Bearriverops, a new Lower Ordovician trilobite genus from the Great Basin, western USA, and classification of the family Dimeropygidae

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Abstract: ***Bearriverops*** n. gen. is a distinctive clade of small, vaulted trilobites from the Lower Ordovician (Ibexian Series; Stairsian Stage) of Utah and Idaho. The genus includes at least seven new species known from silicified material of which five are well enough known to name: ***B. alsacharovi***, ***B. borderinnensis***, ***B. deltaensis***, ***B. ibexensis***, and ***B. loganensis*** (the type species). All are known from the lower Fillmore Formation in western Utah; *B. alsacharovi* and *B. loganensis* are also known from the Garden City Formation of southeastern Idaho. Both units record deposition in shallow subtidal environments above storm wave base. *Bearriverops* is characterized particularly by a suite of pygidial apomorphies apparently related to spiral enrollment. Its close relatives include a large group of mostly undescribed Skullrockian and Stairsian species with more conventional spinose pygidia. Together, the taxa are referred to Dimeropygidae, which is considered a senior synonym of Toernquistiidae. Cladistic parsimony analysis of *Bearriverops* indicates that *B. alsacharovi* and *B. borderinnensis* are sister taxa, and that *B. loganensis*, *B. deltaensis*, and the plesiomorphic *B. ibexensis* are successive sister taxa to this clade.

Résumé : ***Bearriverops*** n. gen. représente un clade distinctif de petits trilobites voûtés de l'Ordovicien inférieur (série ibexienne, étage stairsien) de l'Utah et de l'Idaho. Le genre compte au moins sept nouvelles espèces provenant de matériaux silicifiés, dont cinq sont assez bien connues pour être nommées : ***B. alsacharovi***, ***B. borderinnensis***, ***B. deltaensis***, ***B. ibexensis*** et ***B. loganensis*** (l'espèce type). Toutes les espèces ont été observées dans la Formation de Fillmore de l'ouest de l'Utah, et *B. alsacharovi* et *B. loganensis* ont également été observées dans la Formation de Garden City du sud-est de l'Idaho. Ces deux unités témoignent d'un dépôt en milieux infratidaux peu profonds au-dessus de la limite d'action des vagues de tempête. *Bearriverops* est caractérisé plus particulièrement par une série d'apomorphies pygidiales apparemment associées à un enroulement spiralé. Ses proches parents comprennent un important groupe d'espèces skullrockiennes et stairsiennes, non décrites en bonne partie, présentant des pygidiums épineux plus classiques. Ensemble, ces taxons sont attribués aux Diméropygidés, un nom considéré comme synonyme senior de Toernquistiidé. L'analyse de la parcimonie cladistique de Bearriverops indique que et *B. borderinnensis* sont des taxons frères et que *B. loganensis*, *B. deltaensis* et *B. ibexensis*, une espèce plésiomorphique, sont des taxons frères successifs de ce clade.

[Traduit par la Rédaction]

Introduction

Field-based revision of the Ibexian (Lower Ordovician) trilobite faunas described initially by Ross (1951) from southeastern Idaho and northern Utah and Hintze (1953) from western Utah is yielding an enormous number of new taxa (e.g., Adrain et al. 2003; Adrain and Westrop 2006), as well as much more information on previously described but poorly known forms (e.g., Adrain et al. 2001; Adrain and Westrop 2006). Among these are discoveries that bear on classification of the Dimeropygidae Hupé, 1953. Hypotheses of the content and phylogeny of this group are in a state of flux, with opinions varying widely among recent studies (Chatterton 1994; Adrain and Fortey 1997; Chatterton et al. 1998; Adrain et al. 2001). Complete resolution of the phylogeny of Dimeropygidae and related groups is beyond the scope of the paper. However, the goals of the study are (1) to review the current problems of dimeropygid classification and clarify the questions at issue; (2) to describe a new dimeropygid genus, *Bearriverops*, including five new species from the Stairsian Stage; and (3) to provide a hypothesis of ingroup phylogeny for the new genus based on cladistic parsimony analysis.

Although species of *Bearriverops* are common constituents of mid-Stairsian faunas from both the lower Fillmore Formation in western Utah and the Garden City Formation in southeastern Idaho, only two of them have been reported previously (both in open nomenclature), on the basis of a total of five illustrated sclerites. This is representative of the current state of knowledge of the Stairsian Ross–Hintze faunas.

Received 27 January 2006. Accepted 7 September 2006. Published on the NRC Research Press Web site at http://cjes.nrc.ca on 21 May 2007.

Paper handled by Associate Editor B. Chatterton.

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Although the quality of the original work (Ross 1951; Hintze 1953) was high, there has been virtually no new study in over half a century and most of the genus and species diversity in the sections remains to be formally described and named.

Sampling and biostratigraphy

The faunas of the Garden City Formation in the Bear River Range of southeastern Idaho and northern Utah and the Pogonip Group in the Ibex area of western Utah have formed the foundation for the letter-based Ross–Hintze trilobite zones (Ross 1949, 1951; Hintze 1951, 1953), and these in turn are the basis of the formalized Ibexian Series and its stages (Ross et al. 1997). Intensive field sampling in progress indicates that most trilobite species in at least the Skullrockian and Stairsian stages have almost no stratigraphic range. Trilobites occur in a sequence of distinct faunas, each typically sampled at only one or two horizons in a particular section, with complete faunal turnover between these restricted occurrences. In the upper Skullrockian Red Canyon Member of the House Formation in western Utah, where intensive and closely spaced sampling is possible, this turnover occurs on a metre scale, and there is a nearly bewildering number of distinct, rapidly replaced faunas (Adrain et al. 2003). The Stairsian interval in both the Garden City and Fillmore formations yields fewer, more widely spaced sampling horizons than the upper Skullrockian. However, nearly every horizon yields a unique fauna. There is good reason to suspect, then, that faunal turnover was proceeding at a similar rate as in the upper Skullrockian. In biostratigraphic terms, it is difficult to define "zones" since, except for very closely spaced horizons (e.g., G 26.6–27.0 m, MME 121.6–121.9 m), there are few known Stairsian species with a stratigraphic range that is measurable within a single section. Instead, it may ultimately be preferable to recognize a succession of named faunas. Formal naming of these faunas is deferred until their description is more advanced.

The Stairsian Stage (Ross et al. 1997) is the second of the four stages of the Laurentian Ibexian Series and contains zones D–F of Ross' original (1949, 1951) trilobite biostratigraphy scheme. In the zonal names introduced by Ross et al. (1997), these are the *Leiostegium–Kainella* Zone, the *Tesselacauda* Zone, and the *Rossaspis superciliosa* Zone, respectively. In conodont terms, the stage encompasses the very top of the *Rossodus manitouensis* Zone, the "Lower Diversity Interval," the *Macerodus dianae* Zone, and the lowest part of the *Acodus deltatus – Oneotodus costatus* Zone (Ross et al. 1997). In terms of global correlation, this is equivalent to roughly the upper part of the lower Tremadocian Stage (see Cooper and Sadler 2004, fig. 12.1).

In the Garden City Formation, the Stairsian Stage occupies just over 100 m of section. Ross (1951) named a total of 27 new species from the stage, in addition to eight species reported in open nomenclature and a variety of unassigned sclerites. We resampled the Stairsian of the Garden City Formation at Ross' (1949, 1951) locality 5, on the east side of Hillyard Canyon, Franklin County, Idaho (our section HC5, Figs. 1.4, 1.5), locality 6 on the ridge crest along the west side of Hillyard Canyon (our section HC6), and locality 7 in Franklin Basin (our section FB7). Portions of these sections containing the horizons from which species of *Bearriverops* were collected are shown in graphical logs in Fig. 2.

In western Utah, rocks of the Stairsian Stage mostly make up Hintze's (1973) "basal ledge-forming limestone member" of the Fillmore Formation and occupy ~110–120 m of section. Hintze (1951) recorded the presence of many intraclastic rudstone ("intraformational conglomerate") beds in this unit, and noted (1953, pp. 10–11) for the *Tesselacauda* Zone (E) that "During deposition of these beds the trilobite tests were subjected to much comminution resulting in unidentifiable remains" and for the *Rossaspis superciliosa* Zone (F) that "the fauna is found through about 80 feet of predominantly intraformational conglomerate in which most of the trilobite remains have been broken beyond recognition" (1 foot = 0.3048 m). Hintze recorded only seven positively identified, named species from the Stairsian of the Ibex area (three new, four named from occurrences in the Garden City Formation by Ross), in addition to 10 treated in open nomenclature. Terrell (1973) restudied the interval, adding no new named taxa but illustrating a plethora of species in open nomenclature. He, too, noted the paucity of productive horizons and the preponderance of intraclastic rudstone.

Horizons with well-preserved trilobites are certainly much less common in the lower member of the Fillmore Formation than in the underlying (Skullrockian) Red Canyon Member of the House Formation, where we have collected over 40 rich and evenly spaced horizons in fewer than 70 m of section (Adrain et al. 2003). Nevertheless, we have discovered and collected several abundantly productive horizons. Material described herein from the Fillmore Formation was derived from the lower part of Hintze's (1951, 1953, 1973) section G (Figs. 1.1, 1.3, 3) in the southern Confusion Range and our new section MME (Figs. 1.1, 1.2, 3) on the east slope of Middle Mountain in the northwestern Wah Wah Mountains.

