarded as a cedariid by all authors who have commented on it since it was proposed (Lochman and Duncan, 1944; Lochman, 1950; Palmer, 1955; Deland and Shaw, 1956; Lochman and Hu, 1962; Rasetti, 1965; Hu, 1971, 1983; Hu and Li, 1971; Pratt, 1992; Stitt, 1998; Jell and Adrain, 2003). Species of *Cedarina* have been known only from cephalic and pygidial data. To this point, however, no information on

the morphology of the thorax has been available. In contrast, the thoracic morphology of species of *Cedaria* Walcott, 1924, is well understood. These species are nearly isopygous, with a thorax of seven segments, none of which bear an axial spine (e.g., *Cedaria minor* [Walcott, 1916b, pl. 61, figs. 3, 3a, 3b], *C. prolifica* Walcott, 1924 [Walcott, 1925, pl. 17, fig. 18; Robison, 1988, fig. 14.14]). The cedariid genus *Carinamala* Palmer, 1962, is presently known only from its type species, *C. longispina* Palmer, 1962. However, J.M.A. and S.R.W. have discovered articulated material of a new species of *Carinamala* from the Lincoln Peak Formation in the Schell Creek Range, eastern Nevada (the same locality as for *Cedaria clevensis* n. sp.), and this taxon, too, is isopygous and has seven thoracic segments. Segments four through seven have axial nodes or short spines, but there is no long median spine. New finds in the Weeks Formation of western Utah provide the first knowledge of the thorax of a member of *Cedarina*. The thorax of *C. schachti* n. sp. is not closely similar to that of *Cedaria* or *Carinamala*, but rather is extremely similar to the plesiomorphic condition of remopleuridids.

The thorax of *C. schachti* has ten segments (Figs 6, 7). The segments have a simple morphology (Fig. 5), featuring a well impressed pleural furrow with a transverse course and distal pleural regions that are tapered into blunt, posteriorly directed pleural spines. The eighth segment bears a long median axial spine. None of the other segments bear any axial nodes or spines. This morphology is all but identical to that seen in the articulated "richardsonellines" cited above. The only difference is that the remopleuridids have two additional thoracic segments posterior to the spine-bearing eighth.

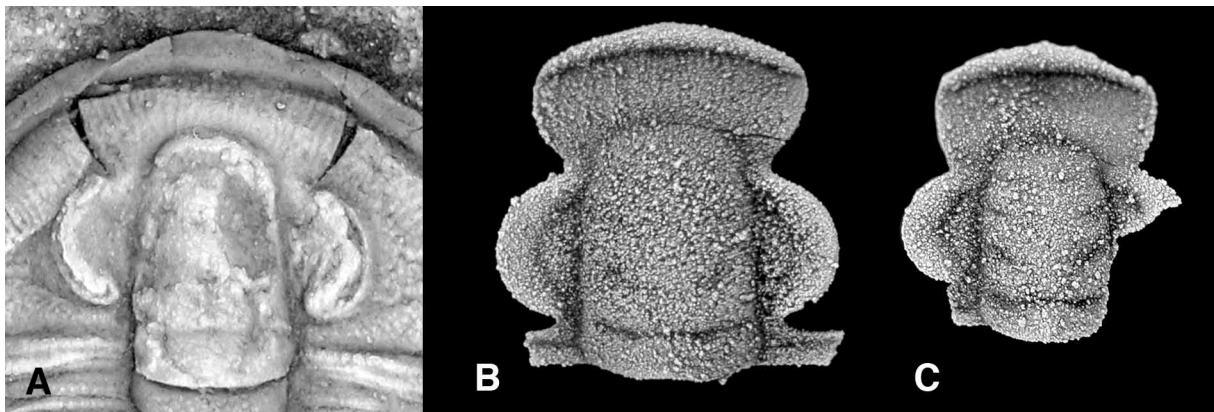


FIGURE 4. Comparison of, A, the cranidium of *Cedarina schachti* n. sp., FMNH PE57116 (see Fig. 5), dorsal view, x12, with, B, C, those of an undescribed species of Sunwaptan "richardsonelline" remopleuridid, *Naustia* n. sp. from the Windfall Formation, Bullwhacker Member, Section CHC 1 219-222T m (see Adrain and Westrop, 2004), Barton Canyon, Cherry Creek Range, White Pine County, Nevada. B, SUI 116034, dorsal view, x15. C, SUI 116035, dorsal view, x20.

Further, the cranidial morphology of *C. schachti* is highly reminiscent of that of the Sunwaptan remopleuridid *Naustia* Ludvigsen, 1982 (Fig. 4). We have discovered silicified material of an undescribed species of *Naustia* from the Windfall Formation in the Cherry Creek Range, eastern Nevada (see Adrain and Westrop, 2004). The silicified specimens record an ontogenetic sequence. Smaller cranidia (Fig. 4B) are extremely similar to holaspid cranidia of *C. schachti* (Fig. 4A) in all cranial dimensions, the presence of radiating caecal trunks on the frontal areas, and the possession of large palpebral lobes with a prominent palpebral furrow. In *C. schachti* the anterior and posterior margins of the palpebral lobe are separated from the glabella by narrow strips of fixigena. The condition in remopleuridids is for the palpebral lobe to abut the glabella anteriorly and posteriorly. However, very small cranidia of *Naustia* have interocular fixigenae in these positions (Fig. 4C), just as in *C. schachti*.

The only significant evolutionary steps required to transform from a *Cedarina* morphology to that of plesiomorphic remopleuridids is the release of an additional two thoracic segments and the loss of the rostral plate and development of a median connective suture. The pygidium of *Naustia* (Ludvigsen, 1982, pl. 64, figs.

Q-S) is not tagmatized, but rather is a fused collection of seven unreleased segments. This contrasts strongly with the reduced number of segments (four or less) typical of remopleuridids. If *Naustia* is a basal member of the clade, it suggests derivation via increased segment generation, which is exactly the mechanism required to transform from the *Cedarina* morphology. The number of thoracic segments in the *Naustia* thorax is unknown, but the rear portion of the pygidium is closely similar to the pygidium of other Sunwaptan richardsonellines such as *Elkanaspis* Ludvigsen (1982, pl. 64, figs H-K). This raises the intriguing and testable possibility that *Naustia* may represent a transitional form with only ten thoracic segments, but with the remaining two segments generated but still incorporated into the holaspid pygidium. Transition from *Naustia* to more typical "richardsonellines" would then require only the release of the anterior two pygidial segments.

A further similarity between cedariids and remopleuridids is that they are two of the groups known to develop prominent pits in the anterior border furrow (see, e.g., *Cedaria prolifica* Walcott - Palmer, 1962, pl. 3, fig. 14). The significance of this pitting has not been fully appreciated and will be dealt with elsewhere, but unpublished evidence suggests that it may be a high level synapomorphy of a broader trilobite group.

The morphological case for a relationship between cedariids and remopleuridids seems very strong. There is, however, a significant gap in the fossil record, spanning the entire Steptoean Stage in Laurentia and equivalents on other paleocontinents, from which no obvious members of the clade are known. The only putative remopleuridid taxon that is older than the equivalent of the Laurentian Sunwaptan Stage is *Oculeus* Poletaeva and Romanenko, 1970, which is known from the Mayan (Marjuman equivalent; *Lejopyge laevigata* Zone) and Sakian (Steptoean equivalent) stages of the Siberian Platform and the Gorny Altay. The status of *Oculeus* as a remopleuridid, however, is dubious. The type species (*O. parvulus* Romanenko in Poletaeva and Romanenko, 1970, pl. 11, figs. 1–5) is known from cranidia and a librigena. The species has extremely large eyes and huge palpebral lobes. The large eye area combined with a narrow frontal region are at least superficially similar to remopleuridids. However, the librigena is very different from that of early remopleuridids, with a very forwardly placed genal spine. It is unclear from the poorly preserved internal molds whether the glabella shows the lateral expansion characteristic (Fortey and Chatterton, 1988, p. 201) of remopleuridids, but deeply incised glabellar furrows are present and in contact with the axial furrow. None of the other assigned species (*O. fidus* Poletaeva in Poletaeva and Romanenko, 1970; *O. parvulus* Egorova in Egorova *et al.*, 1982 [a homonym of the type species]; *O. clivosus* Gogin and Pegel in Pegel and Gogin, 1995) are known from sclerites other than cranidia. Clarification of the affinity of *Oculeus* must await more information, particularly on thoracic and pygidial morphology.

