Zootaxa 2910: 1–45 (2011) www.mapress.com/zootaxa/

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Systematics of the Lower Ordovician pliomerid trilobite *Hintzeia*, with species from the Great Basin, western USA

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Table of contents

Abstract	1
Localities and Stratigraphy	.2
Systematics	. 2
Family Pliomeridae Raymond, 1913	5
Hintzeia Harrington, 1957	5
Hintzeia firmimarginis (Hintze, 1953)	7
Hintzeia parafirmimarginis n. sp.	11
Hintzeia celsaora (Ross, 1951)	12
Acknowledgements	17
Literature cited	18

Abstract

The pliomerid trilobite genus *Hintzeia* Harrington, 1957, includes only species from the early Tulean (upper Tremadocian) of the Great Basin, USA, and from the Northwest Territories, Canada. Previously assigned species reported from Scandinavia, China, South Korea, and Australia do not appear to be closely related to the western Laurentian species and are excluded from the genus. The monophyly of the group needs to be tested in the context of a broader phylogenetic analysis, but *Hintzeia* is rediagnosed with potential synapomorphies including a long, wide anterior border with a large, semicircular median arcuate anterior curve in the posterior margin. *Hintzeia celsaora* (Ross, 1951) and *H. firmimarginis* (Hintze, 1953) are redescribed based on large new collections from Utah and Idaho. Ontogenetic material of *H. celsaora* includes an articulated silicified M13 meraspid. *Hintzeia parafirmimarginis* **n. sp.** is described on the basis of both abundant disarticulated sclerites and a large articulated individual. Large topotype collections indicate that *Hintzeia celsaora* (Ross, 1951) is a senior synonym of *Protopliomerops aemulus* Hintze, 1953; previously claimed differences appear to reflect small original sample sizes, ontogenetic change, and differing photographic orientation.

Key words: Silicified, Utah, Idaho, Ibexian, Tulean, Pliomeridae

Introduction

This is the third work in a series (McAdams and Adrain, 2009a, 2010a) on systematics of Pliomeridae Raymond, 1913, based on description and revision of taxa from rich Lower and Middle Ordovician silicified faunas of western Laurentia. The broader project involves a comprehensive field based revision of the classic Ibexian successions of southeastern Idaho and northern Utah (Ross, 1951) and western Utah and eastern Nevada (Hintze, 1953). Work to date has been summarized by Adrain *et al.* (2009), who also detailed a revised trilobite zonation for the Tulean and Blackhillsian stages which is followed herein.

This paper focuses on *Hintzeia* Harrington, 1957, which was established for the species *Protopliomerops celsaorus* Ross, 1951, and *Protopliomerops firmimarginis* Hintze, 1953, with the type species *Protopliomerops aemu-*

lus Hintze, 1953. The species content of the group has been in flux since its creation. Demeter (1973) recognized *H. aemula* as a junior synonym of *H. celsaora*, and we concur. Only the two Great Basin species remained constant while species previously or subsequently assigned to *Pliomera* Angelin, 1854; *Pliomerops* Raymond, 1905; *Protopliomerops* Kobayashi, 1934; *Pseudomera* Holliday, 1942; and *Kanoshia* Harrington, 1957, were included by different workers (see also Demeter [1973], Laurie and Shergold [1996], Hoel [1999], and Simpson *et al.* [2005]).

A probable contributing factor to this instability is a dearth of well known species. The type species was illustrated from Idaho with nine specimens (Ross, 1951, pl. 31, figs 1–15, pl. 34, figs 9–12, 20) and from Utah with only seven specimens (Hintze, 1953, pl. 22, figs 9, 10, 13–17). Demeter (1973) assigned an additional handful of sclerites to *H. celsaora*, but several of them could also belong to species of *Protopliomerella* Harrington, 1957, or to other pliomerid taxa; problems with interpreting Demeter's specimens were summarized by McAdams and Adrain (2009a). Other species previously assigned to the genus, with the exception of *H. plicamarginis* Simpson *et al.*, 2005, have been poorly known (e.g., *H. glabella* Kobayashi, 1960; *Kanoshia kanoshensis* [Hintze, 1953]) or lack significant modern treatment and illustration (e.g., *"Pliomerops" actinurus* [Dalman, 1824]). Furthermore, the diagnosis of *Hintzeia* given by Harrington (1957, p. 811) was based entirely on symplesiomorphies. That of Simpson *et al.* (2005, p. 538), also contains many symplesiomorphies. Diagnoses based on symplesiomorphies invite chaotic species assignments, as many taxa share these broadly distributed features. A lack of obvious synapomorphies in previous diagnoses also raises the question of whether *Hintzeia* is actually a clade.

Species assigned to *Hintzeia* have been used as outgroup taxa in several phylogenetic analyses of pliomerids (McAdams and Adrain, 2009b, 2010a, 2010b) because they are well known from our new collections, occur stratigraphically early in the Tulean (upper Tremadocian), and possess apparently plesiomorphic morphology. The monophyly of *Hintzeia* is at present an open question. *Protopliomerella* (itself dubiously monophyletic as traditionally conceived) may create paraphyly in *Hintzeia*, and the taxa are surely closely related. A comprehensive phylogenetic analysis of the broader group is necessary to address the question, but cannot proceed until the species involved are adequately described and revised. In this paper, our goals are to restrict *Hintzeia* to a small group of species whose close phylogenetic affinity is apparent, to describe a new species, and to revise the previously established species on the basis of rich new field collections. We provisionally diagnose the genus on the basis of potential synapomorphies, recognizing that these must be tested in future work.

Localities and Stratigraphy

Adrain *et al.* (2009) provided an overview of classic Ibexian localities and sections in the Great Basin and summarized the history of study. This information is not repeated herein. Section G (Hintze, 1951, 1953) in the Ibex area of the Tule Valley of western Utah (Figs 1.1, 1.2) was also recently discussed by McAdams and Adrain (2009c). Additional information on sections HC5 and HC6 (Ross, 1949, 1951) at Hillyard Canyon, Bear River Range, southeastern Idaho (Figs 1.3, 1.4) was given by Adrain and Westrop (2007a, 2007b).

Species of *Hintzeia* occur in the Garden City and Fillmore formations in Idaho and Utah, respectively, and in the Broken Skull Formation in the Northwest Territories, Canada (Simpson *et al.*, 2005). Faunas occurring in the Garden City and Fillmore formations are precisely correlated using the biostratigraphic scheme of Adrain *et al.* (2009). Stratigraphic ranges of species occurring at Section G are shown in Figure 2. Trilobite faunas from the upper part of the Broken Skull Formation are Stairsian to Tulean (Ross-Hintze zones D-G(2)) in age (Ludvigsen, 1975, and references therein). Simpson *et al.* (2005, p. 531) considered their material to be of Stairsian-Tulean boundary age (zones F-G(1)), but their faunal list includes *Psalikilus* Ross, 1951, in addition to *Hintzeia*. Throughout our sampling, these are unambiguously Tulean taxa and it seems likely that the Broken Skull Formation sample is early Tulean in age, broadly equivalent to that of the material we describe herein.

Systematics

Repository. Figured material is housed in the Paleontology Repository, Department of Geoscience, University of Iowa, Iowa City, with specimen number prefix SUI, and the Department of Geology and Geophysics, University of Utah, with specimen number prefix UU.

Terminology. Morphological terms follow Whittington and Kelly (1997) with the exception of the term "doublure". Whittington and Kelly (1997, p. 317) defined the term as the "reflexed continuation of dorsal exoskeleton onto ventral surface". Most morphological terms applied to trilobites reflect homology. "Doublure" is often an exception, as in many trilobites the border continues without interruption in slope and with similar sculpture onto the ventral aspect, and a separate reflexed surface is set off from it, often oriented nearly vertically and not necessarily visible in ventral view. This is the case, for example, in the cephalic ventral region of the hystricurid *Metabowmania* Kobayashi, 1955 (see Adrain and Westrop, 2007b), and it is true of many pliomerids. In pygidia of *Hintzeia*, the innermost effaced surface is held vertically and seen only in anterior view (Pl. 4, fig. 10, Pl. 7, fig. 26, Pl. 10, fig. 29, Pl. 14, fig. 26). We prefer to restrict use the term doublure to refer to this innermost, reflexed surface, regardless of its orientation in any particular trilobite. The inflated, sculptured ventral posterior rim of the pygidium is the pygidial border, which is expressed ventrally because the bases of the pygidial spines protrude above it and the tips extend below it. To simply term any ventral surface of the exoskeleton "doublure" diminishes the biological meaning of the term. With respect to Whittington and Kelly's (1997) definition, we regard the flexure as the critical feature, not the orientation, which is quite arbitrary with respect to the body plan of various trilobites.



FIGURE 1. 1. Road map showing the Ibex area of the Tule Valley, Millard County, western Utah and the location of Section G (black rectangle) in the southern Confusion Range. 2. Portion of U.S. Geological Survey 1: 24,000 Warm Point provisional 7.5' quadrangle topographical map (1991) depicting line of Section G. 3. Road map with location of sections HC5 and HC6 (black box) in Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho. 4. Lines of sections HC6 and HC5 on areas of U.S. Geological Survey Mapleton (1988) and Egan Basin (2005) 1: 24,000 7.5' quadrangle topographical maps, respectively.



FIGURE 2. Section of stratigraphic column of Section G (see Adrain *et al.* [2009] for full columns of sections G and H) showing occurrence of species of *Hintzeia* in the *Psalikilus spinosum* and *Hintzeia celsaora* zones of the Tulean. This part of Section G is a succession of thin beds of intraclastic rudstone ("flat pebble conglomerate") and covered slopes. Note that the lithological symbol appears to the right of the beds because it is too large to fit inside them. Original sampling horizons of Hintze (1951, 1953) are indicated at the corresponding metreage of our (2009) remeasurement.

Family Pliomeridae Raymond, 1913

Hintzeia Harrington, 1957

Type species. *Protopliomerops aemulus* Hintze, 1953 (=*Protopliomerops celsaorus* Ross, 1951); by original designation. This species is from western Utah, USA, and is Tulean (*Hintzeia celsaora* Zone) in age.

Other species. Protopliomerops firmimarginis Hintze, 1953 (Tulean, Psalikilus spinosum Zone); Hintzeia parafirmimarginis **n. sp.** (Tulean, Psalikilus spinosum Zone); H. plicamarginis Simpson, Hughes, Kopaska-Merkel, and Ludvigsen, 2005 (early Tulean).

Diagnosis. Anterior border long, wide, strongly anteriorly bowed, with median arcuate anterior curve in posterior margin of most species; anterior surface of posterior wall of border exposed in anterior view. Glabella rectangular, very gently anteriorly tapered, with small LF partially obscured by anterior border. Palpebral lobes with widest part of arc opposite S2. Pygidium of five segments and small, triangular terminal piece. Pygidial spines short to medium-long, slightly to moderately splayed, and slightly laterally flattened; with dorsally recurved tips in some species.