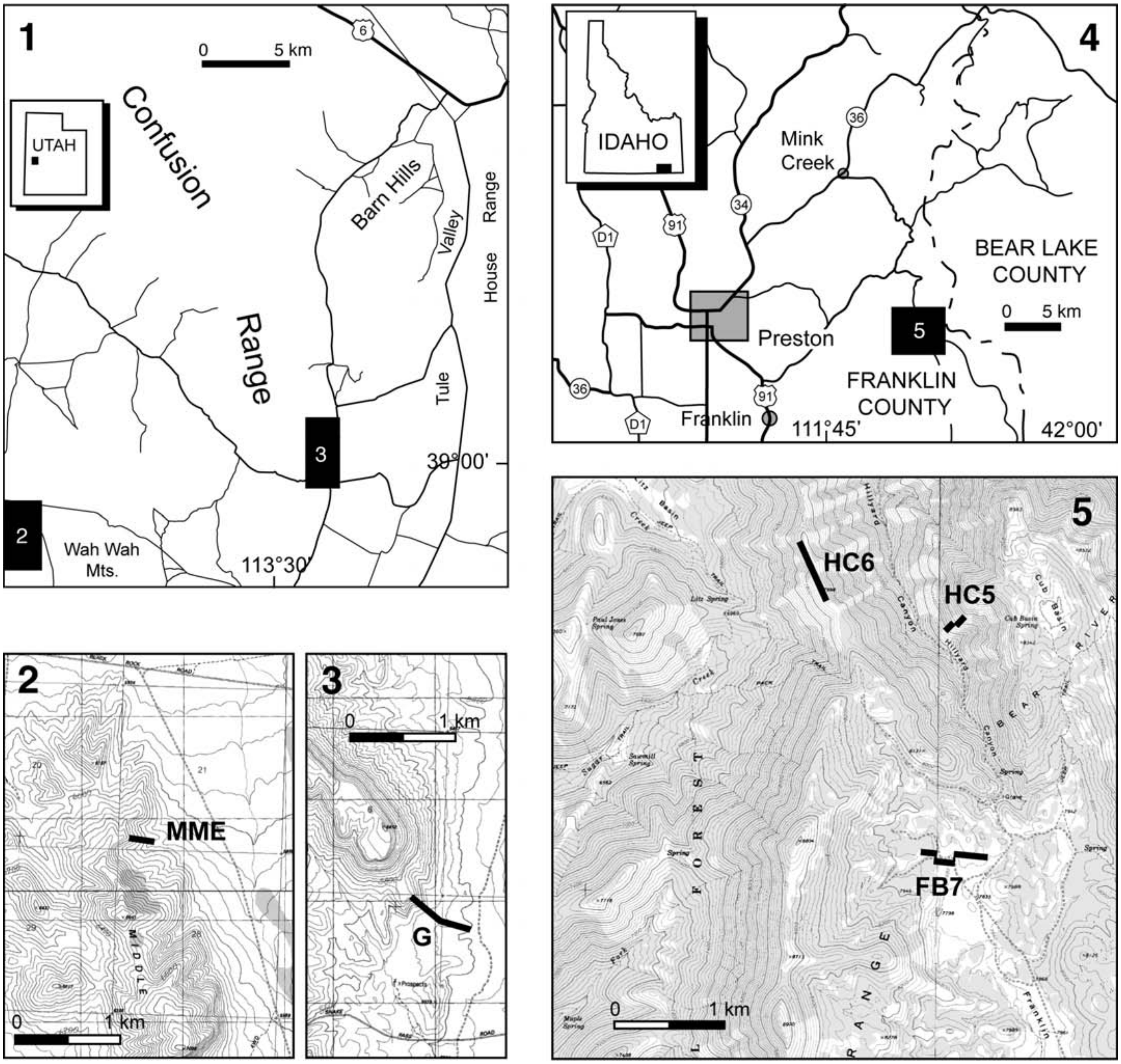
Classification of the dimeropygid trilobites

Classification of Dimeropygidae Hupé, 1953, is in a state of flux. While complete resolution of the problems is beyond the scope of the present manuscript, enough information is now available that the main issues can be outlined. There are four taxic components involved, each of which is composed of species whose close relationship to each other is broadly agreed upon.

(1) Dimeropyge Öpik, 1937, has a range from Middle Ordovician (the oldest known species occur in the Darriwilian Table Cove Formation of Newfoundland, J.M.A., and R.A. Fortey, unpublished data) to Upper Ordovician. Species of *Dimeropyge* are vaulted and tuberculate. As far as is known, they have medially yoked librigenae, a minute hypostome that is evidently not mineralized anteriorly, and seven thoracic segments with a long axial spine on the sixth. They have pygidia with a shallow sagittal depression, which presumably functioned to receive the ventral aspect of the axial spine.

(2) The genera *Chomatopyge* Whittington and Evitt, 1954, and *Mesotaphraspis* Whittington and Evitt, 1954, were assigned to Dimeropygidae by Whittington and Evitt (1954) and were regarded as such by most subsequent workers. Hupé (1953) erected Toernquistiidae to include *Toernquistia* Reed, 1896, and *Pyraustocranium* Ross,

Fig. 1. Locations of measured sections. (1) General location of sections in or near the southern Confusion Range, Ibex area, Millard County, western Utah (inset). Black blocks show position of detailed maps shown in 2 and 3. (2) Position of section MME on the east slope of Middle Mountain. (3) Position of section G on the southeast slope of the Confusion Range. (4) General location of sections in the Bear River Range, Franklin County, southeastern Idaho (inset). (5) Positions of sections HC5 (east side of Hillyard Canyon), HC6 (along ridge crest on west side of Hillyard Canyon), and FB7 (Franklin Basin).



1951 (which Hupé misspelled *Pyraustocrania*). We have sampled abundant new material of *Pyraustocranium orbatum* Ross, 1951, which we will redescribe elsewhere; it does not appear to be related to the taxa under discussion. Whittington and Evitt (1954, note added in proof, p. 100) considered *Toernquistia* to belong to Dimeropygidae, placed Toernquistiidae in synonymy of Dimeropygidae, and excluded *Pyraustocranium* from the family. *Toernquistia* has since usually been regarded as Dimeropygidae (e.g., Churkin 1963; Dean 1974; Webby 1974). *Toernquistina* Rozova in Rozova et al. 1985, was regarded by its author as having affinity with *Toernquistia*. The material is so poorly preserved and illustrated that it is uninterpretable.

The number of thoracic segments in *Mesotaphraspis* is unknown, but *M. inornata* has a long axial spine on the second from last segment (Whittington and Evitt 1954, pl. 24, fig. 24). No species of *Chomatopyge* is known from thoracic material. *Toernquistia sanchezae* (Chatterton, Edgecombe, Waisfeld, and Vaccari, 1998) has seven thoracic segments with a long

Fig. 2. Portions of sections in the Bear River Range, Franklin County, southeastern Idaho, from which samples of *Bearriverops* were collected (see Fig. 1 for locations of sections). Legend for lithological and sedimentological symbols in Fig. 3.