Implications for higher classification. If the hypothesis of relationship outlined above is corroborated, there are two major implications. First, obviously Cedariidae is rendered paraphyletic by Remopleurididae. A likely scenario is that genera of "Cedariidae" become successive sister taxa at the base of the remopleuridoidean tree, with a cedariform suture as a basal apomorphy. *Cedaria* and *Carinamala* may form a clade, depending on whether their shared seven-segment isopygous morphology is apomorphic. They may collectively be sister to *Cedarina*+Remopleurididae.

Second, Remopleurididae have been assigned by Fortey and Chatterton (1988) to a Suborder Asaphina, united with families such as Asaphidae Burmeister, 1843, Nileidae Angelin, 1854, and Ceratopygidae Linnarsson, 1869. These authors considered (Fortey and Chatterton, 1988, text-fig. 1) the key synapomorphy linking remopleuridids to Asaphina to be possession of an "asaphoid protaspis" - a spherical to ovoid larva with an enrolled doublure. Groups with such a larval type underwent metamorphosis after the protaspis period to more adult-like developmental stages.

Fortey and Chatterton's (1988) paper marked one of the first serious attempts to formulate testable and explicit higher level hypotheses of trilobite phylogeny and was a major advance in beginning to unravel the problem of trilobite "cryptogenesis" (Stubblefield, 1959; Whittington, 1981) - the obscure origins and sister group relationships of most post-Cambrian clades. Nevertheless, recent discoveries suggest that remopleuridids are probably not Asaphina, and that similarities of the larvae are probably secondarily acquired.

The examples of asaphoid protaspides in remopleuridids given by Fortey and Chatterton (1988, p. 186, pl. 17, figs. 1–6) were drawn from Whittington's (1959) work on silicified Upper Ordovician species from Virginia. These are some of the latest and most derived members of the group, adults of which were highly specialized for a nektobenthic life habit. Tellingly, Fortey and Chatterton (1988, p. 182) noted that remopleuridids were the exception to a post-larval metamorphosis; unlike true Asaphina, in these most derived taxa the metamorphosis occurs during the meraspid period. As outlined above, these derived pelagic forms did not appear until the Ordovician. The plesiomorphic members of Remopleurididae - the "richardsonellines" - have none of the specialized pelagic adaptations of the taxa whose larvae were figured by Fortey and Chatterton (1988). Obviously, the larval morphology relevant to higher affinity of the family is that of the more basal members of the group.

Recent discoveries indicate that the basal condition for remopleuridid larvae is not asaphoid. Park and Choi (2008) demonstrated that larvae of the Korean Furongian "richardsonelline" *Haniwa sosanensis* Kobayashi, 1933, are flattened, lack an enrolled doublure, and are conventionally adult-like. J.M.A. and S.R.W. have isolated silicified larvae of a Sunwaptan (Furongian) species of *Elkanaspis* from the Windfall Formation in eastern Nevada. These are exceedingly similar to those of *Haniwa*. This suggests, as is typical of other groups, that remopleuridids had a conserved larval morphology shared widely across the group. Further, it appears that the radical morphological changes for a pelagic life habit which took place in Ordovician "remopleuridines" also involved radical changes in the larvae, from an adult-like to an asaphoid form.

Hence, we consider that Remopleurididae is not a component of the Order Asaphida, although we support Fortey and Chatterton's (1988) approach and other general conclusions. Remopleuridids are more compellingly similar to cedariids and other taxa with pits in the anterior border furrow, but full exposition of this case is beyond the scope of the present work.

Systematics

Repositories. Illustrated material is housed in the collections of the Field Museum of Natural History, Chicago (specimen number prefix FMNH), the United States National Museum of Natural History, Smithsonian Institution (prefix USNM), and the Paleontology Repository, Department of Geoscience, University of Iowa (prefix SUI).

Family Cedariidae Raymond, 1937

Discussion. Jell (in Jell and Adrain, 2003) included *Bonneterrina* Lochman, 1936 (= *Holstonia* Resser, 1938; = *Piedmontia* Resser, 1938), *Carinamala* Palmer, 1962, *Cedaria* Walcott, 1924, *Cedarina* Lochman, 1940, *Henadoparia* Öpik, 1967, *Jimachongia* Yuan and Yin, 1998, and *Vernaculina* Lochman and Hu, 1961, in Cedariidae. Of these, *Carinamala*, *Cedaria*, *Cedarina*, and *Vernaculina* are exclusively Laurentian (including reports from the Laurentian-affinity Argentine Precordillera: Borello, 1965; Bordonaro, 2003). *Bonneterrina* is mainly Laurentian, but Siberian (Černyševa, 1960; Rozova, 1964; Egorova *et al.*, 1982) and Uralian (Černyševa, 1968) species have been assigned. The genus is not demonstrably a cedariid. Neither of the two specimens assigned to *B. prima* Lochman, 1936, preserve the posterior projections, and the type of facial sutures present is unknown. The nature of the sutures is also unknown on the other Laurentian species assigned to the genus, none of which are well known. It is far from clear if they are all related to each other or to *B. prima*. The extra-Laurentian species are uniformly poorly known and additional material and better illustrations are required to confirm their status as cedariids. Pegel (2000, fig. 11.3) attributed a Siberian cranidium to *Bonneterrina*, but it lacks a cedariform suture. *Henadoparia* and *Jimachongia* are monotypic. *Henadoparia* is from the Mindyallan (Marjuman equivalent) of Australia, while *Jimachongia* is from strata of similar age in South China.

Henadoparia was assigned to Cedariidae by Öpik (1967, p. 348) on the basis of comparison by A.R. Palmer (verbal communication to Öpik reported by Öpik) and by Öpik himself of its only species, *H. integra* Öpik, 1967, to "*Cedaria*" *woosteri* (Whitfield, 1882), from the *Cedaria* Zone of the Eau Claire Formation of the Upper Mississippi Valley (Minnesota and Wisconsin). "*Cedaria*" *woosteri* has highly modified facial sutures which surround the eye and part of the field, but which do not cut across the cephalic borders. This morphology is apparently unique within Trilobita, and the species was the subject of restudy by Hughes *et al.* (1997), who did not assign it to Cedariidae, considering that (Hughes *et al.*, 1997, p. 103) "The phylogeny of primitive libristomates is currently too poorly known to confirm that sister taxa of "*C.*" *woosteri* occur within *Cedaria*." In any event, there is little detailed similarity between *H. integra* and "*C.*" *woosteri*, which is now known from good photographs provided by Hughes *et al.* (1997). *Henadoparia integra* had functional facial sutures of standard opisthoparian type. They are not cedariform. The species also has a relatively vaulted glabella with complex, well impressed furrows. Laurentian cedariids have uniformly low glabellae with very shallow furrows. While cephalae of *H. integra* and "*C.*" *woosteri* have similar overall dimensions, there is little to support a close phylogenetic relationship.