Discussion. Simpson *et al.* (2005, p. 538) diagnosed *Hintzeia* as possessing an L1 which is larger than L2 or L3. However, their description of *H. plicamarginis* states that its lateral glabellar lobes are equally sized (Simpson *et al.*, 2005, p. 539), and this is true also of the other three species of *Hintzeia*. Simpson *et al.* (2005) also included "S3 anterior or posterior to lateral glabellar corners", but the location of S3 is likely symplesiomorphic, as many pliomerids (e.g., species of *Pseudomera, Protopliomerella*, and *Lemureops* McAdams and Adrain, 2009a) possess a similarly positioned S3. Further, the position of S3 is not variable among illustrated specimens of *H. plicamarginis* nor those of the species described herein, and whether its distal end is anterior or posterior to the "lateral glabellar corner" would appear to depend on how one defined such a feature. Hypostomal characters are excluded from the diagnosis because the species (with the exception of *H. celsaora*) possess an apparently plesiomorphic, subrectangular hypostome with a long posterior border. The character "hypostomal lateral spines near posterolateral corners" is widely distributed among pliomerids, and is also shared with the cheirurid *Rossaspis* Harrington, 1957 (see Ross, 1951, pl. 31, figs 17, 18, 21, 22). Further, Edgecombe and Chatterton (1987, p. 345) considered that the seven marginal spines seen on pliomerid taxa such as *Hintzeia* are shared with some members of Encrinuridae Angelin, 1854, and are likely indicative of a close relationship of Encrinuridae to Pliomeridae.

Hintzeia glabella Kobayashi, 1960, was described from the Tremadocian Bunkoku Formation of South Korea. It is known only from a mold of a crushed partial cranidium, and as such is essentially a *nomen dubium*. It does not possess diagnostic features of *Hintzeia*, but its phylogenetic relationships cannot be confidently assessed without more material. *Hintzeia taoyuanensis* Liu in Zhou *et al.*, 1977, from the Tremadocian Madaoyu Formation of Hunan, China (see also Liu, 1982), was reassigned to *Protopliomerops* by Peng (1990), who revised it on the basis of several articulated individuals and additional disarticulated material. We concur that it is not a species of *Hintzeia*, though *Protopliomerops* is a problematical taxon with a very poorly known type species.

Whittington (1961, p. 917) suggested that *Hintzeia* and the Dapingian (Whiterockian) taxon *Kanoshia* Harrington, 1957, were "similar", and that *Pseudomera* cf. *P. insolita* (Poulsen, 1927) of Hintze (1953) from the upper Blackhillsian resembled the type species of both *Kanoshia* and *Hintzeia*. Demeter (1973, p. 58) assigned *K. kanoshensis* and *P.* cf. *P. insolita* to *Hintzeia*, rendering *Kanoshia* a junior subjective synonym, and Laurie and Shergold (1996) agreed. Hoel (1999) removed *Kanoshia* from synonymy with *Hintzeia*, citing differences in glabellar furrows and the hypostomal margin. We concur that neither *Kanoshia* (which is likely a junior synonym of *Pseudomera* and which we will revise in a forthcoming work) nor any species of *Pseudomera* should be assigned to *Hintzeia*. Knowledge of the morphology of species of *Pseudomera* and *Kanoshia* has been compromised since Hintze (1953, pl. 23, figs 5–13, pl. 25, figs 5, 6, 8–12) misassociated the head and hypostome of his *Cybelopsis* cf. *C. speciosa* Poulsen, 1927, with the tail of his *Pseudomera* cf. *P. insolita* and vice versa. Multiple occurrences of *Pseudomera* and *Cybelopsis* in upper Ibexian-Whiterockian strata at Ibex leave no doubt about the correct association, and Whittington (1961, pl. 100, fig. 17) also figured an articulated specimen of *Pseudomera* cf. *P. barrandei* (Billings, 1865) from the Whiterockian upper Pogonip group of the Toquima Range, Nevada. The mistaken association and its phylogenetic and taxonomic ramifications will be addressed in detail in a forthcoming paper on *Pseudomera*.

Hoel (1999, p. 276) assigned *Protopliomerops rossi* Harrington and Leanza, 1957, from the Tremadocian of Salta Province, Argentina to *Hintzeia*. Waisfeld and Vaccari (2003) also suggested that *P. rossi* was related to *Hintzeia* based on its lack of genal spines and the shape of the distal ends of the fixigenae. However, the short anterior border, lack of frontal areas, 14-segmented thorax, the presence of anterior pleural bands on all segments of its pygidium, and the posteriorly exposed terminal piece rule out its membership. Hoel (1999) also regarded the Floian species *"Pliomerops" actinurus* (Dalman, 1824) from Sweden and Norway as a member of *Hintzeia*, considering that "it is not easy to find any difference between *Hintzeia* and *Pliomerops* Raymond, 1905." *Pliomerops canadensis* (Billings, 1859), the type species of *Pliomerops* from the Mingan Formation (Sandbian) of Quebec, bears little close resemblance to either *"P." actinurus* or to any member of *Hintzeia*. Among many other differences, *Pliomerops canadensis* possesses a thorax of 18 segments (Shaw, 1968, pl. 2, fig. 3); that of *"Pliomerops" actinurus rus* has 14 segments (Hoel, 1999, fig. 16D); and that of species of *Hintzeia* has 15 segments (Plates 8, 11). Further, *"P." actinurus* lacks the distinctive posteriorly indented anterior border of *Hintzeia*.

The identity of specimens of "P." actinurus is not entirely straightforward. The species was illustrated by Angelin (1878, p. 35, pl. 22, fig. 2) as Pliomera actinura (Dalman, 1824) with a new species, Pliomera mathesii (p. 35, pl. 22, figs 1, 1a–1c). In these illustrations, "Pliomerops" actinurus and Pliomera mathesii are depicted as an articulated individuals very similar to the specimen figured by Hoel (1999, fig. 16D), although the specimen of "P." actinurus is approximately 70% as long as that of P. mathesii. Wiman (1908) examined museum collections and considered Pliomera mathesii a junior subjective synonym of "P." actinurus, stating that the former represented immature and tectonically deformed specimens of the latter. He also illustrated some specimens, which differ from Angelin's drawings in having a nearly square glabella with a median furrow on LF and a more widely splayed pygidium with shorter pleural spines. As both Angelin's description states that the glabella is square and some specimens have a faint median LF furrow; the pygidium was not described in detail. Hoel's material and Angelin's drawing clearly show an elongate, ovoid glabella without a median LF furrow, and the pygidia are similar, though the pleural spines are longer on Angelin's drawing. These discrepancies leave open the possibility that several distinct species have been confused as "Pliomerops" actinurus.

Hintzeia sp. indet. of Laurie and Shergold (1996, p. 90, pl. 6, figs 1–6, 9–11; *=Rossaspis* sp. of Legg [1976]), from the Emanuel Formation (Floian), though not well preserved, is similar to Hoel's (1999) material of "P." *actinurus*, and in fact Hoel directly assigned the Australian material to the Baltic species. This is difficult to evaluate given the available material, but there seem to be several differences, including shorter, more downwardly curved pygidial spines in the Australian taxon. One pygidium assigned by Laurie and Shergold (1996, pl. 6, figs 7, 8) is not conspecific with the other material. Based on comparison with our new collections from western Laurentia, it represents an early species of the telephinid *Carolinites* Kobayashi, 1940, and a closely similar Laurentian species will be described in a forthcoming work. "*Pliomerops*" *actinurus*, the Australian species, and "*Protopliomerops*" rossi are all similar to the early Whiterockian *Pliomerops* praematura Fortey, 1980, from the Vallhalfonna Formation of Spitsbergen, Norway, but the relationship of these species to *P. canadensis* and other taxa needs to be examined via phylogenetic analysis.

Toro and Monaldi (1981) erected *Benedettia* with the type species based on a single partial cranidium from the Floian San Juan Formation of Argentina, and assigned it to the subfamily Protopliomeropinae Hupé, 1953. They considered that the closest comparison was to *Kanoshia*, citing a similarly shaped glabella but different glabellar furrows and sculpture. They also compared *Benedettia* with *Hintzeia*, considering that some (unspecified) morphological characteristics were similar, and they differentiated the genera in the shape of the glabella, position of S3, and the cranidial sculpture. Vaccari (2003) figured additional material, including pygidia, librigenae, and two articulated specimens of a second species. He considered that this new information showed that *Benedettia* is related to *Canningella* Legg, 1976, and that together they are most likely closely related to a group of Floian-Darriwilian, mainly Laurentian taxa including *Cybelopsis* Poulsen, 1927, and *Ectenonotus* Raymond, 1920.

As noted above, *Protopliomerella* may cause paraphyly in *Hintzeia*, but we tentatively consider both genera valid until all species involved are revised and described, and a species-level phylogenetic analysis is conducted. *Hintzeia firmimarginis*, *H. parafirmimarginis*, and *H. plicamarginis* all possess a distinctive anteriorly bowed anterior border with a median anteriorly curved indentation in the posterior margin. *Hintzeia celsaora* does not; its border is wide, but is subrectangular. This may be evidence of paedomorphosis, as the anterior border in juvenile cranidia of *H. firmimarginis*, *H. parafirmimarginis*, and *H. plicamarginis* describes a smooth curve, and the inden-

tation develops and strengthens as size increases. *Hintzeia celsaora* possesses a shallow arc formed by the rostral suture on the median anteroventral rim of the anterior border, which is present to a much lesser extent in *H. para-firmimarginis*, and is not noticeable in large specimens of *H. firmimarginis*, but is observable on small cranidia (e.g., Pl. 1, fig. 25). This pattern also suggests paedomorphic development. The rostral suture arc is increasingly prominently developed in species of *Protopliomerella* (e.g., *P. contracta* Ross, 1951, pl. 33, figs 17, 27) and *Lemureops*. It is also present in *Pseudocybele altinasuta* Hintze, 1953, and it may be an important synapomorphy uniting these taxa. Other characters also suggest that *H. celsaora* at least may be more closely related to *Protopliomerella*. Its librigenae are narrow and elongate; its hypostome is strongly posteriorly tapered and the middle body is finely tuberculate; some thoracic segments possess a notch in the pleural spine; and the pygidium is short, with short, narrowly separated spines. This morphology is very similar to that of *P. contracta* and other species of *Protopliomerella* (unpublished data; see also undescribed species on figs 10, 11, 14, 15 of Adrain *et al.* [2009]).

Demeter (1973) figured numerous pliomerid sclerites collected from sections G, 1965 C and C-offset (approximately equal to Section D of Hintze [1951, 1953]; see Adrain *et al.*, 2009, p. 546), and Mesa. Those relevant to *Hintzeia* but which cannot be assigned to a species are dealt with here. Assignments that can be confirmed are included in the synonymy and discussion of the appropriate species of *Hintzeia* below. Demeter's (1973, pl. 3, figs 15a–15c) *Hintzeia* sp. probably represents a species of *Ibexaspis* Přibyl and Vaněk (1985). The cranidia of his pl. 4, figs 1a–1c, 5, 9, 10 do not belong to (respectively) *Kanoshia* cf. *kanoshensis* or *Pseudomera* cf. *P. insolita*, both of which Demeter had also assigned to *Hintzeia*. The cranidia of pl. 4, figs 1a–1c and 5 belong to a new pliomerid genus and to *Ibexaspis*, respectively; those of pl. 4, figs 9, 10 are too poorly preserved to assign with any confidence. *Ibexaspis* will be revised with description of numerous new species in a forthcoming work. Demeter figured two pygidia and a hypostome (1973, pl. 5, figs 2, 3, 7) in open nomenclature. They resemble those of *Hintzeia firmimarginis*, but they occur in the much younger *Heckethornia hyndeae* Zone and belong to a plesiomorphic new species tentatively assigned to *Cybelopsis*.