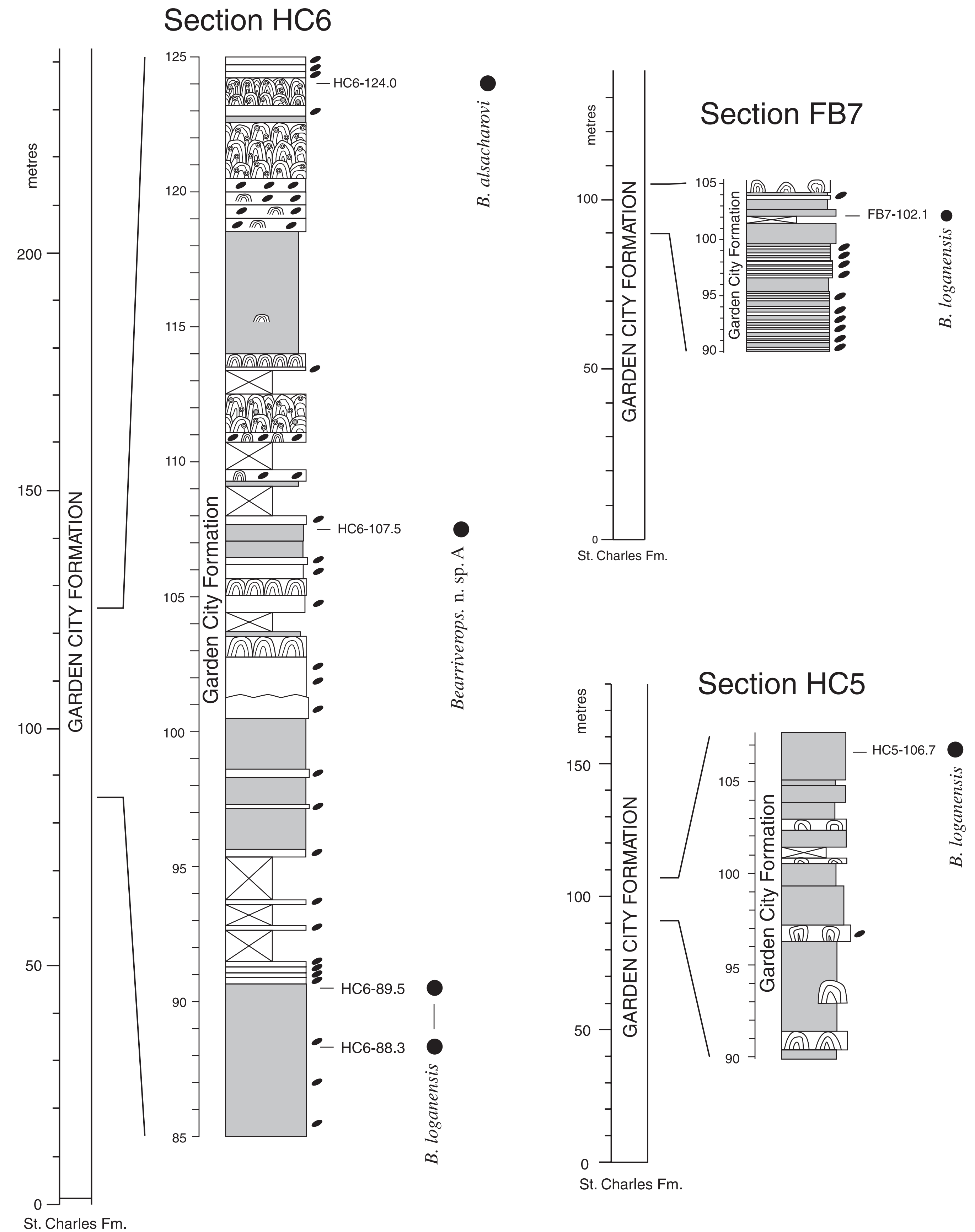
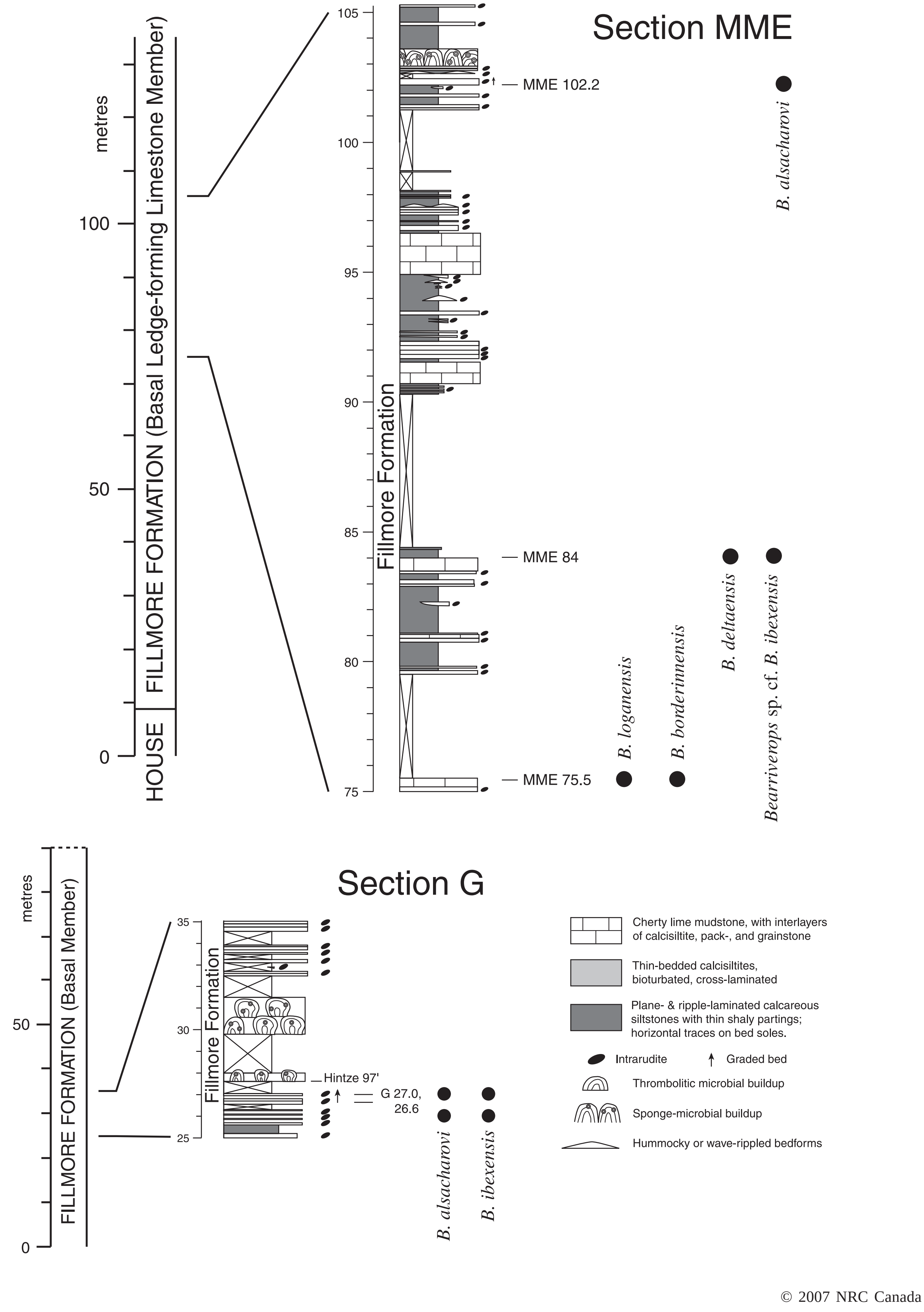


Fig. 3. Portions of sections in the Ibex region, Millard County, western Utah, from which samples of *Bearriverops* were collected (see Fig. 1 for locations of sections).



axial spine on the sixth. All species of *Mesotaphraspis* and *Toernquistia* for which information is available have pygidia, as far as is known, with a sagittal depression to receive the spine. All species of *Chomatopyge*, *Mesotaphraspis*, and *Toernquistia* for which information is available have medially yoked librigena. The only species of any of the genera for which a hypostome has been associated is *T. sanchezae*. This hypostome is tiny, and Chatterton et al. (1998, p. 293) noted that “there are signs that anterior parts of this element were not mineralized (as in *Dimeropyge*)”.

(3) The Middle to Upper Ordovician genus *Celmus* Angelin, 1854 (= *Ischyrophyma* Whittington, 1963; see Adrain and Fortey 1997) was classified in its own monotypic family Celmidae Jaanusson, 1956, but recently has been referred to Dimeropygidae (e.g., Adrain and Fortey 1997; Jell and Adrain 2003). It resembles *Dimeropyge* in its vaulted and tuberculate exoskeleton, but it too differs considerably in detail, including the possession of a thorax with 12 segments lacking any axial spine and a tiny pygidium of only a single segment with a pair of large transversely flattened, dorsally produced flanges.

(4) A group of mainly Lower Ordovician genera, which feature species with tuberculate and vaulted exoskeletons, includes *Dimeropygiella* Ross, 1951, *Ischyrotoma* Raymond, 1925 (see Adrain et al. 2001 for revisions of both), *Pseudohystricurus* Ross, 1951, and *Parahystricurus* Ross, 1951. *Bearriverops* is part of this group, along with a great many undescribed species belonging to additional new genera recovered during the current field sampling program. Collectively, these taxa broadly resemble *Dimeropyge* in their highly vaulted and tuberculate morphology, but differ considerably in detail. For example, although species of *Dimeropygiella* definitely have yoked librigena, all of the other taxa, as far as is known, had functional connective sutures and a rostral plate. All of the taxa, as far as is known, had large hypostomes versus the minute condition seen in *Dimeropyge*. All of the taxa have a greater number of thoracic segments than *Dimeropyge*, ranging from eight in an undescribed Skullrockian form, and in *Ischyrotoma*, to 10 in *Bearriverops*. Further, no species belonging to this group had a thoracic axial spine (this does not require articulated material for determination — it can be proved in large silicified samples by the absence of any spined segment that might be associated).

Current questions revolve around the relationships of these four groups. Dimeropygidae as traditionally conceived (groups 1 plus 2 just listed) appears to have several potential apomorphies; most strikingly, a low number of thoracic segments (seven in all known examples), with a single long axial spine set posteriorly on the second from last segment; and, in three genera, a sagittal groove on the dorsal surface of the pygidium for accommodation of this spine. These features are unknown in any other aulacopleuroidean trilobites. The known hypostomes of *Dimeropyge* and *Toernquistia* are minute and apparently unmineralized anteriorly, another striking potential synapomorphy. The absence of assigned hypostomes for any of the other species of *Toernquistia*, *Mesotaphraspis*, or *Chomatopyge*, is at least consistent with the presence of the minute morphology in these taxa as well.

Despite these rather obvious and highly distinctive apomorphies, the cladistic analysis carried out by Chatterton et al. (1998) failed to retrieve this traditional Dimeropygidae as a clade. Instead, *Dimeropyge* appeared on their strict consensus as a paraphyletic group, which encompassed the Lower Ordovician *Dimeropygiella* and the Lower-Middle Ordovician *Ischyrotoma* (group 4 mentioned earlier), and on the consensus based on successive approximations weighting as sister to these genera. Collectively, the three genera grouped with several species then assigned to *Hystricurus*. On both consensus cladograms *Celmus* (group 3 mentioned earlier) created paraphyly within *Ischyrotoma*. *Toernquistia*, *Mesotaphraspis*, and *Chomatopyge* (group 2 mentioned earlier), meanwhile, were not retrieved as monophyletic groups as conventionally classified, but collectively grouped with a range of other Skullrockian and Stairsian species then assigned to *Hystricurus* (including the type species of the hintzecurines *Hintzecurus* Adrain et al., 2003, *Rossicurus* Adrain et al., 2003, and the hystricurine *Flectihystricurus* Adrain et al., 2003). Chatterton et al. (1998) accordingly classified as Dimeropygidae the tuberculate group, including *Dimeropyge*, *Ischyrotoma*, and *Dimeropygiella* (at the time of their writing regarded as a synonym of *Ischyrotoma*). They resurrected Toernquistiidae for *Toernquistia*, *Chomatopyge*, and *Mesotaphraspis*. Because their analysis failed to retrieve a monophyletic *Toernquistia*, they erected a new genus, *Paratoernquistia*, for their new *P. sanchezae* and several species that grouped with it in their analysis. Finally, they erected a second new genus, *Lasarchopyge*, and assigned it also to Toernquistiidae.