In addition to the Laurentian taxa listed above, *Paracedaria* Lochman and Duncan, 1949, appears to be a cedariid. Jell (in Jell and Adrain, 2003) assigned the genus to Llanoaspididae Lochman in Lochman and Duncan, 1944, but cranidia of all of its species appear to have a cedariform suture. They differ from species of *Cedarina* in having smaller, more anteriorly positioned eyes and in having firmly impressed pleural and interpleural furrows which extend across the pygidial border to the margin.

"*Cedaria*" *woosteri* almost certainly represents a morphologically derived cedariid, but *Henadoparia integra* does not appear to be ingroup Cedariidae. Instead, it may belong to Proasaphiscidae Zhang, 1963. Jago and Cooper (2005, p. 671) considered *Sinocoosella* Yuan and Yin, 1998, to be a junior subjective synonym of *Henadoparia*, considering that "there is no significant difference between" the genera. Independently, however, Peng *et al.* (2004, p. 25) considered *Sinocoosella* to be a junior subjective synonym of the proasaphiscid *Adelogonus* Öpik, 1967. The latter opinion is supported herein, and the pygidium of *H. integra* (Öpik, 1967, pl. 37, fig. 5) compares closely with that of *A. hunanensis* Peng, Babcock, and Lin, 2004 (Peng *et al.*, 2004, pl. 9, figs. 4, 5).

Yuan and Yin (1998, p. 159) erected Jimachongiinae as a new subfamily of Cedariidae. In it they included their new, monotypic, *Jimachongia* from the *Glyptagnostus stolidotus* Zone of South China, along with *Yokusenina* Kobayashi, 1935a, and *Xiaoshiella* Lu and Qian, 1983, each known from several species from the lower Changshanian *Chuangia* Zone (Steptoean equivalent) of the North China block, and the Laurentian upper Marjuman taxa *Verditerrina* Robison, 1988, and (with question) *Wandelella* Robison, 1988. While the affinities of several of these genera are somewhat uncertain, this comprises an almost certainly polyphyletic assemblage, none of whose members is demonstrably ingroup Cedariidae. *Yokusenina* was assigned to Pterocephaliidae Kobayashi, 1933, by Qian (1994), Fortey (1994), and Jell and Adrain (2003). *Xiaoshiella* was assigned to Anomocaridae Poulsen, 1927, by Qian (1994) and to Pterocephaliidae by Jell and Adrain (2003). Robison (1988) considered *Verditerrina* of uncertain familial affinity, but Westrop and Ludvigsen (2000) demonstrated convincingly that it belongs to Menomoniidae Walcott, 1916a. Robison (1988, p. 98) also regarded the family affinity of *Wandelella* as uncertain, but compared it with *Pianaspis* Saito and Sakakura, 1936, of the Papyriaspidae Whitehouse, 1939, to which Jell and Adrain (2003) subsequently assigned it.

Hence, unequivocal cedariids are restricted to Laurentia, and the family may prove to be endemic to that paleocontinent. The group is entirely of Marjuman age.

***Cedarina* Lochman, 1940**

Type species. *Cedarina vale* Lochman, 1940.

Other species. *Cedarina alberta* Lochman in Lochman and Duncan, 1944; *C. clevenensis* n. sp.; *Piedmontia cordillerae* Howell and Duncan, 1939; *C. dakotaensis* Stitt, 1998; *C. obtusans* Duncan in

Lochman and Duncan, 1944; *C. prima* Lochman in Lochman and Duncan, 1944; *C. schachtii* n. sp.; *C. victoria* Lochman in Lochman and Duncan, 1944.

Diagnosis. Eyes and palpebral lobes large; thorax (known from only one species) of ten segments with median axial spine on the eighth; micropygous, with the cephalon four or five times the dorsal area of the pygidium.

Discussion. As noted by Lochman (1940, p. 40), other species currently assigned to *Cedaria* may belong to *Cedarina*. *Cedaria tennesseensis* Walcott, 1925, for example, has pygidia (Rasetti, 1965, pl. 5, figs. 7, 8) with a low number of axial rings and subquadrate outline that are much more like those of *Cedarina* than typical *Cedaria*. Most species of either genus remain difficult to evaluate, however, due to the generally small number of specimens figured with often tiny and inadequate photographs.

Cedarina schachtii n. sp.

Figs. 5–8

Etymology. The species is named in honour of Robert Schacht, who collected and donated the holotype and one of the paratype specimens.

Type Material. Holotype, FMNH PE57116, paratypes SUI 102868, 104476, and additional specimens USNM 437968, 437975, from the Weeks Formation (Marjuman; *Cedaria* Zone), Weeks Canyon, northern House Range, Millard County, western Utah, USA.

Diagnosis. Frontal area and preglabellar field long; anterior border evenly anteriorly arcuate; anterior sections of facial suture strongly anteriorly divergent; palpebral lobes large; pygidium relatively narrow and long.

Description. Cephalon with sagittal length 46.6% (42.9–50.4) width across base of genal spines; cranidium with sagittal length 54.3% (49.5–59.8) maximum width across posterior fixigenae; width across anterior sections of facial suture 96.5% (89.8–103.3) width across midlength of palpebral lobes and 47.6% (45.5–50.0) width across posterior fixigenae; dorsal cephalic sculpture of fine, sparsely distributed granules on borders, prominent caecal ridges, grooves, and pits on genal fields, less well impressed and more finely pitted proximally, deeper and more radially oriented distally; fine granules on interocular fixigena, distal part of posterior fixigena, and all of glabella, and very faint small tubercles scattered over proximal posterior fixigena and rear of glabella, particularly on LO; glabella with sagittal length (including LO) 71.5% (70.0–72.3) cranial sagittal length and maximum width across LO 70.3% (63.2–83.4) sagittal length; glabella low, with only weak to moderate dorsal inflation, trapezoidal in outline; axial furrows with more or less straight, anteriorly convergent course, bowed out slightly around LO, in at SO, gently out around L1, and very slightly inward opposite remaining anterior part of glabella; preglabellar furrow variable from quite strongly anteriorly convex (Fig. 8A) to more transverse (Fig. 6), contact with axial furrow at rounded angle; axial and preglabellar furrows similarly narrow and moderately incised; glabellar furrows effaced, visible distally as very slight indentations in lateral glabellar margin; L1 and L2 expressed mainly as slight swellings, L3 not obvious dorsally; SO with transverse course, very slightly bowed forward medially, very short (sag., exsag.), slightly longer sagittally, shallow laterally, deeper in middle 80%, and deepest sagittally; LO subrectangular, longer (sag., exsag.) than axial rings of anterior thoracic segments, slightly shorter exsagittally than sagittally, with dorsal sculpture of very fine granules, rear margin evenly posteriorly arcuate; preglabellar field long; anterior border longer sagittally than exsagittally owing to oblique course of long connective suture; border dorsally flattened on anterior aspect, sloped sharply towards border furrow posteriorly, lacking dorsal sculpture, anterior margin evenly anteriorly arcuate; anterior border furrow short (sag., exsag.), relatively shallow; anterior sections of facial sutures strongly anteriorly divergent in front of palpebral lobe, bowing near anterior border furrow to run into oblique connective suture; palpebral lobes large, anteroposteriorly elongate, lacking dorsal sculpture, area around lateral margin raised; palpebral furrow expressed as break in slope; eye ridge running obliquely from anterior edge of palpebral lobe to just in front of L3 (best expressed on Fig. 6); interocular fixigenae narrow, lacking sculpture; rear of palpebral lobe nearly abutting glabella;