Hintzeia firmimarginis (Hintze, 1953)

Plates 1-4

- 1953 Protopliomerops firmimarginis Hintze, p. 208, pl. 22, figs 1–8.
- 1953 *Protopliomerops aemula* Hintze (=*Protopliomerops contracta* Ross, 1951); Hintze, pl. 22, fig. 9 (only; *non* pl. 22, figs 13–17 = *Hintzeia celsaora* Ross).
- 1973 *Hintzeia firmimarginis* (Hintze); Demeter, p. 56.
- 1997 Hintzeia firmimarginis (Hintze); Ross et al., p. 19.
- 2005 Hintzeia firmimarginis (Hintze); Simpson et al., p. 538.
- 2009 Hintzeia firmimarginis (Hintze); Adrain et al., p. 557, fig. 8B, E.

Material. Assigned specimens SUI 115119, 115120, 125500-125595, from Section G 99.3 m and G 99T-A m, Fillmore Formation (Tulean; *Psalikilus spinosum* Zone), southern Confusion Range, Ibex area, Millard County, western Utah.

Diagnosis. Cranidium with relatively long frontal areas; anterior border depressed medially over arcuate anterior curve in posterior margin (anterior view); librigena with very wide field and smoothly sloping posterior branch of facial suture along field; pygidium with relatively narrow axis and relatively wide terminal piece, with pleurae and spines dosoventrally flattened, spines long, widely splayed, with slightly dorsally recurved tips.

Description. Cranidium sub-semicircular in outline, long and broad, with sagittal length 50.3% (45.6–52.4%) maximum width across genal angles, highly vaulted (sag., tr.), with very strongly downturned fixigenae, and with dense sculpture of tiny granules all over; anterior border long, wide arc, with broadly anteriorly bowed anterior margin, posterior margin transverse in front of fixigenae and strongly arched anteriorly from glabella, forming arcuate curve slightly less than width of LF, border very strongly dorsally inflated, highest at lateral edges of inner margin arc (anterior view), decreased medially and exsagittally, densely covered in slightly coarser but still very fine granules; doublure mainly expressed as short anterior face of border, leaving bottom half of anterior surface of posterior wall of border exposed in anterior view, with only a short doublural rim ventrally; anterior border furrow (in dorsal view) short, slightly longer medially and near apodemal pits at meeting with axial furrows, overhung by border, extremely deep, broadly arcuate with lateral transverse sections similar to those of border; glabella moder-

ately inflated (sag., tr.), long, moderately narrow, nearly parallel-sided, very slightly anteriorly tapered, subrectangular, with maximum width across L1 93.4% (88.6-95.5%) sagittal length, and with rounded anterior margin (ventral view); lateral lobes slightly independently inflated, separated by short, deeply incised sulci directed anterolaterally at about 20–30° and with slightly backturned inner ends, L1 longest, slightly narrower than L2 and L3, subtriangular, L2 and L3 subrectangular, about 1/3 total glabellar width, frontal lobe wide, short, wedge-shaped; SO shallowly W-shaped, short and moderately deep medially, lengthened laterally over very deep apodemal pits; LO long medially, tapered laterally from midpoint of apodemal pits, moderately inflated, with small median tubercle located slightly posterior of midlength; doublure lens-shaped, fairly long, reaching nearly to SO, slightly laterally tapered, smooth; axial furrows narrow, deep, confluent with all cranidial furrows except palpebrals, roughly parallel-sided, but bowed around edges of LO and expanded back laterally at base of L1; frontal areas strongly downturned (lateral view), long (anterior view), wide, triangular, with scattered small pits; ocular ridges directed posterolaterally at about 50° below transverse, weakly inflated from axial furrows to about mid-width of frontal areas, then increasingly strongly inflated posterolaterally, with slightly coarser granulose sculpture than fixigena; palpebral furrows long, narrow, sigmoid, very shallow until about mid-length of ocular ridge, then deep and incised; palpebral lobes short, narrow, arcuate, slightly dorsolaterally raised, but lower than arch of interocular fixigena (anterior and lateral views), located with furthest exsagittal point on arc of lobe even with abaxial end of S2; interocular fixigena triangular, narrower anteriorly and expanded posteriorly, broadly arched, with steep dropoff into axial furrows; posterior fixigena approximately same length as interocular fixigena and slightly more than twice as wide, very strongly downturned beginning at point even with posterolateral edge of palpebral lobe (anterior view), with gently anteriorly convex anterior margin and smoothly curved lateral margin, entire fixigena with scattered small pits except on very slightly raised ridge following course of posterior border furrow; posterior border furrow short, ventrolaterally tapered, deep, incised, transverse until genal angle, then smoothly anteriorly curved; posterior border shortest adaxially, expanded ventrolaterally until maximum length of about double reached at genal angle, then very strongly anteriorly tapered to a fine point, with small, stubby spine at genal angle, and with extremely short articulating tongue running along transverse section; doublure of inner section expressed as the articulating tongue, then curved inward and expanded into short doublure along genal angle.

Hypostome long, narrow, widest across anterior wings, subrectangular, with width across shoulders 71.5% (69.2–73.0%) sagittal length; hypostomal suture broad, very shallowly arcuate; anterior border vanishingly short medially, longer laterally and merged into large, nearly equilaterally triangular anterior wings with small, deep wing process pits; anterior border furrow strongly anteriorly bowed, very short, moderately deep medially, slightly laterally shallowed into merger with lateral branches of middle body furrow at lateral notch; middle body long, narrow, ovoid, with long, posteriorly tapered, strongly ventrally inflated (sag., tr.) anterior lobe, lobe sculpture of small, very closely spaced granules (coarser anteriorly) rimming central circular effaced area; middle body furrow with narrow, incised, posteriorly convergent lateral sections and barely impressed posteriorly bowed median section; posterior lobe short, U-shaped, with strongly anteriorly tapered lateral sections terminating at junction of middle body and lateral border furrows, weakly inflated, effaced; lateral border furrows moderately narrow, deep, but shallow over lateral branches of posterior lobe; posterior border furrow short, shallow, ill-defined; lateral border narrow at wide, shallow lateral notch, expanded to moderately wide at shoulders, constricted just posterior from shoulders, then expanded to maximum width a little posterior from midway between shoulders and posterolateral corners, moderately inflated, gently downturned (lateral and posterior views), with dense granulose sculpture and small stubby spines at posterolateral corners and at maximum width; posterior border long, moderately downturned, with somewhat effaced area near posterior border furrow, and dense granules posteriorly; doublure moderately long, reaches nearly to posterior border furrow, lateral doublure slightly narrower, effaced.

Rostral plate unknown.

Librigena approximately triangular in outline, with width of librigenal field under midpoint of eye 42.9% (38.3–48.0%) length of lateral border furrow; anterior branch of facial suture fairly short and subvertical to gently posterodorsally sloped along field, long and subhorizontal to anteroventrally sloped at about 30° along anterior projection of lateral border; posterior branch of facial suture long and steeply posteroventrally sloped (about 40°) along field, short and strongly posterodorsally curved along posterior projection of border; eye small, ovoid, moderately inflated, separated from field by short, shallow furrow far posteriorly, otherwise by break in slope, with visual surface of many tiny, closely packed lenses; librigenal field wide, moderately long, subtriangular, gently convex with convexity increasing anteriorly (ventrolateral view), with very dense sculpture of minuscule granules

and with more sparsely distributed small pits concentrated anteriorly and toward the eye; lateral border furrow narrow, moderately shallow, slightly ventrolaterally curved; lateral border strongly inflated, very long, wide, gradually tapered posteriorly to a wide point at tip of posterior projection, widened and rotated posteromedially near tip of very long anterior projection (ventrolateral view), with dense granulose sculpture about twice or three times coarser than that of field, but finer and sparser on anteroventral portion of anterior projection; doublure smooth, wide, slightly tapered and bluntly truncated at about 1/3 length of anterior projection, slightly tapered along curvature of posterior projection, forming point of projection, with inner surface visible as triangle in external view.

Total number of thoracic segments unknown. Segments short, wide, highly arched pleurally and axially with spinose pleurae strongly downturned at fulcrum, and with dense sculpture of very fine granules all over; articulating half ring short, longer medially and tapered laterally; articulating furrow short, deep and incised (Pl. 3, figs 1, 23), or shallow medially (Pl. 3, figs 2, 9, 10), with deep apodemal pits adaxial from axial furrows, course very shallowly U-shaped with wide median section transverse and gradual anterior divergence of lateral ends; axial ring short, moderately narrow, with width of axis 36.8% (34.5–39.5%) width across tips of anterior pleural band, subrectangular, slightly elongated and gently anteriorly divergent near axial furrows, gently inflated medially, more strongly near axial furrows; doublure very short, laterally tapered lens, smooth except for very fine transverse ridge at half length and sigmoid ridge located far laterally, leading from anterior margin to lateral termination of doublure (Pl. 3, fig. 13); axial furrows narrow, slightly widened into triangular shape at junction with pleural furrow, deep (Pl. 3, figs 1, 23) or shallow (Pl. 3, figs 2, 9, 10), subparallel along posterior pleural band, then strongly anteriorly convergent from pleural furrow; anterior pleural band very short, about half length of posterior band, wide, reaching to base of spine, gently independently inflated, with vanishingly short articulating tongue running width of band, set off posteriorly by extremely short, shallow furrow, and with small, hook-like articulating device at ventrolateral tip; pleural furrow short, slightly expanded ventrolaterally, very deep, incised; posterior pleural band wide, moderately long, slightly longer ventrolaterally toward spine, about twice as inflated as anterior band, with rounded inner margin, with very short articulating tongue on posterior margin, tapering out just past fulcrum, set off anteriorly by short, incised furrow (longer near axis; posterior views), and with long, laterally flattened, slightly anteromedially rotated (producing broad facet seen in lateral view; e.g., Pl. 3, figs 12, 16), strongly ventrally tapered, sharply pointed, ventrally directed spine; doublure short, mainly turned out into posterior articulating tongue, but recurved inward at base of spine to merge with wide inner face of spine.