The question arises why, given the striking synapomorphies just noted, the traditional dimeropygid grouping did not emerge from the Chatterton et al. (1998) analysis. The answer is that few of the potential synapomorphies were coded for by Chatterton et al. (1998) in their character analysis. In particular, no characters coded for the hypostome, for the number of thoracic segments, or for presence or position of a thoracic axial spine. Taxon sampling also influenced this analysis. Hystricuridae was traditionally conceived (e.g., Fortey and Owens 1975) as a paraphyletic group within which other aulacopleuroidean (and in some views, proetoidean) families root. Adrain et al. (2003) argued that large components of the “hystricurids,” including a restricted Hystricurinae and their new Hintzecurinae were monophyletic. Species belonging to these clades are largely irrelevant to an analysis of Dimeropygidae, yet in the state of knowledge in 1998 were included in the Chatterton et al. (1998) analysis. This had the effect of changing the polarity of many of the coded characters, as the hystricurids were used as outgroups. Length of genal spine, for example, was polarized with long spines as plesiomorphic on this basis. The long spines of *Dimeropyge* are in our opinion almost certainly derived, as all potential Lower Ordovician dimeropygids have tiny spines in holaspid stages. Results of the Chatterton et al. (1998) analysis must be regarded as suspect because of these problems of character analysis and taxon sampling. We consider that *Dimeropyge*, *Mesotaphraspis*, *Chomatopyge*, and *Toernquistia* are highly likely to make up a clade, recognize this clade as Dimeropygidae, and place Toernquistiidae once more in synonymy of Dimeropygidae.

New data on *Celmus* have come to light as a result of the collection of superbly preserved silicified material from the

Table Cove Formation in the Hare Bay region of western Newfoundland (J.M.A., and R.A. Fortey, unpublished data). Full documentation and discussion will be presented elsewhere, but the evidence based on thoracic, pygidial, and ontogenetic data now seems strong in supporting that *Celmus* is, in fact, not related to Dimeropygidae, but instead closely related to the Ordovician "glaphurids," including *Glaphurus* Raymond, 1905, *Glaphurina* Ulrich, 1930, and *Glaphurella* Dean, 1971. Adrain and Fortey (1997) placed Glaphuridae in synonymy of Raymondinidae Clark, 1924. We hence assign *Celmus* and *Glaphurella* to Raymondinidae.

Lasarchopyge does not appear to be closely related to the genera recognized here as Dimeropygidae. Rather, it is very similar to the scharyiid genus *Panarchaeogonus* Öpik, 1937. We regard it as an obvious member of Scharyiidae, and it was classified as such by Jell and Adrain (2003).

Most recently, Owens (2004) has assigned the Late Ordovician to Early Silurian *Solariproetus* Qu, 1986, to "Toernquistiidae" as a "late, derived member." The genus does not obviously possess any of the synapomorphies of Dimeropygidae as understood earlier in the text. In making the case, Owens (2004, p. 572) compared *Solariproetus* with *Lasarchopyge*, but this is irrelevant as the latter is a scharyiid. *Solariproetus* is not well known, but its general cranidial dimensions, tiny palpebral lobe nearly abutting the glabella, and tiny eye are all similar to taxa of Rorringtoniidae, to which it was assigned by Adrain and Chatterton (1993) and Jell and Adrain (2003).

With those adjustments, the main question remaining is the nature of the relationship, if any, between the mostly Lower Ordovician group 4, which includes *Bearriverops*, and the Middle–Upper Ordovician Dimeropygidae. We tentatively regard these taxa as forming a clade, hence expanding the concept of Dimeropygidae to include the range of earlier forms with a greater number of segments, which lack a thoracic axial spine and possess a large hypostome. Better understanding of phylogenetic structure within the Ibexian taxa and their relationship to the younger genera must await description of the many new species recovered in the current field sampling program, which is beyond the scope of this paper.

Parsimony analysis of *Bearriverops*

Taxa

All five newly named species make up the ingroup. The selected outgroup taxon is an undescribed dimeropygid species from lower in the Stairsian (horizon MME 36.4 m; the oldest *Bearriverops* species occurs at MME 75.5 m), which closely resembles *Bearriverops ibexensis* in cephalic details, but which lacks the prominent pygidial apomorphies of the new genus.

Characters

To explore cranidial shape variation for purposes of character coding, measurements were taken of several length and width parameters on all illustrated specimens. A series of comparisons were carried out using bivariate plots and reduced major axis regression (Imbrie 1956). The results are shown in Fig. 4. Regression equations are given in Table 1, significant pairwise comparisons of slopes in Table 2, and significant pairwise comparisons of intercepts in Table 3. Despite the range of morphology developed, general cranidial dimensions of species of *Bearriverops* are remarkably consistent. There are no significant differences in comparison of relative cranidial widths (Fig. 4.3), length versus width of the cranidium (Fig. 4.5) or length versus width of the glabella (Fig. 4.6). However, several of the species are clearly differentiated from one another based on the relative (exsagittal (exsag.)) length of the posterior fixigena (Fig. 4.1, the length of the palpebral lobe (Fig. 4.2), and the length of the anterior border (Fig. 4.4).

Cranidium

(1) Anterior edge of anterior border: 0, with sagittally rounded contact with forward-facing doublural sector; 1, with sharp transverse ridge marking transition to forward-facing doublural sector.

(2) Palpebral furrow: 0, well impressed; 1, very weakly impressed or absent.

(3) Granulose sculpture on main part of glabella: 0, present; 1, absent.

(4) Tuberculate sculpture on main part of glabella: 0, coarse; 1, small to moderate and subdued; 2, absent.

(5) Preglabellar field: 0, interrupted by median furrow or depression in most specimens; 1, complete medially.

(6) Posterior cranidial projection: 0, generally running slightly posterolaterally; 1, running almost exactly transverse or slightly anterolaterally.

(7) Anterior border exclusive of doublural sector: 0, short (sag.; exsag.) and dorsally convex; 1, long and flat.

(8) Posterolateral end of posterior projection: 0, with rounded, unbroken margin; 1, with short posterolaterally directed spine interrupting margin.

(9) Exsagittal length of posterior fixigena behind palpebral lobe: 0, long; 1, short.

Librigena

(10) Tuberculate sculpture on external surface of field: 0, present; 1, absent.

(11) Eye socle: 0, complete, inflated band; 1, very reduced, band-like only anteriorly, or essentially absent.

(12) Terrace lines on lateral border: 0, absent; 1, numerous fine lines over most of border; 2, two prominent lines abaxially, none adaxially.

Pygidium

(13) Number of strongly expressed axial rings; 0, 4; 1, 3; 2, 1.

(14) Tubercle on first posterior pleural band: 0, absent; 1, large and subconical; 2, obliquely extended, partially or wholly ridge-like.

Results

The character matrix is shown in Table 4. All characters were treated as unordered. Exhaustive search revealed a single most parsimonious tree of length 20, with a consistency index of 0.900 and retention index of 0.900 (Fig. 5.1). Nodal support was evaluated with nonparametric bootstrapping (10 000 replicates, branch and bound search) and Bremer support. Details of character support and the few instances

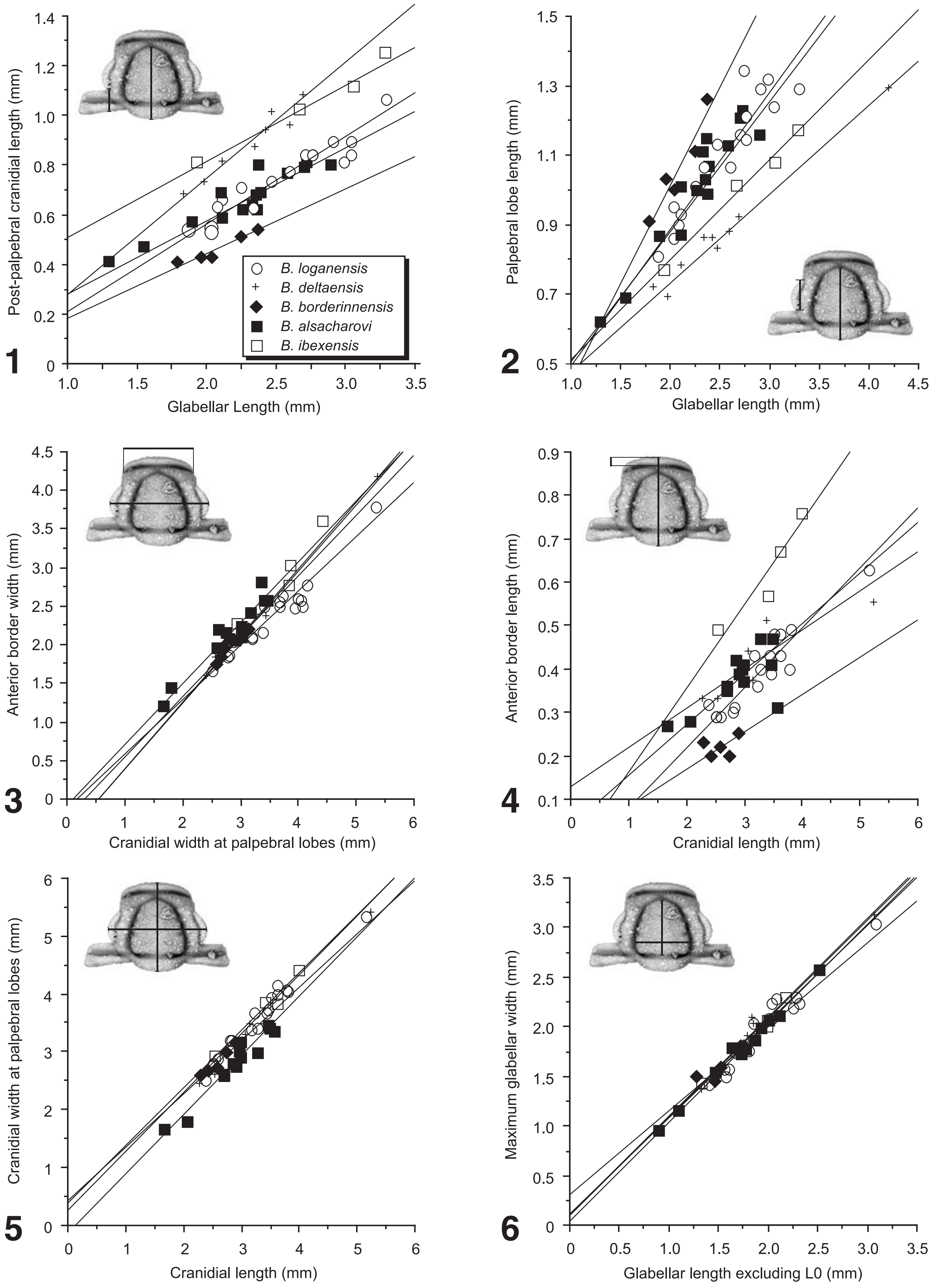

1
Post-palpebral cranidial length (mm)
Glabellar Length (mm)
B. loganensis
B. deltaensis
B. borderinnensis
B. alsacharovi
B. ibexensis
2
Palpebral lobe length (mm)
Glabellar length (mm)
3
Anterior border width (mm)
Cranidial width at palpebral lobes (mm)
4
Anterior border length (mm)
Cranidial length (mm)
5
Cranidial width at palpebral lobes (mm)
Cranidial length (mm)
6
Maximum glabellar width (mm)
Glabellar length excluding L0 (mm)