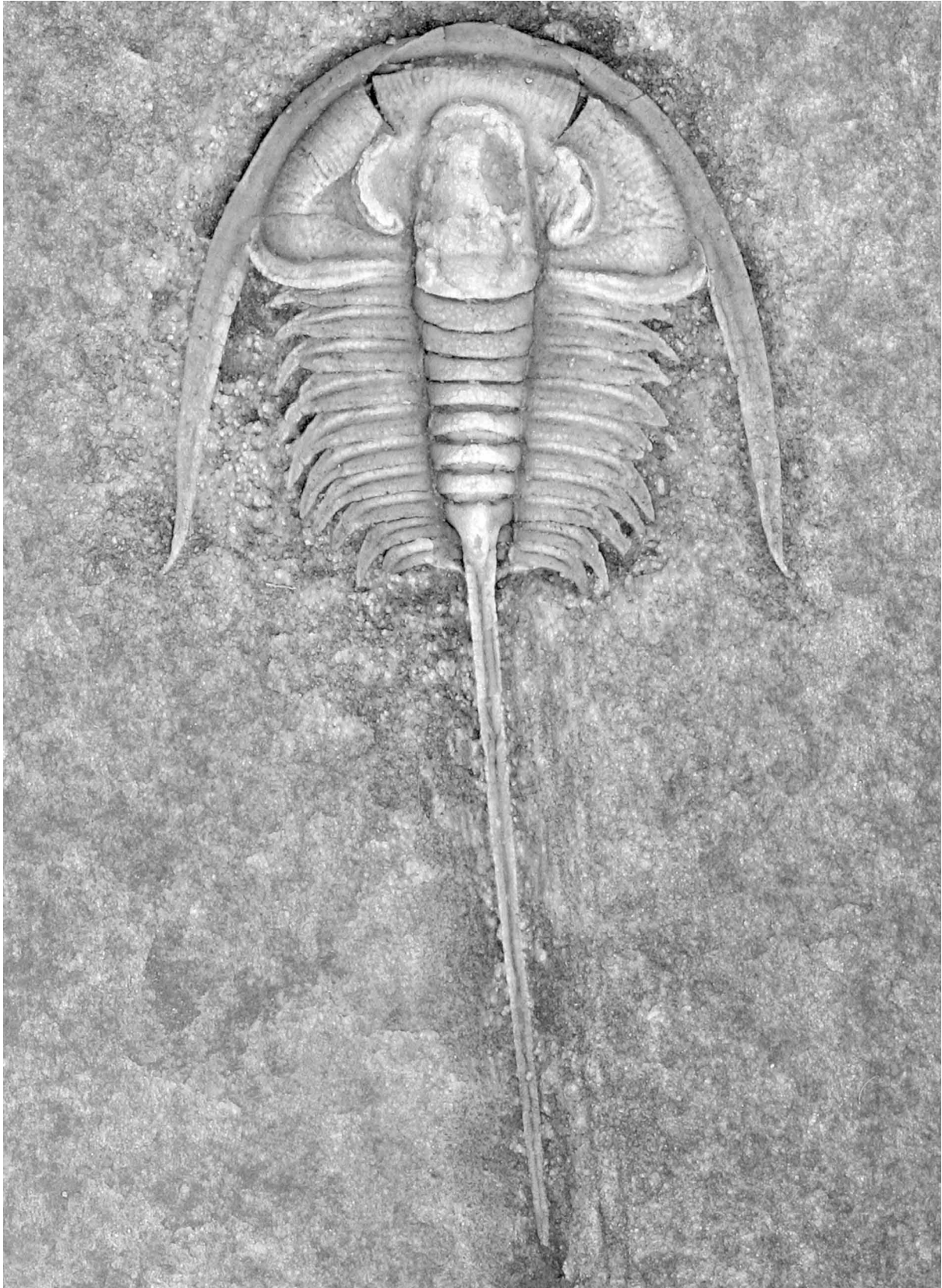


FIGURE 5. *Cedarina schachtii* n. sp., from the Weeks Formation (Marjuman; *Cedaria* Zone), northern House Range, Millard County, western Utah, USA. Dorsal exoskeleton lacking pygidium, **holotype**, FMNH PE57116, dorsal view, x12.



FIGURE 6. *Cedarina schachtii* n. sp., from the Weeks Formation (Marjuman; *Cedaria* Zone), northern House Range, Millard County, western Utah, USA. Dorsal exoskeleton, paratype, SUI 104476, dorsal view, x12.

posterior section of facial suture running transversely at rear of palpebral lobe, turned anteriorly to form cedariform lobe on posterior fixigena; posterior border inflated and semicylindrical, short (exsag.) near axial furrow, longer distally; posterior border furrow deep and short (exsag.); both border and border furrow deflected posteriorly near fulcrum.

Librigena with eye large and long; eye socle not obvious, but region is crushed on all available specimens; furrow separating base of visual surface from field shallow, curved subparallel with outer margin of palpebral lobe; field narrowest about 80% of distance anteriorly, wider immediately in front of eye, and much wider posteriorly at rear of eye, with moderate dorsal inflation, transected by subparallel caecal trunks, with very subdued scattered tubercles on rear part; lateral border furrow narrow, relatively shallow, edge sharply defined along contact with border, contact with field more gently sloping, furrow curved parallel with lateral margin of border; posterior border and lateral border completely confluent across posterior section of facial suture, no sutural ridges developed; lateral border flattened in dorsal aspect anteriorly, more inflated and semicylindrical posteriorly, similar in width to anterior border anteriorly, wider posteriorly to base of genal spine, border lacking dorsal sculpture; genal spine broadest just behind base, long and robust, extending nearly to (Fig. 5) or just past (Fig. 6) rear of pygidium, curved slightly adaxially, tapering more or less evenly to sharp, slightly outwardly turned point.

Hypostome known only from poorly preserved mold (Fig. 7), maximum width anteriorly about 73 percent sagittal length; lateral margins slightly posteriorly convergent, width at rear about 85% anterior width; posterior margin deflected sharply from lateral margin, with moderate posterior curvature; hypostome was apparently quite convex.

Rostral plate unknown.

Thorax of 10 segments, with very long median axial spine on eighth; axial ring of similar length sagittally and exsagittally, with dorsal sculpture of fine granules and relatively densely distributed, very subdued tubercles; axial furrow narrow, sharply incised, deflected laterally around side of axial ring; pleural furrow prominent, deep, but quite short (exsag.), contacts axial furrow, with transversely straight course proximally, deflected and curved posteriorly distally at about fulcrum; both anterior and posterior pleural bands raised and ridge-like, with transverse row of very fine tubercles on each; posterior pleural band shorter distally; anterior and posterior bands unite distally to form laterally protruded, posterolaterally directed, pleural spine; axis of successive segments steadily reduced in width posteriorly; axis of eighth segment almost entirely occupied by base of robust spine; spine somewhat longer than distance from anterior margin of cranidium to posterior margin of pygidium, tapered gradually to sharp point; pleural spines small anteriorly, increasing in size posteriorly to reach maximum around seventh or eighth segment, those of ninth and tenth segment slightly smaller but more posteriorly directed.

Pygidium poorly known; of typical morphology for genus, micropygous, with width about three times sagittal length; apparently composed of 3–4 segments; margin complete, pleurae not extended into spines as in thorax.