Pygidium of five spinose segments and terminal piece, highly vaulted axially and pleurally (sag., tr.; anterior view), with fulcral angle of about 105°, roughly semicircular, long and wide, with sagittal length from articulating furrow 63.5% (59.8–67.2%) width across anterior pleural band of first segment, and with dense, finely granulose sculpture, and somewhat coarser granules on axis, along edges of pleurae and spines, and on pygidial border (ventral view), sculpture increasingly effaced (beginning with main parts of spines and pleurae) on larger specimens; articulating half ring very short, laterally tapered; articulating furrow short, deep (shallower medially on larger specimens), with deep apodemal pits slightly adaxial from axial furrows; axis long, wide anteriorly, strongly tapered posteriorly to point at tip of terminal piece, with width of fifth segment about half that of first segment, strongly vaulted (sag., tr.) anteriorly, with vaulting progressively decreased posteriorly; axial rings short, wide, individually moderately inflated, subrectangular with rounded edges, slightly anteriorly bowed (in dorsal view; shape changes slightly with orientation), particularly fifth ring; terminal piece small, triangular, about as long as wide, moderately inflated, just barely enclosed by pleurae; inter-ring furrows moderately long, slightly tapered laterally, longer in larger specimens, with first furrow longest, deep, shallower medially, with deep apodemal pits near axial furrows; axial furrows narrow, with wider areas at intersections with interpleural furrows, deep, impressed over each pair of pleurae, strongly anteriorly divergent, convergent at tip of terminal piece, and continued as single median furrow separating last pair of pleurae; anterior pleural band fully expressed only on first segment, slightly inflated, very short, wide, reaches to level with base of spines, effaced, with extremely short, thinner articulating tongue running width of band (best visible in lateral view, e.g., Pl. 3, fig. 30; damaged on many specimens) set off by very short, faint furrow, and with small, anteriorly curved hook-like articulating structure at base of band (lateral view, e.g., Pl. 3, fig. 30, Pl. 4, figs 8, 18; damaged on many specimens), weakly expressed on second segment of large pygidia as very short, slightly raised, granulose stripe (Pl. 3, fig. 21, Pl. 4, figs 1, 3, 11, 17; pleural furrow very short, deep, incised, slightly shallower ventrolaterally; posterior pleural bands each moderately inflated dorsally, increasing to very strongly inflated ventrolaterally (lateral view), long, wide, slightly tapered at adaxial ends and at base of spine, section beyond fulcrum laterally flattened, pleurae increasingly posteriorly directed, with fifth

pair subparallel, each with widely separated, wide, tapered, bluntly pointed, slightly flattened (dorsoventrally and laterally) spine projecting posteroventrolateraly, with tips slightly recurved dorsally, from ventrolateral margin of pleurae; interpleural furrows moderately long adaxially, narrower ventrolaterally, deep, incised, increasingly posteriorly directed in course to follow pleurae; pygidial border expressed ventrally as long and wide shelf, with granulose sculpture, and with slightly inflated, effaced inner margin set off by long, fairly shallow furrow; doublure visible only in anterior view (Pl. 4, fig. 10) short, longest at median point and strongly tapered anterolaterally, smooth.

Ontogeny. All figured specimens of *H. firmimarginis* are probably holaspid, but in the cranidia it is possible to observe the lengthening of the anterior border and increasing development of the anterior curve in the posterior margin; the lengthening of the frontal areas; and elongation and narrowing of the glabella as cranidial size increases (cf. specimens of Pl. 1, figs 1–2 with those of Pl. 1, figs 11, 20 and Pl. 2, fig. 6). The hypostome elongates slightly; the middle body furrow shallows; the shoulders broaden; the lateral border broadens at the posterolateral corners; and the posterior border nearly doubles in length (cf. Pl. 2, figs 3–5). Few changes are observable in the librigenae, but the smaller specimens (Pl. 2, figs 24–25) have slightly narrower librigenal fields that are also slightly longer under the eye than the larger specimens, and the pits on the librigenal field are shallower. Ontogenetic changes cannot be observed in the thoracic segments due to the small sample size and variability depending on the position in the thorax. Overall, the pygidium becomes slightly longer, as do the spines; the inter-ring and interpleural furrows lengthen, especially the first interpleural furrow; the second anterior pleural band develops; the axis narrows and tapers more strongly posteriorly; and the spines splay out (cf. Pl. 3, fig. 1, Pl. 4, figs 1, 3 with Pl. 4, figs 17, 20).

Discussion. Specimens of *H. firmimarginis* show little variation. The cranidium of Pl. 1, fig. 2 has a slightly narrower and more tapered glabella than that of Pl. 1, fig. 13. The anterior border arc is wider in that of Pl. 1, fig. 11 compared to that of Pl. 11, fig. 12. The specimen of Pl. 1, fig. 3 has a mildly deformed right S3, which is more anteriorly positioned compared to the left furrow, posterolaterally bowed, and does not reach the anterolateral margin of the glabella. The hypostome of Pl. 2, fig. 4 is narrower and more elongate than that of Pl. 2, fig. 5, but this may be ontogenetic. The librigena of Pl. 2, fig. 22 has a wider field and wider lateral border with a shorter posterior projection than the others. Among pygidia, the length, width, and shape of the terminal piece is somewhat variable (cf. Pl. 4, figs 1, 11). The splay, taper, and degree of recurvature at the tip of the spines also vary slightly.

Hintzeia firmimarginis is compared to *H. parafirmimarginis* in the differential description of the latter taxon, and to and *H. celsaora* in its discussion section. *Hintzeia plicamarginis* Simpson *et al.*, 2005, is better documented than many trilobite taxa in terms of the number of specimens illustrated, but comparison is hindered by the small size of the images and lack of many alternate views. The orientations used by Simpson *et al.* (2005) also differ from those herein: their cranidia and hypostomes are tilted further anteroventrally in dorsal view, their librigena is ventrolaterally tilted compared to those illustrated herein, and the posterior view of the pygidium is tilted much further anteroventrally. Differing orientations can affect the perceived appearance of lengths and widths (e.g., the width of a librigenal field), and convexity (e.g., the shape of the arc of a transverse furrow), and must be considered carefully in differential discussions.

Hintzeia firmimarginis differs from *H. plicamarginis* in possessing a much wider, less anteriorly bowed, less laterally downturned (anterior view) anterior border with a wider, shallower, less depressed (anterior view) arcuate indentation in the posterior margin; a shorter anterior border furrow (medially and laterally in apodemal pits); a slightly wider glabella (across L1), with a larger L1 and narrower LF; narrower axial furrows; longer frontal areas; a more prominent ocular ridge; and shorter, wider posterior fixigenae. The hypostome is relatively shorter and wider; the anterior wings are broader and larger; the middle body is shorter and more strongly posteriorly tapered, with a shorter anterior lobe, much shallower middle furrow, longer posterior lobe, more granulose sculpture anteriorly, and without prominent pits; the lateral border is slightly wider, with the shoulders located more anteriorly; and the posterior border is longer, with a smaller, more rounded median spine. Librigenae are similar, but that of *H. firmimarginis* has a wider field with a more steeply sloped posterior projections; and the doublure is exposed as a wider, narrower triangle in external view. No thoracic segments of *H. plicamarginis* were illustrated. The pygid-ium of *H. firmimarginis* is wider; the pleurae are more strongly anterolaterally arched and splayed further apart; and the pleural spines are shorter, wider and less tapered, and more strongly ventrally directed, with a much shorter recurved tip.

Hintzeia parafirmimarginis n. sp.

Plates 5-9

2003 *Hintzeia* cf. *aemula*; Hintze and Davis, fig. 88.
2009 *Hintzeia* sp. nov. 1; Adrain *et al.*, p. 557, fig. 8C, F.

Material. Holotype, SUI 115122, and assigned specimens SUI 115121, 125533-125558, from Section HC6 165.2, Garden City Formation (Tulean; *Psalikilus spinosum* Zone), Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho; UU 10051.90, exact locality uncertain, Fillmore Formation (presumably Tulean, *Psalikilus spinosum* Zone, but exact horizon unknown), Ibex area, Millard County, western Utah.

Etymology. Latin para, against, and the specific epithet firmimarginis.

Diagnosis. Glabella nearly square; hypostome with fine tubercles and granules on anterior half to two-thirds of anterior lobe of middle body; pygidial spines conical, strongly tapered, and moderately splayed.

Description. *Hintzeia parafirmimarginis* **n. sp.** is morphologically very similar to *H. firmimarginis* (Hintze, 1953) and is treated via differential discussion. Ratios are given to facilitate comparison with the other species.

Cranidia of *H. parafirmimarginis* are only subtly different from those of *H. firmimarginis*, with sagittal length 46.4% (41.3–51.1%) maximum width across genal angles and maximum glabellar width across L1 97.6% (91.1–105.9%) sagittal length; with shorter frontal areas (anterior view); a weakly developed rostral suture arc on the median anteroventral rim of the anterior border; a shorter anterior border furrow more overhung by the anterior border; narrower LF; anterior of LF also more obscured by border; slightly more straight-sided glabella; slightly wider interocular fixigenae; more inflated and prominent eye ridges and palpebral lobes; wider posterior fixigenae; and with slightly coarser granulose sculpture and deeper, denser fixigenal pitting.

The hypostomes are also very similar, but that of *H. parafirmimarginis* is slightly shorter, with width across shoulders 68.9% (67.0, 70.7%) sagittal length; anterior wings slightly shorter and narrower; middle body more strongly inflated, more densely granulose, without posteromedian effacement; lateral branches of middle body furrow less posteriorly convergent, shallower, extend only to about half length of middle body; posterior border shorter, more strongly posteromedially tapered; and with spines on lateral and posterior borders very small points rather than larger rounded nubs.

Hintzeia parafirmimarginis is the only species of the genus for which a rostral plate has been found. It is attached to the articulated specimen (Pl. 8, fig. 4), so only the anterior face is exposed. Rostral plate sub-equilaterally triangular, with dorsal edge slightly longer than lateral edges, wider than long, densely granulose.

Librigenae of *H. parafirmimarginis* are narrower than those of *H. firmimarginis*, with width of librigenal field measured at midpoint of eye 34.9% (32.0–37.0%) length along lateral border furrow; field shorter, more strongly posteriorly tapered, less densely and less deeply pitted; lateral border wider, especially near anterior edge of field, and posteriorly tapered along length of field; and with slightly shorter anterior and posterior projections of border.

The thoracic segments are virtually identical. The axial width is 38.4% (35.8–39.9%) width across anterior pleural band.

The pygidia differ most significantly (cf. Pl. 3, fig. 28, Pl. 7, fig. 13). Those of *H. parafirmimarginis* are shorter and narrower, with sagittal length from articulating furrow 60.9% (58.7–64.0%) width across anterior pleural band of first segment; axis less strongly vaulted; inner pleurae narrower (anterior views); posterior pleural bands shorter, more roundly inflated, not flattened; interpleural furrows shorter; pleurae more strongly posteriorly directed; spines longer, narrower, more strongly tapered, more inflated, not recurved, less widely separated; sculpture slightly coarser; doublure slightly longer medially.

Ontogeny. As in *H. firmimarginis*, the anterior border of *H. parafirmimarginis* lengthens, the lateral sections widen, and the median posterior arcuate curve develops; the glabella becomes shorter and wider; the median LO tubercle lessens in prominence; the axial furrows broaden; the eye ridges become more distinct from the arc of the palpebral lobe; the posterior fixigenae broaden; the genal spine is reduced in size, although a small spine remains even on very large cranidia (Pl. 8, fig. 5); and the coarseness of the granulose sculpture is slightly decreased (cf. Pl. 5, figs 1, 31, Pl. 9, fig. 1). The hypostomes (Pl. 7, figs 1, 3, 4) are very close in size, but it is possible to observe the anterior wings becoming broader; the lateral border widening, especially at the posterolateral corners; and the posterior border lengthening, especially medially. The librigenal field widens and elongates slightly; the pits deepen; the eye decreases in size relative to the field; and the lateral border also widens, but the anterior and posterior projections become relatively shorter as the field increases in length (cf. Pl. 6, figs 9, 11 with Pl. 6, fig. 1 and Pl. 9, fig. 2). Thoracic morphol-

ogy varies by the position of the segment, but the axis and axial furrows widen; the furrows for the posterior articulating tongue become more incised; the flange of the spines lengthens; and the granulose sculpture decreases in coarseness (cf. segments of Pl. 6 with thorax of articulated individual, Pl. 8). Pygidia widen; the inter-ring, axial, and interpleural furrows lengthen or widen; the terminal piece elongates; the anterior pleural band develops on the second segment (Pl. 7, fig. 12, best seen on left side); the pleural spines lengthen and splay further apart; and the granulose sculpture decreases in coarseness (cf. Pl. 7, fig. 23, Pl. 9, fig. 5).