Fig. 4. Bivariate plots of various cranidial measurements on five new species of *Bearriverops*, with reduced major axes regression lines. Measurements are illustrated on a cranidium belonging to *Bearriverops loganensis*. Regression equations are shown in Table 1. Significant differences in pairwise comparison of slopes are shown in Table 2. Significant differences in pairwise comparison of intercepts are shown in Table 3. (1) Glabellar length versus posterior fixigenal exsagittal length. (2) Glabellar length versus palpebral lobe length. (3) Width across midlength of palpebral lobes versus width across anterior border. (4) Cranidial length versus anterior border length. (5) Cranidial length versus width across midlength of palpebral lobes. (6) Glabellar length, excluding LO, versus maximum glabellar width.

Table 1. Regression equations for reduced major axes depicted in Fig. 4.

Figure	Species	Slope	Constant	R^2	Standard error
4.1	*borderinnensis*	0.261	–0.08	0.904	0.027
4.1	*alsacharovi*	0.279	0.03	0.851	0.029
4.1	*ibexensis*	0.322	0.17	0.97	0.031
4.1	*loganensis*	0.348	–0.134	0.904	0.027
4.1	*alsacharovi*	0.466	–0.19	0.943	0.044
4.2	*borderinnensis*	0.565	–0.115	0.977	0.014
4.2	*alsacharovi*	0.418	0.015	0.898	0.036
4.2	*ibexensis*	0.288	0.224	0.98	0.023
4.2	*loganensis*	0.395	0.21	0.917	0.028
4.2	*alsacharovi*	0.261	0.21	0.977	0.014
4.3	*borderinnensis*	0.783	–0.08	0.932	0.118
4.3	*alsacharovi*	0.79	–0.08	0.924	0.066
4.3	*ibexensis*	0.918	–0.122	0.933	0.047
4.3	*loganensis*	0.702	–0.122	0.933	0.047
4.3	*alsacharovi*	0.859	–0.479	0.992	0.037
4.4	*borderinnensis*	0.085	–0.001	0.094	0.047
4.4	*alsacharovi*	0.116	0.041	0.479	0.025
4.4	*ibexensis*	0.193	–0.031	0.893	0.045
4.4	*loganensis*	0.138	–0.058	0.875	0.013
4.4	*alsacharovi*	0.09	0.13	0.744	0.023
4.5	*borderinnensis*	0.921	0.432	0.944	0.126
4.5	*alsacharovi*	1.02	–0.134	0.951	0.068
4.5	*ibexensis*	0.977	0.377	0.973	0.116
4.5	*loganensis*	1.02	0.247	0.973	0.043
4.5	*alsacharovi*	1.001	0.112	0.991	0.048
4.6	*borderinnensis*	0.833	0.34	0.804	0.213
4.6	*alsacharovi*	0.976	0.1	0.983	0.039
4.6	*ibexensis*	0.922	0.095	0.986	0.082
4.6	*loganensis*	0.999	0.032	0.949	0.059
4.6	*alsacharovi*	1	0.087	0.98	0.07

of homoplasy are discussed under treatment of individual species as follows.

Worthy of discussion is the degree to which the very well-supported hypothesis of phylogenetic relationship matches the sampled stratigraphic occurrence. We have commented at length (Adrain and Westrop 2001) on the inappropriateness of using stratigraphic order as a criterion to determine phylogeny and on the extreme and uneven habitat-based sampling biases in the Laurentian trilobite record. The *Bearriverops* cladogram is fully pectinate, but of its internal nodes (excluding the root), only one of three are stratigraphically consistent (following Huelsenbeck's (1994) definition of stratigraphic consistency, as when the oldest first occurrence of the taxa subtended by the node is the same age or younger than the oldest first occurrence of the sister taxon of the node). Huelsenbeck's stratigraphic consistency index (SCI, the number of consistent nodes divided by the number of internal nodes excluding the root) for the cladogram is, therefore, 0.33. The most plesiomorphic species, *B. ibexensis*, occurs at the youngest horizon, the opposite of the expectation if sampled order is an accurate representation of true temporal order. The next most plesiomorphic species, *B. deltaensis*, is younger than two of the species in its derived sister clade. And finally, *B. alsacharovi* is younger than its sister species. All of these mismatches with sampled order must be accounted for by range extensions (for *B. ibexensis*, *B. deltaensis*, and *B. alsacharovi*) as shown in Fig. 5.2.

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Table 2. Significant differences in pair-wise comparison of slopes of reduced major axis regression lines of Fig. 4. *z*, z-statistic; *p*, probability.

Figure	Species pair	*z*	*p*
4.1	*loganensis–alsacharovi*	2.27	<0.05
4.1	*prestonensis–alsacharovi*	3.53	<0.01
4.1	*ibexensis–alsacharovi*	2.67	<0.01
4.1	*borderinnensis–alsacharovi*	3.95	<0.01
4.2	*loganensis–alsacharovi*	4.47	<0.01
4.2	*prestonensis–alsacharovi*	4.2	<0.01
4.2	*loganensis–ibexensis*	3.57	<0.01
4.2	*prestonensis–ibexensis*	3.47	<0.01
4.2	*borderinnensis–alsacharovi*	3.01	<0.01
4.2	*borderinnensis–ibexensis*	2.7	<0.01
4.4	*ibexensis–alsacharovi*	2.06	<0.05

Note: Comparisons not listed did not reveal significant differences. All comparisons with $p > 0.01$ are not significant using the Bonferroni correction for multiple comparisons.

Table 3. Significant differences in pairwise comparison of intercepts of reduced major axis regression lines of Fig. 4.

Figure	Species pair	*z*	*p*
4.1	*loganensis–ibexensis*	8.19	<0.01
4.1	*loganensis–borderinnensis*	4.62	<0.01
4.1	*prestonensis–borderinnensis*	4.53	<0.01
4.1	*prestonensis–ibexensis*	13.96	<0.01
4.1	*borderinnensis–ibexensis*	3.42	<0.01
4.2	*alsacharovi–borderinnensis*	4.45	<0.01
4.2	*loganensis–borderinnensis*	2.8	<0.01
4.2	*prestonensis–borderinnensis*	3.51	<0.01
4.2	*ibexensis–alsacharovi*	3.09	<0.01
4.4	*ibexensis–loganensis*	3.74	<0.01
4.4	*ibexensis–prestonensis*	6.1	<0.01
4.4	*ibexensis–borderinnensis*	5.67	<0.01
4.4	*prestonensis–borderinnensis*	3.14	<0.01
4.4	*alsacharovi–borderinnensis*	8.37	<0.01

Note: Comparisons not listed did not reveal significant differences. All comparisons remain significant using the Bonferroni correction for multiple comparisons.

tory, Department of Geoscience, University of Iowa, Iowa City, Iowa, USA, with specimen number prefix SUI.

Family Dimeropygidae Hupé, 1953
= Dimeropygidae Whittington and Evitt, 1954
= Toernquistiidae Hupé, 1953

INCLUDED GENERA: *Dimeropyge* Öpik, 1937; *Chomatopyge* Whittington and Evitt, 1954; *Mesotaphraspis* Whittington and Evitt, 1954; *Toernquistia* Reed, 1896 (= *Paratoernquistia* Chatterton, Edgecombe, Waisfeld, and Vaccari, 1998).

TENTATIVELY INCLUDED GENERA: *Bearriverops* n. gen.; *Dimeropygiella* Ross, 1951; *Ischyrotoma* Raymond, 1925; *Parahystricurus* Ross, 1951; *Pseudohystricurus* Ross, 1951.

REJECTED GENERA: *Celmus* Angelin, 1854 (Raymondinidae); *Glaphurella* Dean, 1971 (Raymondinidae); *Lasarchopyge* Chatterton, Edgecombe, Waisfeld, and Vaccari, 1998 (Scharyiidae); *Solariproetus* Qu, 1986 (Rorringtoniidae).

NOMEN DUBIUM: *Toernquistina* Rozova in Rozova et al. 1985.

DIAGNOSIS: (This diagnosis applies to the abovementioned core group of genera.) Aulacopleuroidean trilobites with long genal spines; yolked librigenae; minute hypostome; seven thoracic segments with a long axial spine on the sixth; and pygidial axis typically with a dorsal sagittal groove to receive the underside of the thoracic axial spine.

REMARKS: The rationale for current classification of Dimeropygidae was discussed earlier in the text.

Genus ***Bearriverops*** n. gen.

TYPE SPECIES: *Bearriverops loganensis* n. sp., from the Ibexian (Stairsian) of southeastern Idaho and western Utah, USA.

OTHER SPECIES: All Stairsian in age: *Bearriverops alsacharovi* n. sp.; *B. borderinnensis* n. sp.; *B. deltaensis* n. sp.; and *B. ibexensis* n. sp.; *Bearriverops* n. sp. A and *Bearriverops* sp. cf. *B. ibexensis* both represent distinct but as yet unnamed species.