Discussion. *Cedarina vale* Lochman, 1940, the type species from the Bonnetterre Dolomite of Missouri, is known only from tiny photographs of one cranidium, one librigena, and one pygidium in the original description. Hu (1983, pl. 1, figs. 34–38) assigned and illustrated two cranidia, a librigena, and a pygidium. These are clearly morphologically distinct from Lochman's species. Hu (1983, p. 278) recognized this, but opined that "Comparing these morphologic differences with the present studied materials, it might assume that this species has a broad morphologic varieties within the same species population." (sic) It is not clear why one would assume this, as a more likely explanation is that they are simply different taxa. Although Hu's material was collected by Lochman and was said to be (Hu, 1983, p. 275) "from the same general area Saline Creek at Avon, Ste. Genevieve County, Missouri," (sic) no further stratigraphic information was given and whether Hu's material is from the same horizon as Lochman's is not known. *Cedarina schachtii* differs from *C. vale* in the possession of an evenly forwardly arcuate anterior border, versus one with a strong posterior inflection medially. The anterior border is concomitantly shorter sagittally. The anterior sections of the facial sutures are more anteriorly divergent in *C. schachtii*, the preglabellar field is longer, and the frontal areas

occupy a larger area. The glabella is more nearly parallel sided, and relatively narrower at the base. The librigenal field of *C. schachtii* is considerably wider. Although the pygidium of *C. schachtii* is not well known, its outline (Fig. 7) clearly shows that it is relatively narrower and longer than that of *C. vale*.

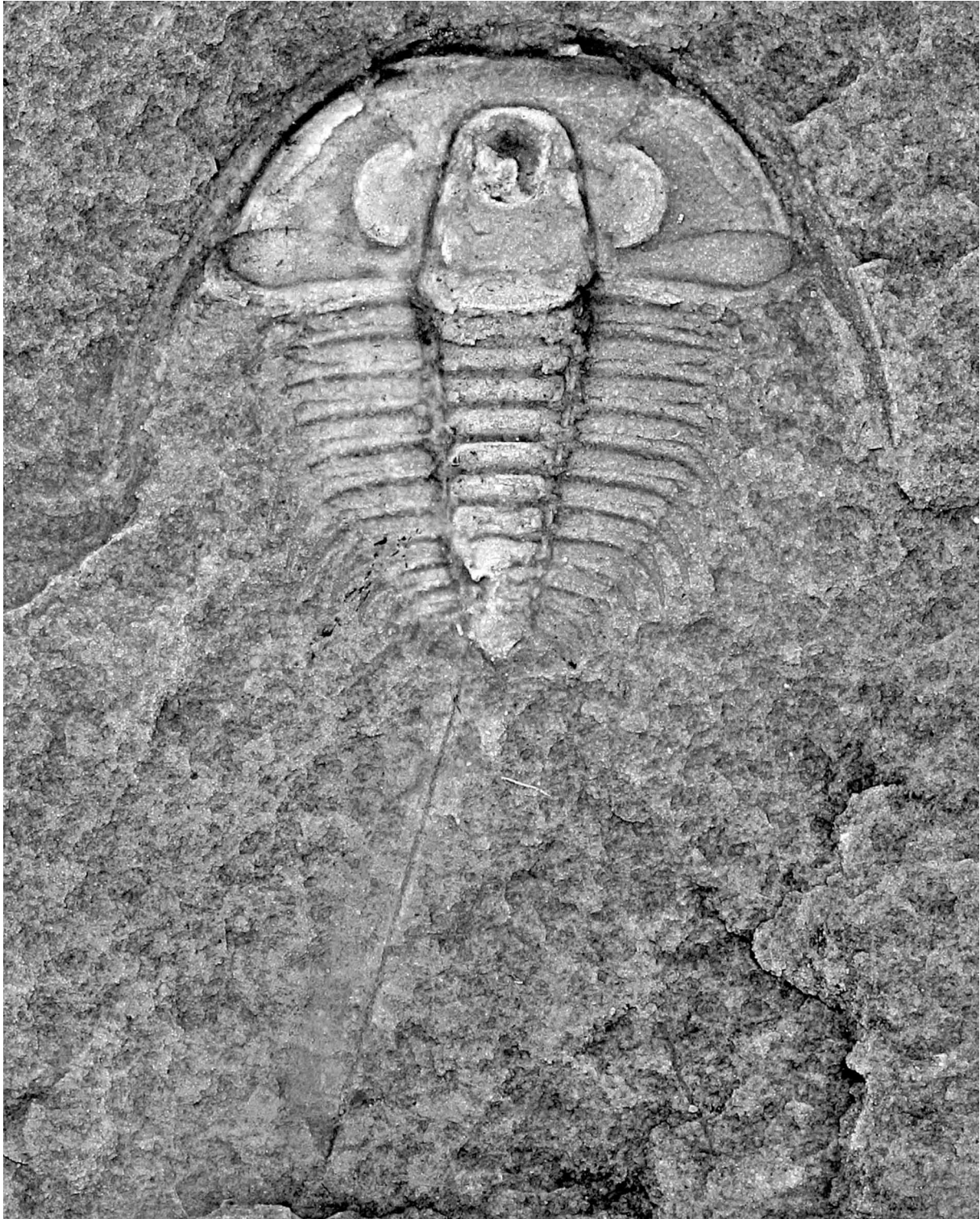


FIGURE 7. *Cedarina schachtii* n. sp., from the Weeks Formation (Marjuman; *Cedaria* Zone), northern House Range, Millard County, western Utah, USA. Dorsal exoskeleton (internal mold), SUI 102868, dorsal view, x12.