Discussion. There is little intraspecific variation in *H. parafirmimarginis*. Cranidia of the same sizes (Pl. 5, figs 3, 15; 18, 19; and 26, 31) are essentially identical, although the amount of LF covered anteriorly by the anterior border varies slightly. The slope of the posterior branch of the facial suture along the librigenal field, and the point of the change in slope are also slightly different. The pygidium of Pl. 7, fig. 14 has a smaller terminal piece relative to its axis. The splay of the pygidial spines differs slightly among the specimens, but that could also be due partly to preservation, as those of Pl. 7, figs 12, 13 are slightly crushed. The hypostomes are not comparable in size, and the thoracic segments require a larger sample for comparison.

Compared to Hintzeia plicamarginis Simpson et al., 2005, H. parafirmimarginis has a shorter, wider, less strongly anteriorly bowed anterior border with a wider, shorter median anteriorly arcuate curve in the posterior margin, the border is much less depressed medially over the curve in anterior view, and it also seems to develop the median curve in relatively larger cranidia (cf. Pl. 5, fig. 15 with fig. 12.10 of Simpson et al. [2005]); the anterior border furrow is shorter, especially medially and laterally in the apodemal pits; L1 is slightly wider and larger relative to the other lateral glabellar lobes; the median node on LO is less distinct; the interocular and posterior fixigenae are slightly wider; and the granulose sculpture overall is slightly denser and finer. The hypostome (cf. Pl. 7, fig. 1 with fig. 14.9 of Simpson et al. [2005]) is relatively shorter and broader; with wider anterior wings; a shorter, wider middle body with a much longer (medially) posterior lobe, closely spaced granules anteriorly, and without distinct pits; narrower shoulders with the widest part located much further anteriorly; and with smaller spines spaced further apart on the lateral border; and a longer, more granulose posterior border. Librigenae of *H. parafirmimarginis* are very similar, but the librigenal field is narrower, especially posteriorly, and much less pitted; the lateral border furrow is more strongly curved; the lateral border is also more strongly curved, especially along the posterior projection; and less doublure is visible in external view. The pygidium is shorter, with a broader axis; shorter, relatively wider terminal piece; much shorter (measured obliquely), more conical pleurae that curve strongly posteroventrally and lack a lengthy recurved tip; and the ventral pygidial border is shorter, without a raised anterior rim.

Cranidia of *H. parafirmimarginis* differ from those of *H. celsaora* in possessing a more strongly anteriorly bowed anterior border with a median anteriorly arcuate curve in the posterior margin and with a shallow, ill-defined rostral suture arc on the edge of the doublure only of larger specimens (anterior view); a longer, narrower glabella with a longer or more anteriorly exposed LF; a slightly shorter, deeper SO; and a more prominent median node on LO. Hypostomes are very similar, but that of *H. parafirmimarginis* is more elongate; the middle body has fine granules on only the anterior portion of the anterior lobe; the lateral border is wider, and the spines are only small nubs; and the posterior border is slightly longer and more finely granulose. Librigenae are wider in both the librigenal field and lateral border; the field is much wider anteriorly and less deeply pitted; the lateral border is wider, more so anteriorly, and slightly more finely granulose. Thoracic segments of the two species are nearly identical, except that some of those belonging to *H. celsaora* (Pl. 14, figs 4, 12) display a slight notch near the ventrolateral tip of the spine, and no segments of *H. parafirmimarginis* show this feature. Pygidia are also very similar, but that of *H. parafirmimarginis* is wider, with a narrower axis; the terminal piece is shorter; the pleurae are longer (oblique), less strongly posteriorly directed, more anterolaterally bowed, and splayed more, with much more space between the tips of the spines; the ventral pygidial border is slightly longer and wider; the doublure is much shorter and more strongly medially pointed; and the sculpture is much denser.

Hintzeia celsaora (Ross, 1951)

Plates 10-14

- 1951 *Protopliomerops celsaora* Ross, p. 135, pl. 31, figs 1–5, 8–15 (*non* pl. 31, figs 6–8), pl. 34, figs 9–12, 20, pl. 35, fig. 29?
- = 1953 Protopliomerops aemula Hintze, p. 206, pl. 22, figs 13–17 (non pl. 22, fig. 9 =Hintzeia firmimarginis [Hintze]).
- ? 1953 Protopliomerops aff. P. celsaora Ross; Hintze, p. 207, pl. 22, fig. 10.

- 1957 *Hintzeia aemula* (Hintze); Harrington, p. 811.
- 1957 *Hintzeia celsaora* (Ross); Harrington, p. 811.
- 1961 *Hintzeia aemula* (Hintze); Whittington, p. 917.
- 1973 Hintzeia celsaora (Ross); Demeter, pp. 56, 58, pl. 3, figs 11–13 (only).
- 1973 Genus and species undetermined; Demeter, pl. 5, fig. 17 (only).
- 1973 *Hintzeia aemula* (Hintze); Hintze, p. 17.

?

?

- 1986 *Hintzeia aemula* (Hintze); Ingham *et al.*, p. 503.
- 1987 Hintzeia aemula (Hintze); Edgecombe and Chatterton, p. 345.
- 1989 *Hintzeia celsaora* (Ross); Dean, pp. 13, 20.
- 1997 *Hintzeia celsaora* (Ross); Lee and Chatterton, p. 691.
- 1997 *Hintzeia celsaora* (Ross); Ross *et al.*, p. 19
- 1998 *Hintzeia celsaora* (Ross); White and Lieberman, pp. 61, 106.
- 1999 Hintzeia celsaroa [sic] (Ross); Hoel, p. 276.
- 2003 *Hintzeia celsaora* (Ross); Hintze and Davis, p. 73.
- 2003 Hintzeia celsora [sic] (Ross); Hintze and Davis, p. 301 (Correlation Chart 3).
- 2003 *Hintzeia aemula* (Hintze); Jell and Adrain, p. 384.
- 2005 *Protopliomerops celsaora* Ross; Simpson *et al.*, p. 538.
- 2005 Hintzeia aemula (Hintze); Simpson et al., p. 541.
- 2009 Hintzeia celsaora (Ross); Adrain et al., p. 559, fig. 9A, E.

Material. Assigned specimens SUI 125559-125567, from Sections HC5 186.5 m and HC6 171.0 m, Garden City Formation (Tulean; *Hintzeia celsaora* Zone), Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho; SUI 125568, 125569 from Section D 59T m, Fillmore Formation (Tulean; *Hintzeia celsaora* Zone), southern House Range, Ibex area, Millard County, western Utah; SUI 115142, 115143, 125570-125595 from Section G 118.6 m, Fillmore Formation (Tulean; *Hintzeia celsaora* Zone), southern Confusion Range, Ibex area, Millard County, western Utah; Suit 115142, 115143, 125570-125595 from Section G 118.6 m, Fillmore Formation (Tulean; *Hintzeia celsaora* Zone), southern Confusion Range, Ibex area, Millard County, western Utah.

Diagnosis. Anterior border without median curve in posterior margin and with shallow rostral suture arc in anteroventral rim (anterior view); glabella wider than long; librigenae narrow, with narrow field and abrupt change in slope of posterior branch of facial suture midway along field; hypostome teardrop-shaped, with densely, finely tuberculate anterior lobe and effaced posterior lobe; thoracic segments with long articulating furrow, and some with notch in pleural spine; pygidium subquadrate, with short, slightly splayed spines.

Description. Cranidium moderately short, wide, subtrapezoidal in outline, with sagittal length 47.8% (44.7– 50.0%) maximum width across genal angles, highly vaulted (sag., tr.) axially and fixigenally, with dense, finely granulose sculpture on all areas; anterior border highly inflated, wide, long medially and abruptly tapered at lateral margins, very gently anteriorly bowed; doublure expressed mainly as anterior face of border, exposing ventral half of anterior face of posterior wall of border, doublure only a rim ventrally, rim with broad, shallow median arc formed by course of rostral suture (anterior view); anterior border furrow short, longer laterally and in apodemal pits at junctions with axial furrows, very deep, very gently anteriorly bowed, slightly overhung by border medially; glabella fairly short and wide, nearly square, with width across L1 108.9% (101.5–117.3%) sagittal length, parallel sided to slightly anteriorly tapered, moderately vaulted (sag., tr.), with independently inflated lateral lobes; lateral lobes roughly equal in length and width, but L1 more subtriangular in shape rather than rectangular, lobes each about 1/3 total glabella width, frontal lobe short, narrow, subtriangular; glabellar sulci short (S1 longer), deep, incised, producing strong ventral apodemes, with slightly posteriorly elongate inner ends, anterolaterally directed at about $30-50^{\circ}$ from transverse; SO short medially, flared laterally into apodemal pits located level with about half width of L1, moderately deep medially, very deep in pits, confluent with axial furrows; LO long medially, abruptly tapered to about half median length at and lateral from apodemal pits, moderately inflated, with small median tubercle located at half length; doublure reaches not quite to SO, elliptical, laterally tapered, smooth except for very fine transverse ridge at midlength (Pl. 10, fig. 20, Pl. 12, fig. 17); axial furrows narrow, deep, incised, subparallel (e.g., Pl. 10, fig. 1, Pl. 12, fig. 13) or gradually anteriorly convergent (e.g., Pl. 10, fig. 13, Pl. 12, fig. 1) and slightly laterally bowed, intersect all other cranidial furrows except palpebrals; frontal areas very short, narrow, small, triangular (best seen on Pl. 10, figs 6, 8, 9, 16), set off from eye ridges by line of small pits; eye ridges mildly inflated, arcuate, short (oblique) and narrow; palpebral furrows long (oblique), narrow, incised, with arcuate to shallowly sigmoid course, define posterior edge of eye ridges and palpebral lobes; palpebral lobes located level with S2, short, arcuate, with narrow anteriorly recurved posterior section, slightly dorsolaterally raised, but lower than curvature of fixigena (anterior view); interocular fixigena short, wide, triangular, nearly horizontal between axial fur-

rows and fulcrum; posterior fixigena slightly longer than interocular, more than twice as wide, rectangular, with rounded anterolateral margin, strongly downturned from fulcrum (anterior view), entire fixigena with dense scatter of small pits on top of very fine granules, and with slightly raised, unpitted border along axial and posterior border furrows; posterior border furrow mostly transverse, with strong, rounded forward curvature at genal angle, short adaxially, slightly longer along middle section of course, then rapidly tapered anterolaterally at genal angle, mostly deep, but shallower along anterolateral section; posterior border short adaxially, expanded laterally to maximum length of about double adaxial length at genal angle, then sharply tapered to a point, genal angle rounded, with very small stubby spine; doublure of short rim adaxially, rotated outward and partially expressed dorsally as extremely short articulating tongue set off anteriorly by extremely short, incised furrow (Pl. 10, fig. 20), expanded laterally to maximum length just before genal angle, and shallowly cut by facial suture just adaxial from genal angle (Pl. 10, fig. 20).