Derivation of name: After the Bear River Range, Idaho, and the Greek noun *ops*, eye. Gender is masculine.

DIAGNOSIS: Anterior part of cephalic doublure turned outwards and forwards, so as to be plainly visible in anterior view and not visible in ventral view; librigenal field narrow, eye long and large; librigenal lateral border with abaxial raised line sculpture; genal spine slender to (more typically) tiny or absent; thorax of ten segments, lacking any axial spines; pygidium with one to three low rings, pleural bands, and furrow expressed only on narrow proximal area, and large, generally steeply declined, distal pleural region with smooth or, at most, granulose sculpture; first pygidial posterior pleural band typically with conical spine, serial homologues that are set in longitudinal series in progressively more distal positions on successively anterior thoracic segments.

REMARKS: *Bearriverops* species encompass a surprising range of morphological diversity, given that the clade includes only five well known taxa and has a known distribution restricted to the later Stairsian of Utah and Idaho. Nevertheless, the shared anterior border morphology and that of the posterior of the thorax and especially the pygidium is unique among Lower Ordovician dimeropygids, and the genus appears to represent an unambiguous clade.

Four of the species have a prominent conical tubercle on the proximal part of the posterior pleural band of the first pygidial segment. *Bearriverops borderinnensis* is the only species lacking this tubercle, but has a strongly effaced dorsal morphology coupled with an extremely small proximal pygidial pleural area. All five named species have pygidia with strongly downturned, unsculptured, distal faces. Three species are known from articulated complete or nearly complete thoraces, which make clear that the pygidial morphology

Table 4. Data matrix for parsimony analysis of *Bearriverops*.

Taxa	Characters 1	2	3	4	5	6	7	8	9	10	11	12	13	14
B. loganensis	0	0	0	1	0	1	0	1	1	1	0	1	1	1
B. deltaensis	0	0	0	1	0	0	0	0	0	0	0	1	1	1
B. alsacharovi	1	1	1	2	1	1	1	1	1	1	1	2	2	2
B. borderinnensis	1	1	1	2	1	1	0	1	1	1	1	2	2	2
B. ibexensis	1	0	0	0	0	0	1	0	0	0	0	1	1	1
MME 36.4	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Note: “MME 36.4” is outgroup taxon, an undescribed species of dimeropygid from section MME 36.4 m, Middle Mountain, northwestern Wah Wah Mountains.

is probably an aptation to facilitate spiral enrollment, with most of the pygidium and the distal tips of the posterior thoracic segments accommodated within the cephalic doublure.

The Upper Ordovician (Ashgill) genus *Carmon* Barrande, 1872, type genus of the monotypic Carmonidae Kielan, 1960, is at least superficially similar to *Bearriverops*. The type and only species, *Carmon mutilus* (Barrande, 1852) from the Králův Dvůr Formation of the Prague Basin, Czech Republic, is not well known. Horný and Bastl (1970, p. 20, fig. 10) figured an outstretched, articulated specimen, and Shaw (2000) provided tiny photographs of three others. All are internal molds. Kielan (1960) assigned better preserved external molds from the *Staurocephalus clavifrons* Zone of the Holy Cross Mountains, Poland, to Barrande’s species. Kielan had Králův Dvůr Formation material available for direct comparison, but in the present state of knowledge of the Czech material, the species identity remains to be firmly established.

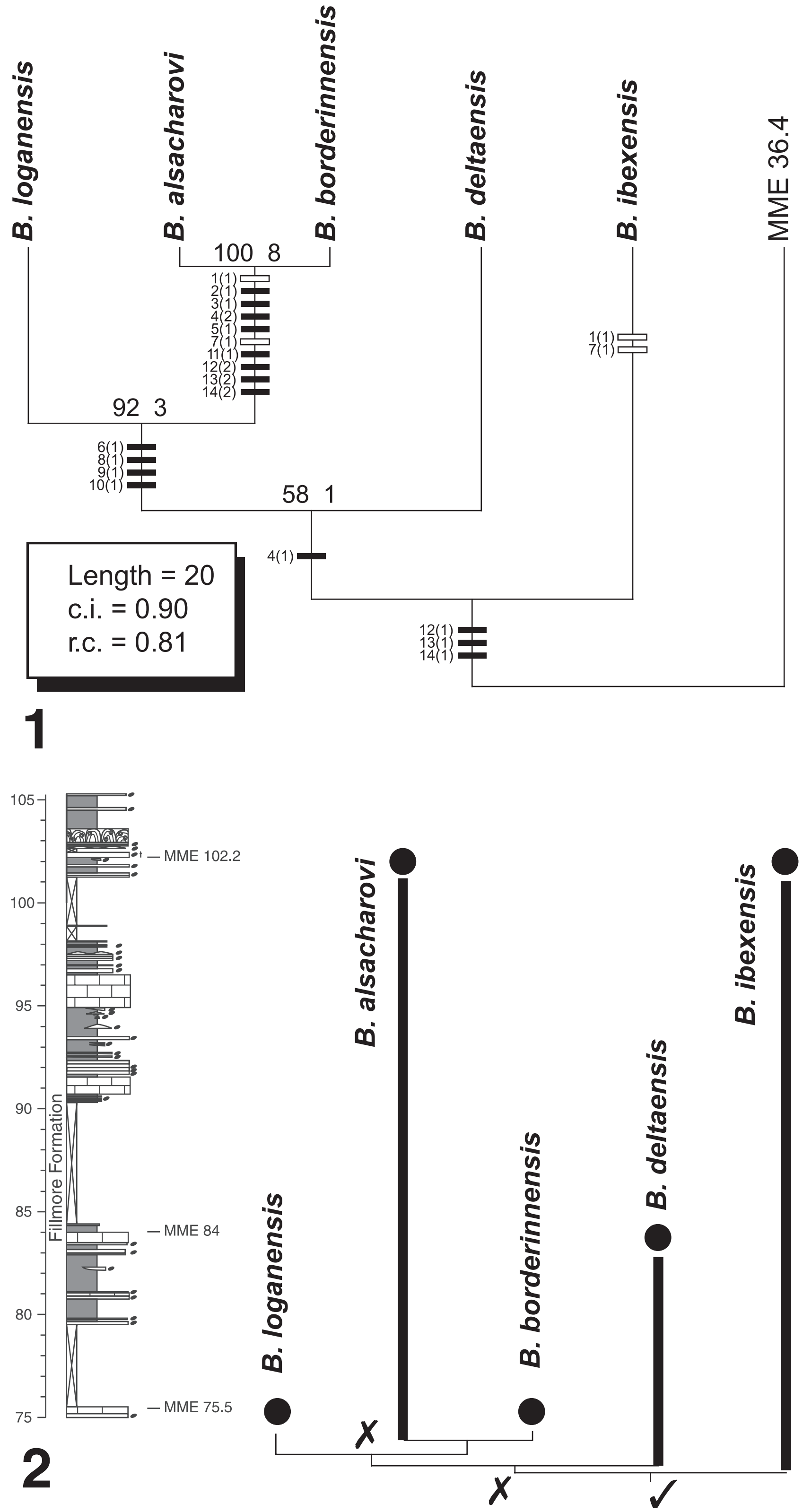
Carmon mutilus is a vaulted trilobite approximately similar in overall dimensions to species of *Bearriverops* (cf. Kielan, 1960, pl. 17, fig. 2; with Fig. 6.1 herein). It lacks genal spines and has a dorsal sculpture of tubercles set atop granules, which is very similar to that of *B. loganensis*. Pygidia of the species are strikingly similar (cf. Kielan 1960, pl. 17, fig. 5; with Fig. 6.8 herein), as both are small and medially bowed, with a broad effaced posterior region, a low number of axial rings, and a protuberance on the posterior pleural band of the first segment. The pygidium of *C. mutilus* has only two axial rings, while that of *B. loganensis* has three, but the thorax of *C. mutilus* contains 11 segments, whereas that of *B. loganensis* has 10 — hence either species has a thoracopygidium composed of 13 segments. Nevertheless, there are also very significant differences between the taxa. *Carmon mutilus* is blind and has a much reduced librigena formed mainly of its thick lateral border. The anterior border and border furrow of *C. mutilus* is of fundamentally different structure, abutting the front of the glabella with no sign of a preglabellar field, and with a strong scarp along the posterior edge. This morphology is reminiscent of calymenoideans, as is the hypostome (Kielan 1960, pl. 17, fig. 3), which is also very different from the aulacopleuroidean form of that of *Bearriverops*. *Carmon mutilus* has a very narrow rostral plate (Kielan 1960, pl. 17, fig. 6), which expands anteriorly, a completely different morphology than the broadly transverse plate of *B. loganensis* (Fig. 6.11). While a dimeropygid relationship of *Carmon* should not be ruled out pending new data, in the present state of knowledge, we regard the similarities between the genus and *Bearriverops*, while striking, as most likely uninformative of relationship. If a relationship exists, it implies a ghost lineage spanning much of the Ordovician.

A genus much closer in age to *Bearriverops* is *Holubaspis* Přibyl, 1950, from the Milina Formation (lower Tremadocian; Mergl 1984) and Třenice Formation (upper Tremadocian; Mergl 1994) of the Czech Republic. The genus has been classified by Vaněk (1965) and Mergl (1984, 1994) as Hystricuridae Hupé 1953. Its possible affinities were discussed by Adrain et al. (2003, p. 560), who concluded that it may well represent an aulacopleuroidean but that further information was required to establish its affinities with confidence. The hypostome of *H. perneri* (Růžíčka, 1926) (Mergl 1984, pl. 4, fig. 9) is closely comparable to those of *Bearriverops loganensis* (Fig. 6.11) and *B. deltaensis* (Fig. 10.11). Cephalic dimensions are also similar to those of *B. loganensis*, with the exception of the complete lack of a preglabellar field in *Holubaspis*. Nevertheless, the anterior border is closely comparable, with a dorsal sculpture of raised subparallel lines, and the general dorsal cephalic sculpture of fine tubercles atop background granulation is nearly identical. *Holubaspis* also has an extremely reduced genal spine (Mergl 1994, p. 4, fig. 9). A major point of difference, however, is pygidial morphology. Although the pygidium of *Holubaspis* is apparently quite micropygous as in *Bearriverops*, it has an extremely prominent, raised axis that occupies a majority of its area, very well-incised pleural furrows, and a strong border, none of which are at all comparable with what is seen in *Bearriverops* or, for that matter, any other Laurentian Lower Ordovician dimeropygid. The possibility that *Holubaspis* is a dimeropygid, or at least an aulacopleuroidean, remains compelling, but the question can only be resolved with the discovery of new data.