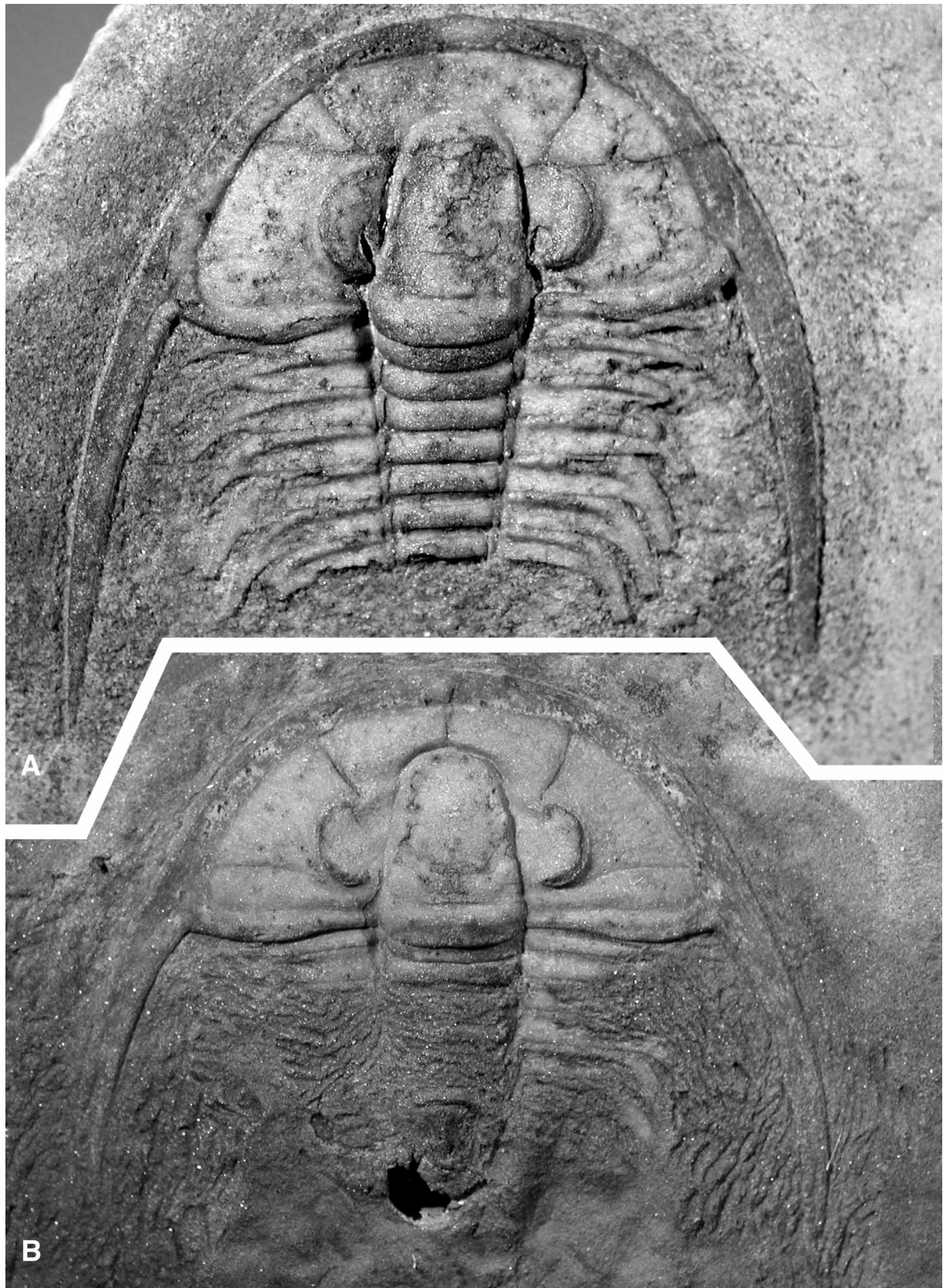


FIGURE 8. *Cedarina schachtii* n. sp., from the Weeks Formation (Marjuman; *Cedaria* Zone), northern House Range, Millard County, western Utah, USA. A. Anterior part of dorsal exoskeleton, USNM 437975, x12. B. Anterior part of dorsal exoskeleton, USNM 437968, x12.

Cedarina alberta Lochman in Lochman and Duncan, 1944, from the Pilgrim Formation of south-central Montana, is based on inadequate material, including two poorly preserved cranidia, a nearly uninterpretable librigena, and one pygidium. Lochman and Hu (1962) subsequently assigned material from the DuNoir Limestone of Wyoming to the species. Despite the poor preservation of the type material, the Wyoming specimens do appear to be consistent with it, and this assignment is reasonable. *Cedarina alberta* differs from *C. schachtii* in its much longer (exsag.) and narrower posterior fixigena, shorter preglabellar field, narrower frontal area, more forwardly tapering glabella, and narrower pygidium.

Cedarina cordillerae (Howell and Duncan, 1939) is ostensibly the most widely distributed species. The type material is from the Pilgrim Formation in the Big Snowy Mountains of central Montana, and is poorly preserved. Lochman and Duncan (1944, pp. 89–90, pl. 17, figs. 1–10) subsequently reillustrated the holotype along with additional material. Lochman (1950, p. 347, pl. 50, figs. 20, 21) illustrated another cranidium and librigena from the Pilgrim Formation in the Little Snowy Mountains, Montana, and Hu and Li (1971, p. 171, pl. 2, figs. 1–37, text-fig. 2a–m) illustrated many specimens, including an essentially complete ontogenetic series. Material has subsequently been assigned from the Riley Formation, Texas (Palmer, 1955, p. 727, pl. 80, figs. 8, 10), the Wasatch Mountains, Utah (Hu, 1971, p. 87, pl. 13, figs. 1–29, text-fig. 42), the Rabbitkettle Formation, Northwest Territories, Canada (Pratt, 1992, p. 82, pl. 31, figs. 17–21), and the Deadwood Formation, South Dakota (Stitt, 1998, p. 1038, fig. 6.14). Many of these records involve sparse, poorly preserved material, and the presence of a median occipital spine has possibly led to the identification of any *Cedarina* cranidia bearing such a spine as *C. cordillerae*. The species, its putative distribution, and the quality of the evidence comprise another example of the common phenomenon discussed by Adrain and Westrop (2005), in which inadequate, or inadequately illustrated, material from geographically widespread areas are assigned to species that are themselves poorly documented. Although the various sets of material are generally similar, the available quality and numbers of both specimens and illustrations simply preclude modern systematic evaluation. *Cedarina cordillerae* differs from *C. schachtii* and all other species of *Cedarina* in its median occipital spine. It is similar to *C. vale*, and differs from *C. schachtii*, in having a posteromedian deflection of its anterior border furrow.

Cedaria prima Lochman in Lochman and Duncan, 1944, from the Pilgrim Formation, Montana, is based on mostly flattened material. It is distinguished from *C. schachtii* by its shorter preglabellar field, less anteriorly divergent anterior facial sutures, much more anteriorly convergent axial furrows, apparently smaller eye, and longer pygidium.

Cedarina victoria Lochman in Lochman and Duncan, 1944, from the Pilgrim Formation in the Big Snowy Mountains, Montana, is characterized by very large and long lateral extensions of the posterior fixigenae and a long librigenal field. The cranidial morphology is not evident on the material from the Wind River Mountains of Wyoming assigned to the species by Lochman and Hu (1962, p. 23, pl. 3, figs. 9–14), which seems to represent a separate species. *Cedarina victoria* is further distinguished from *C. schachtii* in its narrower frontal area, longer anterior border, more forwardly positioned palpebral lobes, apparently smaller eye, and much narrower librigenal field.

Cedarina obtusans Duncan in Lochman and Duncan, 1944, from the Pilgrim Formation in the Big Snowy Mountains, Montana, is a very distinctive species, characterized by a very long anterior border and very wide anterior part of the librigenal lateral border. It further differs from all other species in the possession of a pygidium with a pair of posteriorly directed pleural spines on the first segment.

Cedarina dakotaensis Stitt, 1998, from the Deadwood Formation, Black Hills, South Dakota, was erected on the basis of material mostly preserved as coarse molds in a sandstone. It is not clear that all of the sclerites assigned by Stitt are conspecific. One librigena (Stitt, 1998, fig. 6.10) in particular appears to have a much longer field than either of the other examples (Stitt, 1998, fig. 6.8, 6.12). One assigned pygidium (Stitt, 1998, fig. 6.11) is considerably longer and narrower than the others. The holotype cranidium (Stitt, 1998, fig. 6.6) differs from those of *C. schachtii* in the possession of a posteromedially inflected anterior border furrow, less anteriorly divergent anterior facial sutures, smaller palpebral lobes, and longer, narrower posterior fixigenae.

***Cedarina clevensis* n. sp.**

Figs. 9, 10

Etymology. After Cleve Creek, the type locality.

Type material. Holotype, pygidium, SUI 109011 (Fig. 10M, P, T, U), and paratypes SUI 109001-109010, 111860, 111861, from the Lincoln Peak Formation (Marjuman; *Crepicephalus* Zone), Cleve Creek, Schell Creek Range, White Pine County, eastern Nevada, USA.

Diagnosis. Anterior border furrow weakly posteriorly deflected medially; preglabellar field about same length as anterior border; palpebral lobes long but very narrow; glabella broadest at base, tapering forward; librigena with relatively narrow field; genal spine of only moderate length, tapered to sharp point; thoracic axial spine narrow; pygidium with four fully expressed axial rings.