Hypostome long and narrow, posteriorly tapered, widest across anterior wings, with width across shoulders 74.6% (70.1–78.0%) sagittal length; anterior border extremely short medially, flared laterally into small, roughly equilaterally triangular anterior wings with small, deep wing process pits; anterior border furrow extremely short, deep, incised medially, shallower laterally toward meeting with lateral branches of middle body furrow, strongly anteriorly bowed, nearly semicircular in course on most specimens (narrower on specimens of Pl. 10); middle body elliptical, long, narrow, only slightly tapered, nearly same width posteriorly as anteriorly; anterior lobe strongly ventrally inflated, ovoid, roughly three times longer than posterior lobe, with dense, coarse sculpture of small tubercles; middle body furrow strongly impressed only on short, narrow, anteriorly divergent lateral branches, effaced medially; posterior lobe of middle body mainly defined by effacement, U-shaped, wider than anterior lobe, longer medially than laterally, with long lateral branches wrapping about halfway up sides of anterior lobe, weakly ventrally inflated; lateral border furrows narrow, deep, incised, shallower anteriorly at intersection with anterolateral end of middle body furrow and posteriorly toward posterior border furrow; posterior border furrow, short, shallow, weakly posteriorly convex; lateral border moderately inflated, narrowest at long, shallow lateral notch, posteriorly expanded to shoulders, narrowed, then expanded again to maximum width at pair of spines anterior to posterolateral corners, slightly tapered adaxially to posterolateral corners, with small, pointed spines at shoulders, posterolateral corners, and point slightly posterior from halfway in between, densely granulose, with slightly finer granules than on middle body; posterior border moderately long, slightly longer than maximum width of lateral border, narrow, posteriorly tapered, strongly downturned (lateral view), with same granulose sculpture as lateral border, and slightly larger pointed median spine; doublure short, reaches about half length of posterior border and nearly entire width of lateral borders, strongly dorsomedially upturned, smooth.

Rostral plate unknown.

Librigena long and narrow, very roughly subtriangular in outline; anterior branch of facial suture very short along field, almost three times longer along anterior projection of lateral border, with junction angle of about 90°; posterior branch of facial suture very long, steep and gently posteriorly bowed from eye to about midlength, then less steeply angled at about 30° to lateral border, then posterodorsally curved along posterior projection of lateral border, all three segments of approximately equal length; eye not well known, but small, elliptical (Pl. 13, fig. 5), located on steeply raised platform (Pl. 13, figs 1, 3); librigenal field irregularly triangular, narrow, long, with width of field under midpoint of eye 27.2% (25.1–31.0%) length along lateral border, gently laterally convex (ventrolateral views), densely granulose and pitted like fixigenae; lateral border furrow moderatly narrow, deep, gently laterally bowed; lateral border long, with long anterior and posterior projections, anterior projection somewhat posteromedially rotated, creating triangular flange (ventrolateral views), border very wide anteriorly, widest level with anterior edge of field, increasingly tapered posteriorly to blunt point, strongly inflated, with inflation highest anteriorly and decreasing posteriorly, densely granulose with coarser granules matching those of anterior border; doublure effaced, wide, not quite as long as librigena, bluntly terminated anteriorly at about half length of anterior projection, gradually tapered posteriorly, with small portion of inner face visible in external view at posterior end.

Thorax of 15 segments, widest anteriorly, with sides subparallel to about segment seven, then increasingly strongly tapered posteriorly, with each segment highly vaulted pleurally and axially (sag., tr.), with fulcral angle of approximately 115–120° separating steep distal portions of pleurae from horizontal proximal parts, and with very fine granulose sculpture; articulating half ring short, approximately equal to length of axial ring medially, tapered laterally, semilunate; articulating furrow long medially, sharply anterolaterally tapered into very deep apodemal pits located just adaxial from axial furrows, shallow medially, deep laterally; axial ring short, subrectangular with

rounded lateral margins and slightly anterolaterally directed ventrolateral sections, 39.3% (36.6–42.6%) width across anterior band of segment, moderately inflated; doublure short, laterally tapered, elliptical, effaced but for fine transverse median ridge (Pl. 14, fig 7); axial furrows narrow except widened triangularly at junction with pleural furrows, deep, incised, subparallel along axial ring, then strongly anteriorly convergent; anterior pleural band slightly inflated, very short, about half length of posterior band, wide, with about 1/3 width distal to fulcrum, with extremely short, wide articulating tongue set off from anterior edge by extremely short, incised furrow, and with small, anterodorsally directed articulating hook structure at ventral tip (Pl. 14, fig. 12); pleural furrow short, very deep, incised, very slightly shallowed and anteriorly directed at tips; posterior pleural band wide, short, lengthened ventrolaterally into long, gently anteromedially rotated facet and spine base (lateral and anterior views), moderately inflated, with long, strongly tapered spine projecting ventrolaterally from base, with very shallow notch on some specimens (Pl. 14, figs 4, 12); doublure short adaxially until spine base, posterodorsally rotated to form very short articulating tongue separated from inflated band by short (longer adaxially; posterior view), deep furrow, doublure very rapidly expanded to long, wide inner face of spine.

Pygidium of five segments and terminal piece, short, moderately wide, subrectangular, with sagittal length from articulating furrow 72.6% (69.0–74.9%) width across anterior pleural band of first segment, highly vaulted axially and pleurally (sag., tr.); articulating half ring short, semilunate, laterally tapered; articulating furrow long, fairly shallow medially, deeper laterally into apodemal pits; axis highly vaulted anteriorly, progressively less vaulted posteriorly to gently inflated terminal piece, with each axial ring strongly independently inflated, short, wide anteriorly, strongly posteriorly narrowed, with fifth ring a little less than half width of first ring, more coarsely tuberculate than pleurae; terminal piece triangular, narrow, elongate, enclosed by fifth pair of pleurae; inter-ring furrows long (first furrow slightly laterally shortened; subsequent furrows shorter overall), deep, but shallower medially, with deep apodemal pits just adaxial from axial furrows; axial furrows strongly anteriorly divergent from tip of terminal piece, narrow, wider at intersections with interpleural furrows, deep anteriorly, shallower posteriorly over fourth and fifth pleurae and along terminal piece; anterior pleural band well expressed only on first segment, gently inflated, short, a little more than 1/3 length of posterior pleural band, wide, reaching to level with base of spines, strongly posteriorly directed, with very short transverse articulating flange on anterior edge separated from posterior portion of band by very short, incised furrow (Pl. 14, fig. 23), and with small anterodorsally curved hook structure at tip (Pl. 10, fig. 23) like that of thoracic segments, expressed as short raised stripe on second segment of large pygidia only (Pl. 14, fig. 19) and pinched out just past fulcrum; pleural furrow short, deep, shallower ventrolaterally, strongly anterolaterally bowed in course; posterior pleural band long, highly inflated, with rounded inner margin, strongly posteriorly directed, with each pair increasingly so, third and fourth pair subparallel, fifth pair posteriorly convergent, posterior pairs decreasing in length (exsag.), each band gently laterally flattened, with spines more strongly compressed into buttress shape (lateral view), spines long, moderately wide, tapered to bluntly pointed tips, narrowly but well separated, gently anteroventrally curved, segments with coarser granules lining edges (dorsal view) and on ventral edge of spine (lateral view); interpleural furrows short (first furrow longer), deep, increasingly shallower posteriorly, posteriorly directed to follow pleural curvature; pygidial border expressed ventrally (Pl. 10, fig. 28, Pl. 14, figs 25, 30), short, broadly U-shaped, coarsely granulose on small specimens (Pl. 10, fig. 28) or smooth (Pl. 14, figs 25, 30); pygidial doublure (anterior views; Pl. 10, fig. 29, Pl. 14, fig. 26) very long medially, broadly rounded and strongly anterolaterally tapered, effaced.

Ontogeny. The ontogeny of *Hintzeia celsaora* is the best known of the Great Basin species, and the material includes an articulated M13 meraspid individual (Pl. 11, figs 1–8) missing only the librigenae, rostral plate, hypostome, and the pleurae of the 12th thoracic segment. This specimen is likely also the best known example of a pliomerid meraspid (but see also Ross [1951], pl. 33, figs 3, 6–8, 12). Compared to *H. plicamarginis* Simpson *et al.*, 2005, the cranidium is very close in size to that of their fig. 12.2, and the transitory pygidium is equivalent to their stage G (fig. 5.3). The cranidia show most of the differences present in larger specimens. The immature cranidium of *H. celsaora* is shorter and wider overall; the anterior border is much less anteriorly curved, although that of *H. plicamarginis* has not begun to develop the median posterior arcuate curve; the glabella is shorter and wider, with wider lateral lobes and median region, and LF is narrower; and the fixigenae are longer. Likewise, the pygidia show the same differences as in more mature specimens; that of *H. celsaora* is shorter and narrower, with a relatively wider axis; the pleurae are shorter, more inflated, and more strongly posteriorly directed; and the pleural spines are shorter, narrower, and strongly downturned. The pygidium of *H. celsaora* also appears to be more densely tuberculate, but the SEM image of Simpson *et al.* is also figured at a size too small to show the sculpture.

The *H. parafirmimarginis* cranidium of Pl. 5, fig. 26 is slightly smaller. It has not yet developed the indentation in the posterior margin of the anterior border, but the glabella is longer and narrower; the fixigenae are shorter; and LO is shorter. The latter may be an ontogenetic difference; the *H. parafirmimarginis* cranidium of Pl. 5, fig. 22 is closer in size to that of the *H. celsaora* meraspid and its LO is much longer. However, the cranidium is crushed and unsuitable for general comparison. Cranidia of *H. firmimarginis* are too large for suitable comparison, as are pygidia of both it and *H. parafirmimarginis*.

Ontogenetic changes are well exemplified in the specimens of *H. celsaora*. As in other species of *Hintzeia*, the anterior border lengthens and widens, but it does not develop the median posterior indentation; the glabella shortens, narrows anteriorly, and the lateral lobes increase in width as the median lobe narrows; the axial furrows widen; the fixigenae widen slightly; and the granulose sculpture becomes less well developed (cf. Pl. 10, figs 1, 15, Pl. 12, fig. 1 and articulated individual of Pl. 11). The hypostome elongates; the anterior wings grow longer and wider; the middle body elongates and the sculpture on the anterior lobe decreases in density; the middle body furrow deepens; the lateral border widens slightly and its spines become blunter; and the posterior border lengthens slightly (cf. Pl. 10, fig. 14, hypostomes of Pl. 13). Librigenae are all of nearly the same size and therefore uninformative. The granulose sculpture of the thoracic segments becomes finer and sparser, especially on the pleurae. The pleurae may also develop a small notch in the anterior margin of the posterior pleural band, near the tip of the spine. The notch is visible on two of the larger segments (Pl. 14, figs 4, 12), but is not apparent on any segments of the articulated individual (Pl. 11), although it may simply be hidden by spines of other segments. Pygidia widen, especially anteriorly; inter-ring furrows and interpleural furrows lengthen; the anterior pleural band of the second segment develops; axial furrows widen slightly; the axis increases in width and its posterior taper is stronger; spines splay slightly and the tips become very slightly more pointed; and sculpture becomes finer, especially in the reduction of the coarse granules on the axial rings (cf. Pl. 14, figs 19, 24).

Discussion. Demeter (1973) suggested that *Protopliomerops aemula* Hintze, 1953, is a junior synonym of *H. celsaora* (Ross, 1951). Simpson *et al.* (2005, p. 538), on the other hand, not only rejected this synonymy but excluded *Protopliomerops celsaora* from the genus *Hintzeia*. We have recovered large samples of both species and these indicate that they are certainly synonyms. Confusion probably stems from small original sample sizes, misassociated sclerites, and differing photographic orientations. Comparison of similarly sized sclerites from Ibex illustrated on Plates 12–14 with those from the Garden City Formation illustrated on Plates 10 and 11 reveals no obvious morphological differences. They occur together with multiple other species also shared between all of the horizons (see Adrain *et al.*, 2009, pp. 557–559 for a summary).