Bearriverops loganensis n. sp.
(Figs. 6–8)

DERIVATION OF NAME: After the town of Logan, Utah, our base of operations for Bear River Range fieldwork.

TYPE SPECIMENS: Holotype dorsal exoskeleton SUI 99859, from section FB7 102.1 m, Garden City Formation (Stairsian, Zone E – *Tesselacauda* Zone), Franklin Basin, Bear River Range, Franklin County, southeastern Idaho (paratype specimen from this horizon: SUI 99867). Also occurs at section HC 5 106.7 m (figured specimens: SUI 99860 – SUI 99866, SUI 99868, SUI 99870 – SUI 99876, SUI 99878 –



SUI 99880) and HC6 88.3–89.5 m (figured specimens form HC6 88.3: SUI 99869, SUI 99877), Garden City Formation, Hillyard Canyon, Bear River Range, and section MME 75.5 m, Fillmore Formation (Stairsian, Zone E – *Tesselacauda* Zone), Middle Mountain, Ibex area, Millard County, western Utah (figured specimens: SUI 99881 – SUI 99907).

Fig. 5. (1) Singlemost parsimonious cladogram derived using exhaustive search of the data matrix of Table 4. Character-state optimizations shown using accelerated transformation. Black bars are characters with a consistency index (c.i.) of 1.0; white bars are characters which contain homoplasy. Numbers to left of nodes are nonparametric bootstrap values based on 10 000 pseudoreplicates using branch and bound. Numbers to right of nodes are Bremer support values. (2) Singlemost parsimonious cladogram (excluding outgroup species, which occurs 38.6 m down section from lowest level depicted) mapped against stratigraphy. Diagram uses stratigraphic column for section MME and assumes that *B. ibexensis*, which co-occurs with *B. alsacharovi* at G 26.6 m and G 27.0 m, would occur at the same horizon at MME, though it has not been sampled there. The cladogram has a stratigraphic c.i. (Huelsenbeck 1994) of 0.33. Necessary range extensions, implying the unsampled presence of their respective lineages, are shown in bold. Check mark, stratigraphically consistent node. X, stratigraphically inconsistent node. r.c., re-scaled consistency index.

DIAGNOSIS: Palpebral lobe long, with strong palpebral furrow; librigenal field broad; genal spine almost completely lost in large specimens; pygidium with strong posteromedian flexure.

DESCRIPTION:

Cranidium: Cranidial measurements are based on the specimens of Figs. 7.1–75, 7.20, 7.22, 7.23, 8.1–8.4, 8.11, 8.17, 8.18, 8.20, and 8.30. Cranidium with sagittal length 91.4% (range 87.2%–96.5%) width across midlength of palpebral lobes; width across anterior border 66.8% (61.1%–73.0%) width across midlength of palpebral lobes; glabella with sagittal length (excluding LO and S0) 98.5% (91.2%–105.4%) maximum width; glabella with overall shape nearly subtriangular, axial furrows anteriorly divergent opposite rear half of L1, strongly anteriorly convergent from opposite anterior half of L1 forward, running without obvious change in depth or break in course into preglabellar furrow; preglabellar furrow with anteromedian inflection in most specimens, in some cases with slightly deepened pit, so that front of glabella forms slight anterior point; axial furrows and preglabellar furrow deep, axial furrows broader posteriorly opposite L1 and L2, narrower anteriorly; glabella with dorsal sculpture of fine, closely spaced granules surmounted by more widely scattered, subdued, small- and moderate-sized tubercles; L1 and L2 with moderate but obvious independent inflation, S1 with contact with axial furrow approximately opposite midlength (exsag.) of palpebral lobe, course curved posteromedially, variable in length but a clearly expressed furrow in all specimens; S2 with contact with axial furrow just posterior to anterior end of palpebral furrow, running very slightly anteromedially in most specimens, but slightly posteromedially in a few, expression ranging from distinct furrow to mainly lateral notch; S3 discernible in most specimens as very faint lateral indentation; S0 long and of similar length in median two thirds, much shorter and deeper behind L1, contact with front of LO sharper than that with rear of median glabellar lobe, but both contacts very distinct; LO longest sagittally, progressively shorter exsagittally to lateral terminus, with very subdued median tubercle set on anterior third of ring and sculpture of fine granules and small tubercles similar to that on rear of median glabellar lobe, posterior margin of LO with stronger posterior curvature than anterior margin; axial furrow very shallow opposite LO; preglabellar field short and not complete medially, median area depressed into shallow furrow connecting anterior border furrow and preglabellar furrow; anterior sections of facial suture nearly subparallel to slightly anteriorly convergent in overall course; frontal area with granulose sculpture but lacking tubercles or with only faint, small tubercles; anterior border furrow fairly deep and incised laterally, with pronounced posterior deflection medially in most specimens to meet median depression on preglabellar field; general course transverse to slightly anterior arc; anterior border with sagittal length 12.0% (10.6%–13.6%) sagittal length of cranidium, with moderate to strong dorsal inflation, lacking sculpture dorsally, grading into doublural sector, which is produced forward to face slightly anterodorsally, doublural sector with sculpture of fine, closely spaced raised lines with slightly irregular course, generally subparallel with curvature of border and anterior margin; interocular fixigena with moderate dorsal inflation, sculpture of granules and small tubercles similar to that on glabella, many large specimens with larger primary fixigenal tubercles expressed in exsagittal row; palpebral lobe long and very narrow, with substantial but slightly uneven lateral curvature, curve strongest at midlength of lobe, held in horizontal plane, lacking sculpture; palpebral furrow strongly impressed, widest opposite midlength of palpebral lobe, narrower anteriorly and posterior, curved anteriorly and posteriorly around edges of lobe, lateral curvature less pronounced than that of palpebral lobe; posterior fixigena extended into fairly long, almost exactly transverse posterior projection; posterior border furrow short (exsag.) proximally, but much longer over most of its course, shallow, with an abrupt posterior scarp making the front of the posterior border and a shallower, more gradational contact anteriorly with the rear of the fixigena, furrow runs to lateral termination of projection, interrupted distally only by small sutural ridge; posterior border with strong dorsal convexity, lacking sculpture, short proximal to fulcrum, progressively longer distally, posterior edge with very faint furrow running along it for articulation with first thoracic segment; lateral terminus of posterior projection with posterolateral point but no development of spine; doublure forming articulatory surface underlying LO, lacking sculpture, and narrow edge underlying posterior border, expanded distally; doublure of anterior border facing forward (as described earlier) and surface not visible in ventral view.

Librigena: Librigenal measurements are based on the specimens of Figs. 7.25, 7.27, 7.28, 7.33, 7.35, 7.36, 7.40, 8.31, 8.33, 8.34, and 8.36–8.40. Librigenal field with width at midlength of eye 36.4% (29.9%–44.0%) exsagittal length; eye long and low, with considerable convexity; eye socle of single prominent, continuous band, increasing in width anteriorly, set off from visual surface by deeply incised, narrow furrow and from field by broader, less incised depression; field with sculpture of many densely spaced fine granules, no tubercles present dorsally, though positions of faint tubercles on middle part of field are indicated by pits on internal surface (Fig. 7.32); middle of field more inflated than adaxial or abaxial part, so as to form broadly inflated band along length; lateral border furrow

Fig. 6. *Bearriverops loganensis* n. gen. n. sp., from the Garden City Formation (Stairsian), Bear River Range, Franklin County, south-eastern Idaho. (**figs. 6.1, 6.2, 6.5, 6.8, 6.9, 6.13, 6.17**) Dorsal exoskeleton, holotype, SUI 99859, dorsal, posterior, anterior, dorsal pygidium, ventral, right lateral, and oblique views, ×7.5 (FB7 102.1 m). (**figs. 6.3, 6.4, 6.6, 6.7, 6.11**) Cephalon, SUI 99860, dorsal, left lateral, oblique, anterior, and ventral views, ×6 (HC5 106.7 m). (**figs. 6.10, 6.12, 6.14–6.16, 6.18**) Dorsal exoskeleton lacking librigenae, SUI 99861, dorsal, oblique, left lateral, posterior, anterior, and ventral views, ×7.5 (HC5 106.7 m). (**figs. 6.19, 6.20**) Cranidium and thoracic segments, SUI 99862, dorsal and ventral views, ×10 (HC5 106.7 m).