Description. Cranidium with glabella elongate and broad at base; axial furrows narrow and deeply incised, shallowest and bowed laterally around L1, moderately anteriorly convergent, turned without interruption to grade into anteriorly arcuate preglabellar furrow; glabella with dorsal sculpture of very fine granules; S1-S3 visible as faint impressions with suppressed granulation; L1 and L2 very weakly inflated, but slightly swollen laterally; preglabellar field about same sagittal length as anterior border; field and frontal areas with granular sculpture similar to that of glabella, set atop fine radiating series of caecal trunks; anterior sections of facial sutures strongly anteriorly divergent, maximum point of divergence just behind contact with anterior border furrow; anterior border furrow very short (sag., exsag.) and strongly incised, with only gentle anterior arc, deflected very slightly posteriorly across median portion; anterior border longest sagittally, length constrained by long, obliquely set connective sutures abaxially, with moderate dorsal inflation in sagittal profile, sculpture of fine granules on posterior region, and widely spaced fine raised lines running subparallel to margin on anterior region; preglabellar field sloped down at about 40° from plane of palpebral lobes; eye ridge prominent in small and medium-sized specimens, progressively subdued with size, set about 30° posteriorly from a transverse plane, running from anterior corner of palpebral lobe to near indistinct junction of axial and preglabellar furrows, in smaller specimens course is more transverse; eye ridge not obviously bicomposite, but forming a raised, moderately inflated ridge, separated from fixigena anteriorly and posteriorly by short (exsag.) shallow furrows; palpebral lobe long but very narrow, slightly inclined toward glabella, with sculpture of fine granules; palpebral furrow expressed only at posteriormost edge of lobe, otherwise palpebral lobe grades into interocular fixigena with no break in slope; interocular fixigena narrow, with weak dorsal inflation and granular sculpture identical to that of palpebral lobe; posterior border short proximally; posterior border furrow very short (exag.) and incised proximally; posterior projections not preserved in large specimens; LO long, only slightly longer sagittally than exsagittally, with granular sculpture similar to that on rear of median glabellar lobe; very faint median node set at ring midlength; occipital lobes weakly differentiated behind L1; glabella moderately inflated in sagittal profile, occipital ring flat.

Rostral plate and hypostome not found.

Librigena with long, narrow field, posterior portion of field broader and subtriangular; eye narrow and strongly curved, reniform, separated from field by shallow furrow; field with strong caecal sculpture of pits and ridges adaxially and radiating trunks abaxially; posterior section of facial suture indicates posterior projection was not lobate as in some other cedariids; posterior border furrow not developed on librigena, cut entirely by suture immediately above base of genal spine; lateral border furrow very narrow, deeply incised anteriorly, progressively shallower posteriorly, effaced completely just in front of and atop base of genal spine; lateral border flat, separated from ventral aspect by sharp, blade-like lateral edge, with sculpture of very fine granules and somewhat irregular, meandering and very sparsely distributed fine raised lines; raised lines more robust and more densely crowded posteriorly, and continued along dorsal aspect of genal spine; genal spine about same length as remainder of librigena, curved adaxially, flattened in same manner as lateral border, tapered rapidly to sharp tip; ventral aspect of border turned sharply under dorsal aspect to form ventrally concave furrow subparallel to lateral margin, separated from doublural sector by raised ridge;

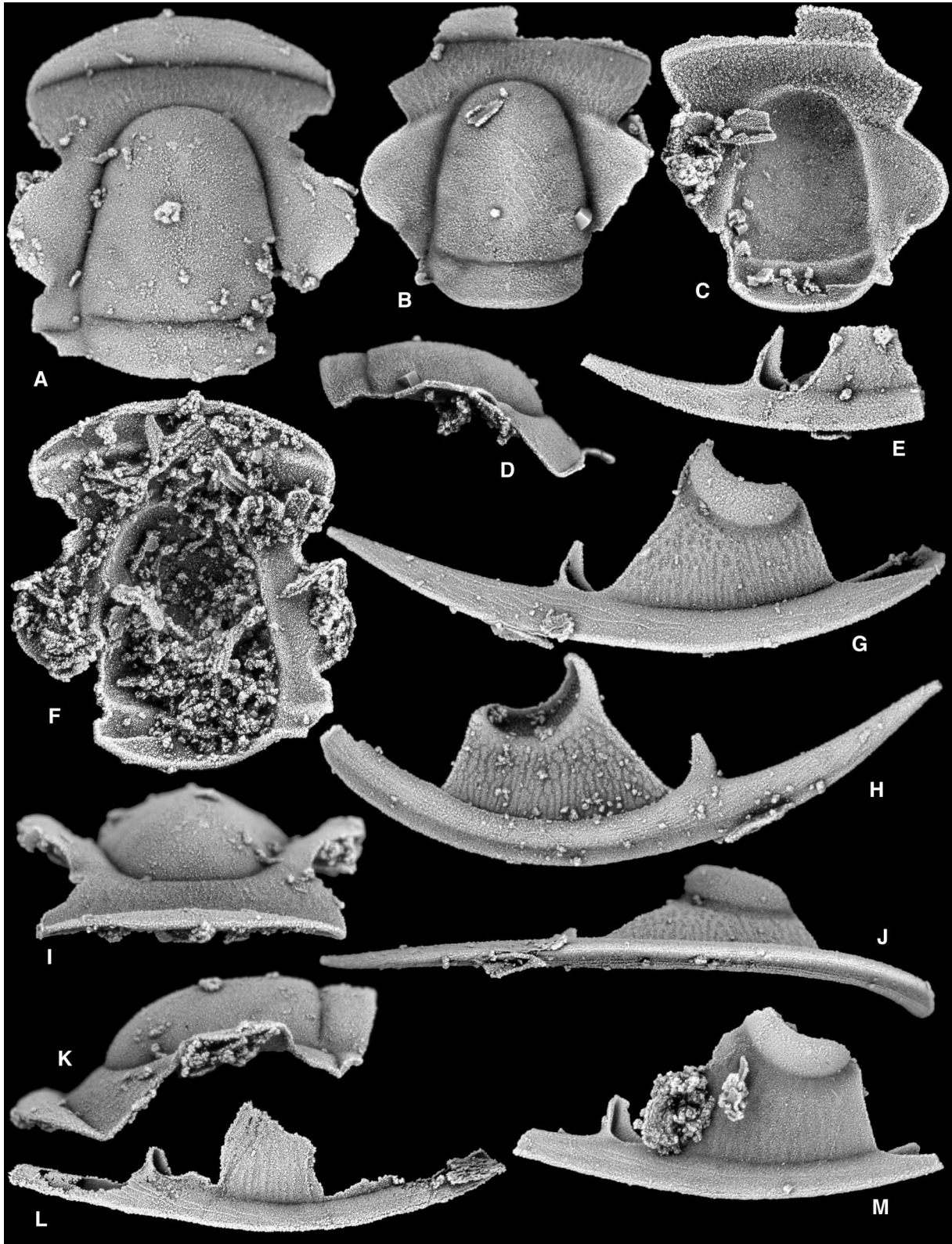


FIGURE 9. *Cedarina clevensis* n. sp., from the Lincoln Peak Formation (Marjuman; *Crepicephalus* Zone), Cleve Creek, Schell Creek Range, White Pine County, eastern Nevada. Magnifications are x15 except where noted. A, F, I, K. Cranidium, SUI 109001, dorsal, ventral, anterior, and left lateral views (CLC 70.5T m). B-D. Cranidium, SUI 109004, dorsal, ventral, and right lateral views (CLC 67.5T m). E. Right librigena, SUI 109007, external view, x12 (CLC 67.5T m). G, H, J. Right librigena, SUI 109002, external, internal, and ventrolateral views (CLC 70.5T m). L. Right librigena, SUI 109005, external view, x10 (CLC 67.5T m). M. Right librigena, SUI 109003, external view (CLC 67.5T m).