Hintze assigned a small cranidium (1953, pl. 22, fig. 9) from Section G-8/306' (99.3 m) to "*H. aemula*", but this is the type horizon of *H. firmimarginis*, and that is the identity of the cranidium. All of the material figured by Ross (1951) comes from a single horizon, limiting the possibility of incorrect association. However, his pygidium (Ross, 1951, pl. 31, figs 6–8) is incorrectly associated, though its affinity is uncertain. Most notably, it is longer (sag.) than our figured *H. celsaora* pygidia, but retains distinct tuberculate sculpture whereas there is a clear ontogenetic process of effacement illustrated in our specimens. We recovered several pygidia from Section HC6 171.0 (likely Ross' type horizon) which are direct matches for those from Section G 118.6 m at Ibex.

Intraspecific variation in *H. celsaora* is low. In the cranidia, the glabella varies slightly in length (cf. Pl. 10, figs 13, 15), although it also shortens as the overall size of the cranidium increases (cf. Pl. 12, figs 1, 3). The lengths and widths of cranidial furrows also vary slightly (cf. Pl. 11, fig. 12, Pl. 12, fig. 1). The hypostome in Pl. 13, fig. 18 is narrower and more elongate than the others, and has shorter spines. Among librigenae, the slopes of the posterior branch of the facial suture vary slightly, as does the position of the change in slope relative to the length of the field. The thickness of the pygidial spines varies slightly, as does the splay between spines (posterior view; cf. Pl. 14, figs 21, 22).

Hintzeia celsaora was compared to *H. parafirmimarginis* in the discussion of the latter taxon. It differs in much the same way from *H. firmimarginis*: the anterior border is not strongly anteriorly bowed nor is the posterior margin medially curved, and it has a rostral suture arc in the anteroventral rim; the anterior border furrow is shorter and nearly transverse in dorsal view; the glabella is shorter and wider; the median LO node is less prominent; the interocular fixigenae are wider, but the posterior fixigenae are narrower and longer; and the sculpture overall is slightly coarser, with larger fixigenal pits. The hypostome is shorter, with smaller anterior wings; the middle body is less strongly posteriorly tapered, the posterior lobe is slightly shorter, and the anterior lobe has much coarser sculpture extending further posteriorly; the middle body furrows are less incised, but the lateral border furrows are

deeper; the lateral border is narrower, especially at the shoulders and toward the posterolateral corners, and its spines are longer and more sharply pointed; and the posterior border is much shorter, with a longer, more sharply pointed median spine. The librigena has a much shorter anterior branch of the facial suture; an abrupt change in slope midway along the posterior facial suture; a much narrower field; and a relatively wider lateral border, with a longer posterior projection and shorter anterior projection, and coarser sculpture. Thoracic segments are very similar, but those of *H. celsaora* have a longer articulating furrow, and on some segments the posterior band is notched near the base of the spine. Pygidia are very different: they are much narrower, with a wider axis; a slightly longer and narrower terminal piece; shorter, narrower, and more conical pleurae; much shorter, blunter, more closely spaced, and more ventrally directed pleural spines; a much shorter and narrower, smooth ventral pygidial border; and a much longer doublure.

The morphology of *H. plicamarginis* is much more similar to that of *H. firmimarginis* and *H. parafirmimarginis* than to that of *H. celsaora*. *Hintzeia celsaora* has a wider, much less anteriorly bowed anterior border without an indentation in the posterior margin and with a rostral suture arc in the anteroventral rim; a shorter, nearly transverse anterior border furrow; a shorter, wider glabella with a narrower LF; a less prominent LO node; and wider interocular fixigenae and longer posterior fixigenae. The hypostome is shorter and wider, as is the middle body; the anterior lobe of the middle body is shorter; the middle furrow is much shallower; the posterior lobe is longer; the anterior lobe is tuberculate, and both lobes are less pitted; the anterior wings are wider and larger; the shoulders are located more anteriorly; the lateral border is slightly wider, with more pointed spines which are spaced further apart near the posterolateral corners; and the posterior branch of the facial suture is much shorter and the posterior branch has a change in slope at mid-length; the lateral border is slightly narrower, more curved, and has a longer posterior projection and shorter anterior projection. The pygidium is much shorter and slightly narrower; the axis is wider; the pleurae are much shorter, narrower, more conical, and strongly posteriorly directed; the spines are much shorter, slightly closer set, strongly downturned, and lack a lengthened recurved tip; and the ventral pygidial border is much shorter and narrower, without an inflated inner rim.

Hintze (1953) reported *Hintzeia* aff. *H. celsaora* (Ross) from a talus block at Section G 462', and figured a single partial cranidium (pl. 22, fig. 10). We have recently collected talus from this interval and the range of *Hintzeia celsaora* may be extended upward. It is also possible that Hintze's specimen is a new species of *Hintzeia* very similar to *H. celsaora*, as it is not very well preserved, and the other sclerites are unknown.

Demeter (1973, p. 53) claimed that *H. celsaora* ranged through 488 feet of the Fillmore Formation, but this is largely based on misidentification of specimens. He also figured a number of specimens from Section G and Mesa (Demeter, 1973, pl. 3, figs 9–14) as *H. celsaora*. The pygidia of his figures 11–13 are from Mesa, but are stratigraphically approximately equivalent to G 112–116 m, morphologically similar to *H. celsaora*, and are likely conspecific. The other sclerites represent a new species of *Protopliomerella* Harrington, 1957 (unpublished work in progress). An unidentified transitory pygidium from the same equivalent range at Mesa (Demeter, 1973, pl. 5, fig. 17) may also belong to *H. celsaora*, but it is very small and figured at low magnification. It could also belong to any other pliomerid from the *H. celsaora* Zone.

Acknowledgements

Research was supported by National Science Foundation grant DEB 0716065. Fieldwork in 2009 and 2010 was supported by an award from the University of Iowa Department of Geoscience Max and Lorraine Littlefield Fund to N.E.B.M. Stephen Westrop logged and produced the stratigraphic column for Section G. Ed Landing remeasured and logged Section HC5 and logged Section HC6. Sahale Casebolt, TracyAnn Champagne, and Marc Spencer assisted with field collections. Richard Robison kindly allowed us to study a specimen in his collection. Tiffany Adrain provided assistance with SUI numbers and curation. We are grateful for helpful reviews by John Laurie and Helje Pärnaste.

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PLATE 1.

PLATE 1. *Hintzeia firmimarginis* (Hintze, 1953), from Section G 99.3 m and G 99T-A m, Fillmore Formation (Tulean; *Psa-likilus spinosum* Zone), southern Confusion Range, Ibex area, Millard County, western Utah.

^{1, 4, 5.} Cranidium, SUI 125500, dorsal, anterior, and right lateral views, x6 (G 99.3 m).

^{2, 6, 8, 10.} Cranidium, SUI 125501, dorsal, right lateral, anterior, and ventral views, x10 (G 99.3 m).

^{3, 7, 9.} Cranidium, SUI 125502, dorsal, left lateral, and anterior views, x6 (G 99T-A m).

^{11, 14, 15, 17, 23.} Cranidium, SUI 125503, dorsal, anterior, left lateral, ventral, and oblique views, x10 (G 99.3 m).

^{12, 21, 22, 25.} Cranidium, SUI 125504, dorsal, oblique, left lateral, and anterior views, x10 (G 99.3 m).

^{13, 16, 19.} Cranidium, SUI 115119, dorsal, anterior, and left lateral views, x10 (G 99.3 m).

^{18, 20, 24.} Cranidium, SUI 125505, right lateral, dorsal, and anterior views, x12 (G 99.3 m).



PLATE 2.

PLATE 2. *Hintzeia firmimarginis* (Hintze, 1953), from Section G 99.3 m and G 99T-A m, Fillmore Formation (Tulean; *Psa-likilus spinosum* Zone), southern Confusion Range, Ibex area, Millard County, western Utah.

^{1, 2, 3, 9.} Hypostome, SUI 125506, posterior, left lateral, ventral, and dorsal views, x9 (G 99T-A m).

^{4, 10, 11, 15.} Hypostome, SUI 125507, ventral, right lateral, posterior, and dorsal views, x7.5 (G 99T-A m).

^{5, 12, 13, 16.} Hypostome, SUI 125508, ventral, left lateral, posterior, and dorsal views, x7.5 (G 99T-A m).

^{6-8.} Cranidium, SUI 125509, dorsal, left lateral, and anterior views, x12 (G 99T-A m).

^{14, 18, 20.} Right librigena, SUI 125510, external, internal, and ventrolateral views, x7.5 (G 99.3 m).

^{17.} Right librigena, SUI 125511, external view, x5 (G 99T-A m).

^{19, 21.} Left librigena, SUI 125512, external and ventrolateral views, x6 (G 99T-A m).

^{22.} Right librigena, SUI 125513, external view, x7.5 (G 99.3 m).

^{23, 24, 27.} Left librigena, SUI 125514, ventrolateral, external, and internal views, x10 (G 99.3 m).

^{25.} Right librigena, SUI 125515, external view, x10 (G 99.3 m).

^{26, 29.} Right librigena, SUI 125516, ventrolateral and external views, x6 (G99T-A m).

^{28.} Right librigena, SUI 125517, external view, x6 (G 99T-A m). 30. Right librigena, SUI 125518, external view, x10 (G 99.3 m).





PLATE 3. *Hintzeia firmimarginis* (Hintze, 1953), from Section G 99.3 m and G 99T-A m, Fillmore Formation (Tulean; *Psa-likilus spinosum* Zone), southern Confusion Range, Ibex area, Millard County, western Utah.

^{1, 3, 4, 5, 8.} Thoracic segment, SUI 125519, dorsal, anterior, posterior, right lateral, and ventral views, x12 (G 99.3 m).

^{2, 6, 7, 14.} Thoracic segment, SUI 125520, dorsal, posterior, anterior, and left lateral views, x7.5 (G 99.3 m).

^{9, 12, 18, 19.} Thoracic segment, SUI 125521, dorsal, right lateral, anterior, and posterior views, x7.5 (G 99.3 m).

^{10, 13, 16, 17, 20.} Thoracic segment, SUI 125522, dorsal, ventral, right lateral, posterior, and anterior views, x7.5 (G 99.3 m).

^{11, 15, 22–24.} Thoracic segment, SUI 125523, posterior, anterior, right lateral, dorsal, and ventral views, x12 (G 99.3 m).

^{21, 25, 26.} Pygidium, SUI 125524, dorsal, posterior, and left lateral views, x5 (G 99T-A m). 27, 28, 32. Pygidium, SUI 125525, right lateral, dorsal, and posterior views, x12 (G 99T-A m).

^{29-31.} Pygidium, SUI 125526, posterior, right lateral, and dorsal views, x15 (G 99T-A m).



PLATE 4.

PLATE 4. *Hintzeia firmimarginis* (Hintze, 1953), from Section G 99.3 m and G 99T-A m, Fillmore Formation (Tulean; *Psa-likilus spinosum* Zone), southern Confusion Range, Ibex area, Millard County, western Utah.

^{1, 4, 7.} Pygidium, SUI 115120, dorsal, posterior, and right lateral views, x7.5 (G 99T-A m).

^{2, 5, 8.} Pygidium, SUI 125527, dorsal, posterior, and right lateral views, x10 (G 99.3 m).

^{3, 6, 9, 10, 13.} Pygidium, SUI 125528, dorsal, posterior, left lateral, anterior, and ventral views, x10 (G 99T-A m).

^{11, 12, 14, 15.} Pygidium, SUI 125529, dorsal, ventral, posterior, and left lateral views, x7.5 (G 99T-A m).

^{16, 20, 24.} Pygidium, SUI 125530, left lateral, dorsal, and posterior views, x20 (G 99T-A m).

^{17, 21, 22.} Pygidium, SUI 125531, dorsal, posterior, and left lateral views, x7.5 (G 99.3 m).

^{18, 19, 23, 25.} Pygidium, SUI 125532, right lateral, dorsal, ventral, and posterior views, x12 (G 99T-A m).



PLATE 5.

PLATE 5. *Hintzeia parafirmimarginis* **n. sp.**, from Section HC6 165.2, Garden City Formation (Tulean; *Psalikilus spinosum* Zone), Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho.

^{1, 4, 7.} Cranidium, SUI 125533, dorsal, anterior, and left lateral views, x6.

^{2, 5, 9.} Cranidium, SUI 125534, dorsal, anterior, and left lateral views, x6.

^{3, 6, 10, 11.} Cranidium, SUI 125535, dorsal, ventral, left lateral, and anterior views, x10.

^{8, 12, 16.} Cranidium, SUI 125536, right lateral, dorsal, and anterior views, x7.5.

^{13, 17, 18.} Cranidium, SUI 125537, left lateral, anterior, and dorsal views, x12.

^{14, 15, 21, 24, 27.} Cranidium, SUI 115121, left lateral, dorsal, ventral, anterior, and oblique views, x10.

^{19, 20, 23.} Cranidium, SUI 125538, dorsal, left lateral, and anterior views, x12.

^{22, 25, 28.} Cranidium, SUI 125539, dorsal, anterior, and right lateral views, x15. 26, 29, 32. Cranidium, SUI 125540, dorsal, right lateral, and anterior views, x15.

^{30, 31, 33.} Cranidium, SUI 125541, left lateral, dorsal, and anterior views, x15.



PLATE 6.

PLATE 6. *Hintzeia parafirmimarginis* **n. sp.**, from Section HC6 165.2, Garden City Formation (Tulean; *Psalikilus spinosum* Zone), Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho.

^{1.} Right librigena, SUI 125542, external view, x7.5.

^{2, 3, 5.} Left librigena, SUI 125543, ventrolateral, external, and internal views, x12.

^{4, 7.} Left librigena, SUI 125544, external and ventrolateral views, x12.

^{6, 8.} Left librigena, SUI 125545, external and internal views, x12.

^{9.} Right librigena, SUI 125546, external view, x15.

^{10.} Left librigena, SUI 125547, external view, x12.

^{11.} Right librigena, SUI 125548, external view, x12.

^{12-14, 16, 18.} Thoracic segment, SUI 125549, dorsal, ventral, right lateral, anterior, and posterior views, x12.

^{15, 17, 22, 26.} Thoracic segment, SUI 125550, anterior, posterior, dorsal, and left lateral views, x7.5.

^{19, 20, 24, 25, 27.} Thoracic segment, SUI 125551, anterior, posterior, doral, right lateral, and left lateral views, x12.

^{21, 23, 28–30.} Thoracic segment, SUI 125552, anterior, posterior, right lateral, ventral, and dorsal views, x12.



PLATE 7.

PLATE 7. *Hintzeia parafirmimarginis* **n. sp.**, from Section HC6 165.2, Garden City Formation (Tulean; *Psalikilus spinosum* Zone), Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho.

^{1, 2, 5, 6.} Hypostome, SUI 125553, ventral, dorsal, left lateral, and posterior views, x10.

^{3, 7, 9, 10.} Hypostome, SUI 125554, ventral, dorsal, posterior, and left lateral views, x12.

^{4, 8, 11.} Hypostome, SUI 125555, ventral, posterior, and left lateral views, x10.

^{12, 15, 18.} Pygidium, SUI 125556, dorsal, posterior, and right lateral views, x10.

^{13, 16, 19, 22.} Pygidium, holotype, SUI 115122, dorsal, posterior, ventral, and left lateral views, x12.

^{14, 17, 20, 25, 26.} Pygidium, SUI 125557, dorsal, posterior, ventral, left lateral, and anterior views, x15.

^{21, 23, 24.} Pygidium, SUI 125558, left lateral, dorsal, and posterior views, x15.



PLATE 8. *Hintzeia parafirmimarginis* **n. sp.**, float collected in southern Confusion Range, exact locality uncertain, Fillmore Formation (presumably Tulean, *Psalikilus spinosum* Zone, but exact horizon unknown), Ibex area, Millard County, western Utah. 1–5. Dorsal exoskeleton, specimen in private collection of R. A. Robison, University of Kansas, dorsal, oblique, posterior, anterior, and right lateral views, x6.





PLATE 9. *Hintzeia parafirmimarginis* **n. sp.**, float collected in southern Confusion Range, exact locality uncertain, Fillmore Formation (presumably Tulean, *Psalikilus spinosum* Zone, but exact horizon unknown), Ibex area, Millard County, western Utah. 1–5. Dorsal exoskeleton, UU 10051.90, dorsal cephalic view, x12, external view of right librigena, x12, right lateral view of pygidium, x10, right lateral view of cephalon, x12, and dorsal view of pygidium, x10.



PLATE 10.

PLATE 10. *Hintzeia celsaora* (Ross, 1951), from Sections HC5 186.5 m and HC6 171.0 m, Garden City Formation (Tulean; *Hintzeia celsaora* Zone), Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho.

^{1, 6, 7.} Cranidium, SUI 125559, dorsal, anterior, and right lateral views, x10 (HC6 171.0 m).

^{2, 8, 11.} Cranidium, SUI 125560, dorsal, anterior, and right lateral views, x10 (HC6 171.0 m).

^{3–5.} Cranidium, SUI 125561, dorsal, left lateral, and anterior views, x10 (HC5 186.5 m).

^{9, 12, 15, 16, 20.} Cranidium, SUI 125562, oblique, left lateral, dorsal, anterior, and ventral views, x12 (HC6 171.0 m).

^{10, 13, 17.} Cranidium, SUI 125563, right lateral, dorsal, and anterior views, x12 (HC5 186.5 m).

^{14, 18, 19, 22.} Hypostome, SUI 125564, ventral, posterior, dorsal, and left lateral views, x15 (HC6 171.0 m).

^{21, 25, 26.} Hypostome, SUI 125565, ventral, right lateral, and posterior views, x15 (HC6 171.0 m).

^{23, 24, 27-29.} Pygidium, SUI 125566, right lateral, dorsal, posterior, ventral, and anterior views, x15 (HC6 171.0 m).



PLATE 11.

PLATE 11. *Hintzeia celsaora* (Ross, 1951), from Section HC6 171.0 m, Garden City Formation (Tulean; *Hintzeia celsaora* Zone), Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho.

^{1–8.} Dorsal exoskeleton, SUI 125567, dorsal, ventral, oblique, dorsal cephalic, dorsal thoracic, ventral cephalic, dorsal pygidial, and right lateral views, x14.

Hintzeia celsaora (Ross, 1951), from Section D 59T m, Fillmore Formation (Tulean; *Hintzeia celsaora* Zone), southern House Range, Ibex area, Millard County, western Utah.

^{9, 11.} Left librigena, SUI 125568, ventrolateral and external views, x10.

^{10, 12, 13.} Cranidium, SUI 125569, anterior, dorsal, and right lateral views, x10.



PLATE 12.

PLATE 12. *Hintzeia celsaora* (Ross, 1951), from Section G 118.6 m, Fillmore Formation (Tulean; *Hintzeia celsaora* Zone), southern Confusion Range, Ibex area, Millard County, western Utah.

^{1, 4, 9, 12, 16.} Cranidium, SUI 115142, dorsal, anterior, right lateral, oblique, and ventral views, x10.

^{2, 5, 6, 11.} Cranidium, SUI 125570, dorsal, left lateral, anterior, and ventral views, x10.

^{3, 7, 8. 3, 7, 8.} Cranidium, SUI 125571, dorsal, anterior, and left lateral views, x7.5.

^{10, 13, 14, 17, 21.} Cranidium, SUI 125572, right lateral, dorsal, anterior, ventral, and oblique views, x10.

^{15, 18, 22.} Cranidium, SUI 125573, dorsal, left lateral, and anterior views, x10.

^{19, 20, 23.} Cranidium, SUI 125574, dorsal, left lateral, and anterior views, x10.

^{24–26.} Cranidium, SUI 125575, anterior, left lateral, and dorsal views, x12.



PLATE 13.

PLATE 13. *Hintzeia celsaora* (Ross, 1951), from Section G 118.6 m, Fillmore Formation (Tulean; *Hintzeia celsaora* Zone), southern Confusion Range, Ibex area, Millard County, western Utah.

^{1, 4.} Left librigena, SUI 125576, ventrolateral and external views, x10.

^{2.} Right librigena, SUI 125577, external view, x10.

^{3, 6, 9.} Left librigena, SUI 125578, ventrolateral, external, and internal views, x10.

^{5.} Left librigena, SUI 125579, external view, x10. 7, 10. Right librigena, SUI 125580, external and internal views, x10.

^{8.} Left librigena, SUI 125581, external view, x10.

^{11.} Left librigena, SUI 125582, external view, x10.

^{12.} Right librigena, SUI 125583, external view, x10.

^{13.} Left librigena, SUI 125584, external view, x10.

^{14, 16, 20.} Hypostome, SUI 125585, ventral, right lateral, and posterior views, x15.

^{15, 17, 21.} Hypostome, SUI 125586, ventral, left lateral, and posterior views, x12.

^{18, 19, 22, 24.} Hypostome, SUI 125587, ventral, dorsal, right lateral, and posterior views, x12.

^{23, 25–27.} Hypostome, SUI 125588, posterior, left lateral, ventral, and dorsal views, x12.



PLATE 14.

PLATE 14. *Hintzeia celsaora* (Ross, 1951), from Section G 118.6 m, Fillmore Formation (Tulean; *Hintzeia celsaora* Zone), southern Confusion Range, Ibex area, Millard County, western Utah.

^{1, 4, 9, 14.} Thoracic segment, SUI 125589, dorsal, left lateral, posterior, and anterior views, x9.

^{2, 7, 13, 16, 17.} Thoracic segment, SUI 125590, dorsal, ventral, left lateral, anterior, and posterior views, x8.

^{3, 10, 11, 15, 18.} Thoracic segment, SUI 125591, left lateral, dorsal, ventral, anterior, and posterior views, x8.

^{5, 6, 8, 12.} Thoracic segment, SUI 125592, anterior, posterior, dorsal, and right lateral views, x9.

^{19, 21, 25, 29.} Pygidium, SUI 115143, dorsal, posterior, ventral, and left lateral views, x10.

^{20, 22, 26, 27, 30.} Pygidium, SUI 125593, dorsal, posterior, anterior, right lateral, and ventral views, x10.

^{23, 24, 28.} Pygidium, SUI 125594, left lateral, dorsal, and posterior views, x20.

^{31, 32.} Pygidium, SUI 125595, left lateral and dorsal views, x10.