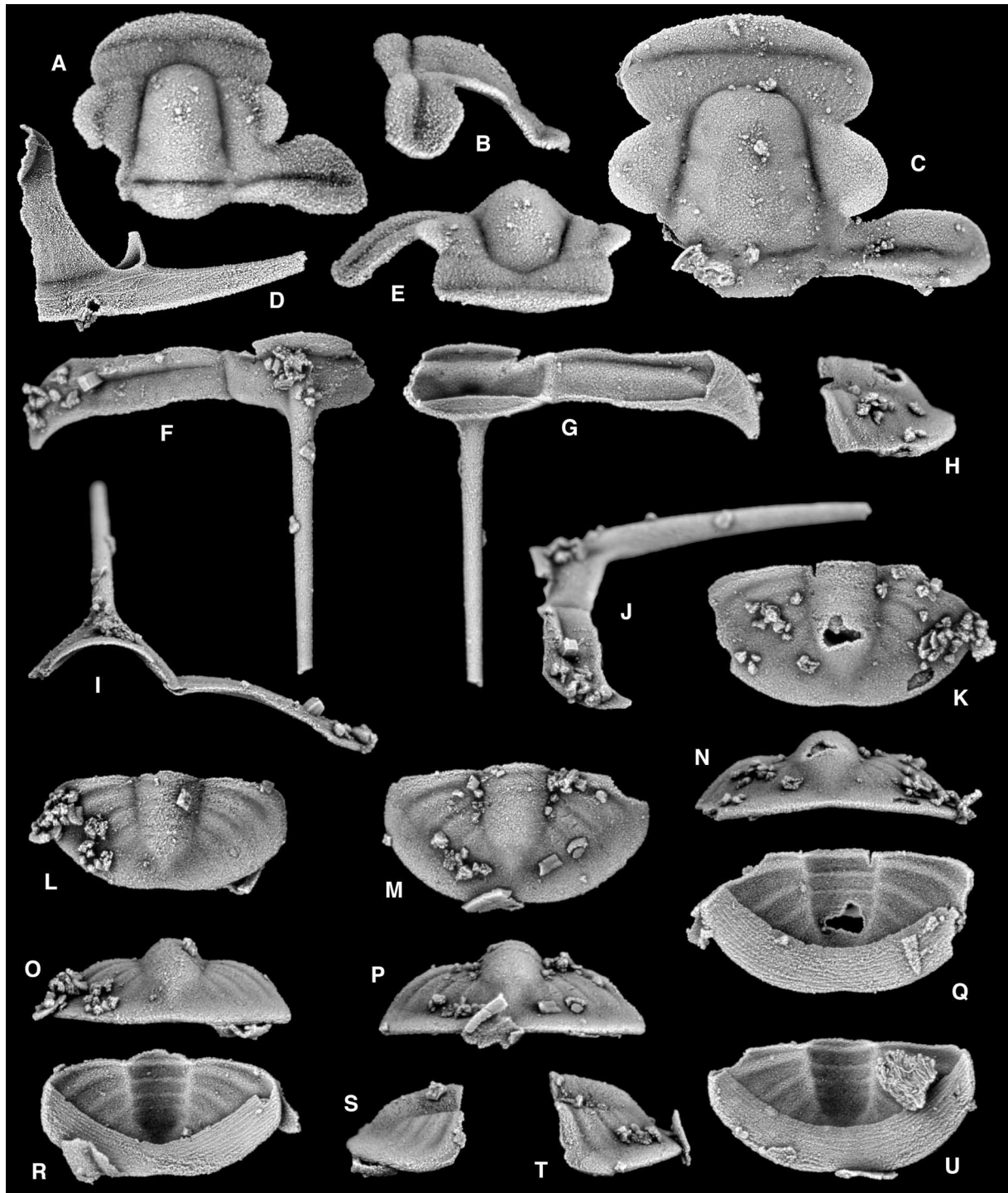


FIGURE 10. *Cedarina clevensis* n. sp., from the Lincoln Peak Formation Marjuman; *Crepicephalus* Zone), Cleve Creek, Schell Creek Range, White Pine County, eastern Nevada. All magnifications are x15. Juvenile specimens in A-C and E are questionably assigned. A, B, E. Cranidium, SUI 111860, dorsal, right lateral, and anterior views, x30 (CC1). C. Cranidium, SUI 111861, dorsal view, x25 (CC1). D. Left librigena, SUI 109006, external view, x10 (CLC 67.5T m). F, G, I, J. Thoracic segment, SUI 109008, dorsal, ventral, anterior, and left lateral views (CLC 67.5 T m). H, K, N, Q. Pygidium, SUI 109009, left lateral, dorsal, posterior, and ventral views (CLC 67.5 T m). L, O, R, S. Pygidium, SUI 109010, dorsal, posterior, ventral, and right lateral views (CLC 67.5 T m). M, P, T, U. Pygidium, **holotype**, SUI 109011, dorsal, posterior, left lateral, and ventral views (CLC 67.5 T m).

doublure turned up underneath lateral border furrow, with sculpture of closely spaced and regular fine raised lines set subparallel to inner margin; contact between rear of posterior border and genal spine sharp, angle about 90°.

Spine-bearing thoracic segment with narrow axis; articulating half ring short, slightly longer sagittally than exsagittally, separated from ring by moderately deep furrow; ring lacking dorsal sculpture; narrow and gracile median spine with base set at about midlength of ring, posterior edge of ring drawn back to form small oblique ridge on either side which merges with spine posteriorly, small furrow developed between ridge and spine; length of spine unknown, but probably would have reached past rear of pygidium; axial furrow narrow and incised, but quite shallow, running slightly obliquely; pleural region distinctly bowed, with margins describing shallow M shape; posterior pleural band about twice length (exsag.) of anterior band, both lacking sculpture; region of anterior band distal to fulcrum developed into wide, short subtriangular facet; pleural furrow short and finely incised proximally, longer and deeper distally; fulcrum set close to axis; distal pleural regions with posterior and anterior bands merged into flattened, posteriorly turned pleural spine; doublure beneath rear of ring with fine subparallel raised lines; doublure present as very short (exsag.) strip underneath rear edge of pleura, longer distally, and underlying entire pleural spine distal to termination of pleural furrow, with sculpture of relatively robust and widely spaced raised lines cutting anterolaterally across doublure.

Pygidium subtrapezoidal, with narrow axis; axis with subparallel sides, four weakly expressed rings (easiest to discern ventrally) and a transverse terminal piece and faint, subtriangular post-axial ridge; rings and ring furrows almost effaced dorsally, but short; dorsal sculpture absent from rings; axial furrows relatively deep anteriorly, becoming progressively shallower posteriorly, interrupted posteromedially by post-axial ridge; four pleural furrows expressed, but progressively weaker and more difficult to discern posteriorly; anterior edge of pleura with short facet across most of its width; anterior and posterior pleural bands subequal in length; entire pleural region lacking sculpture; interpleural furrows very weakly expressed; broad, flat border against which furrows terminate; margin and border with slight anterior inflection medially; doublure broad, underlying border, with sculpture of closely spaced fine raised lines running subparallel to margins.

Discussion. Although material is rare and somewhat fragmentary, *Cedarina clevensis* nevertheless becomes one of the better known members of the genus, and the first for which ventral information is available. It confirms the presence of a thoracic axial spine, indicating that this is likely the common condition for members of the genus. Juvenile cranidia (Fig. 10A, C; assignment to *C. clevensis* tentative) represent the first ontogenetic information for a member of *Cedarina*, showing the presence of a shallow median furrow on the preglabellar field in early ontogeny, better expression of the eye ridge, a distinct palpebral furrow that is effaced in later ontogeny, independently inflated L1, and stronger expression of the median occipital node.

Compared with *C. schachtii*, the only other adequately known species, *C. clevensis* differs in the possession of a shorter preglabellar field, shorter glabella with broader base, smaller and particularly narrower palpebral lobes lacking expression of a palpebral furrow in large specimens, a shorter occipital ring, a much narrower thoracic axial spine, and a longer, more subquadrate pygidium.

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