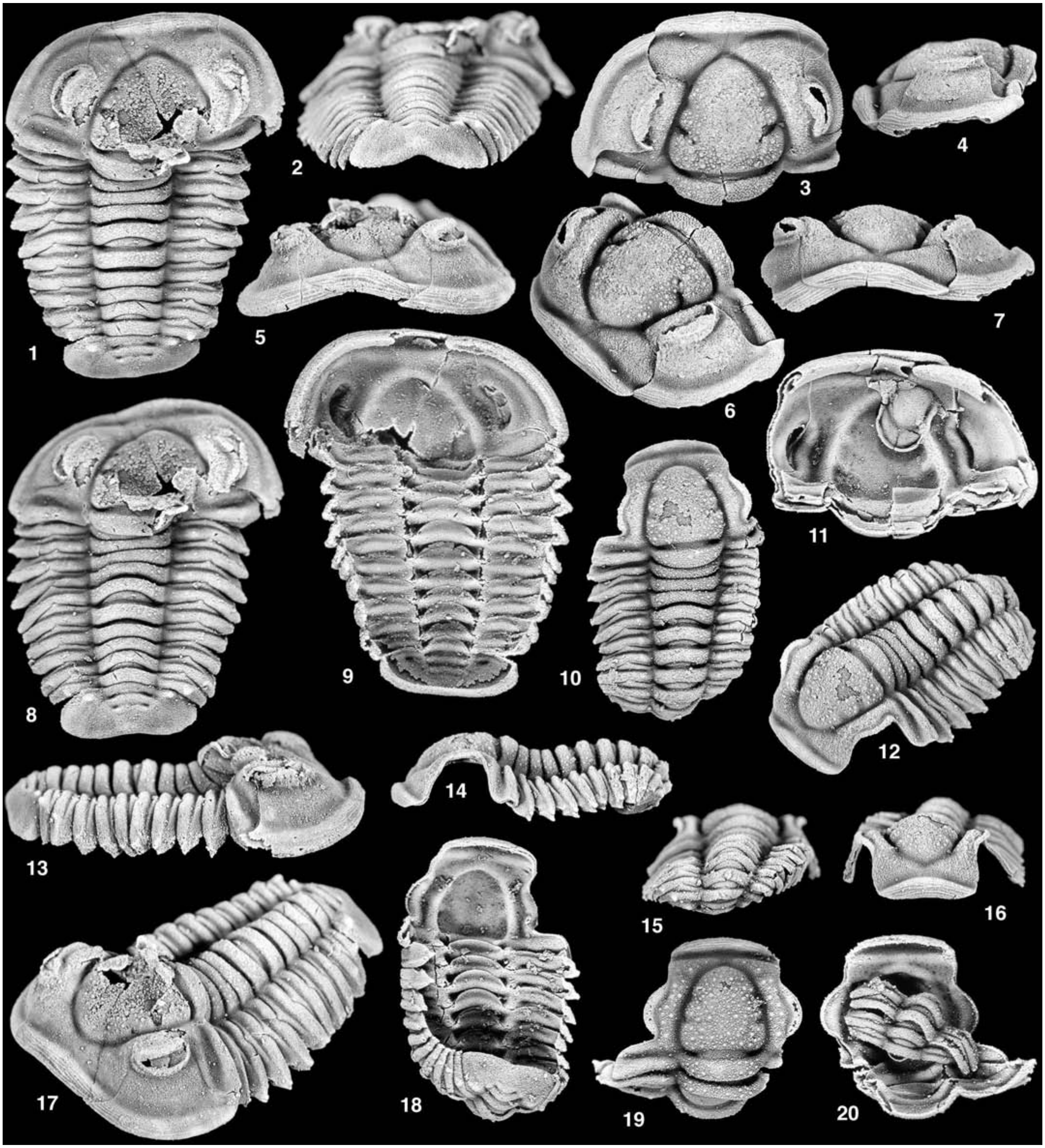
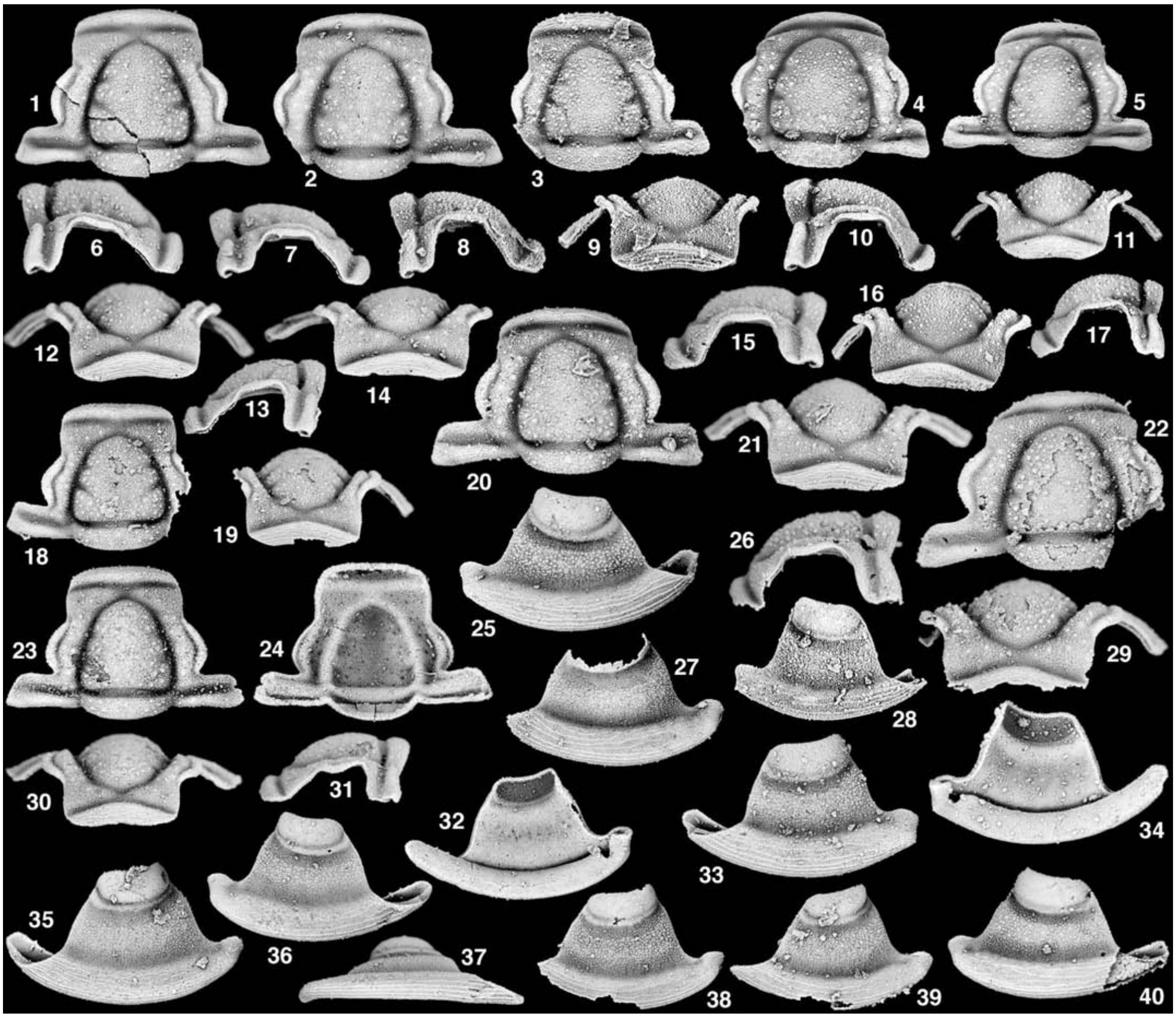


Fig. 7. *Bearriverops loganensis* n. gen. n. sp., from the Garden City Formation (Stairsian), Bear River Range, Franklin County, southeastern Idaho. From Section HC5 106.7 m and ×7.5, except where noted. (**figs. 7.1, 7.6, 7.12**) Cranidium, SUI 99863, dorsal, right lateral, and anterior views. (**figs. 7.2, 7.7, 7.14**) Cranidium, SUI 99864, dorsal, right lateral, and anterior views. (**figs. 7.3, 7.8, 7.9**, cranidium) SUI 99865, dorsal, right lateral, and anterior views. (**figs. 7.4, 7.10, 7.16**) cranidium, SUI 99866, dorsal, right lateral, and anterior views. (**figs. 7.5, 7.11, 7.17**) Cranidium, SUI 99867, dorsal, anterior, and left lateral views (FB7 102.1 m). (**figs. 7.13, 7.18, 7.19**) Cranidium, SUI 99868, left lateral, dorsal, and anterior views. (**figs. 7.15, 7.20, 7.21**) Cranidium, SUI 99869, left lateral, dorsal, and anterior views, ×10 (HC6 88.3 m). (**figs. 7.22, 7.26, 7.29**) Cranidium, SUI 99870, dorsal, left lateral, and anterior views, ×10. (**figs. 7.23, 7.24, 7.30, 7.31**) Cranidium, SUI 99871, dorsal, ventral, anterior, and left lateral views, ×10. (**fig. 7.25**) Right librigena, SUI 99872, external view, ×10. (**fig. 7.27**) Left librigena, SUI 99873, external view. (**fig. 7.28**) Right librigena, SUI 99874, external view, ×10. (**figs. 7.32, 7.36, 7.37**) Right librigena, SUI 99875, internal, external, and ventrolateral views. (**figs. 7.33, 7.34**) Left librigena, SUI 99876, external and internal views, ×10. (**fig. 7.35**) Left librigena, SUI 99877, external view (HC6 88.3 m). (**fig. 7.38**) Left librigena, SUI 99878, external view. (**fig. 7.39**) Left librigena, SUI 99879, external view. (**fig. 7.40**) Right librigena, SUI 99880, external view, ×10.



broad and shallow, in some specimens (Figs. 7.27, 7.33) with fairly sharp and steep contact with adaxial edge of lateral border, contact less pronounced in most specimens, furrow with broad lateral curvature subparallel with that of lateral margin; lateral border with width opposite midlength of eye 66.5% (51.7%–76.9%) width of field in same position, width similar over most of course, in some specimens (e.g., Fig. 7.35) narrower posteriorly; border with sculpture of fine raised lines over entire surface, less closely spaced and more irregular in course adaxially, closely spaced and nearly exactly parallel with lateral margin abaxially; posterior border not developed, cut entirely out by posterior facial suture; genal angle subrectangular and tab-shaped, in most specimens with very small thorn-like spine, entirely absent in some

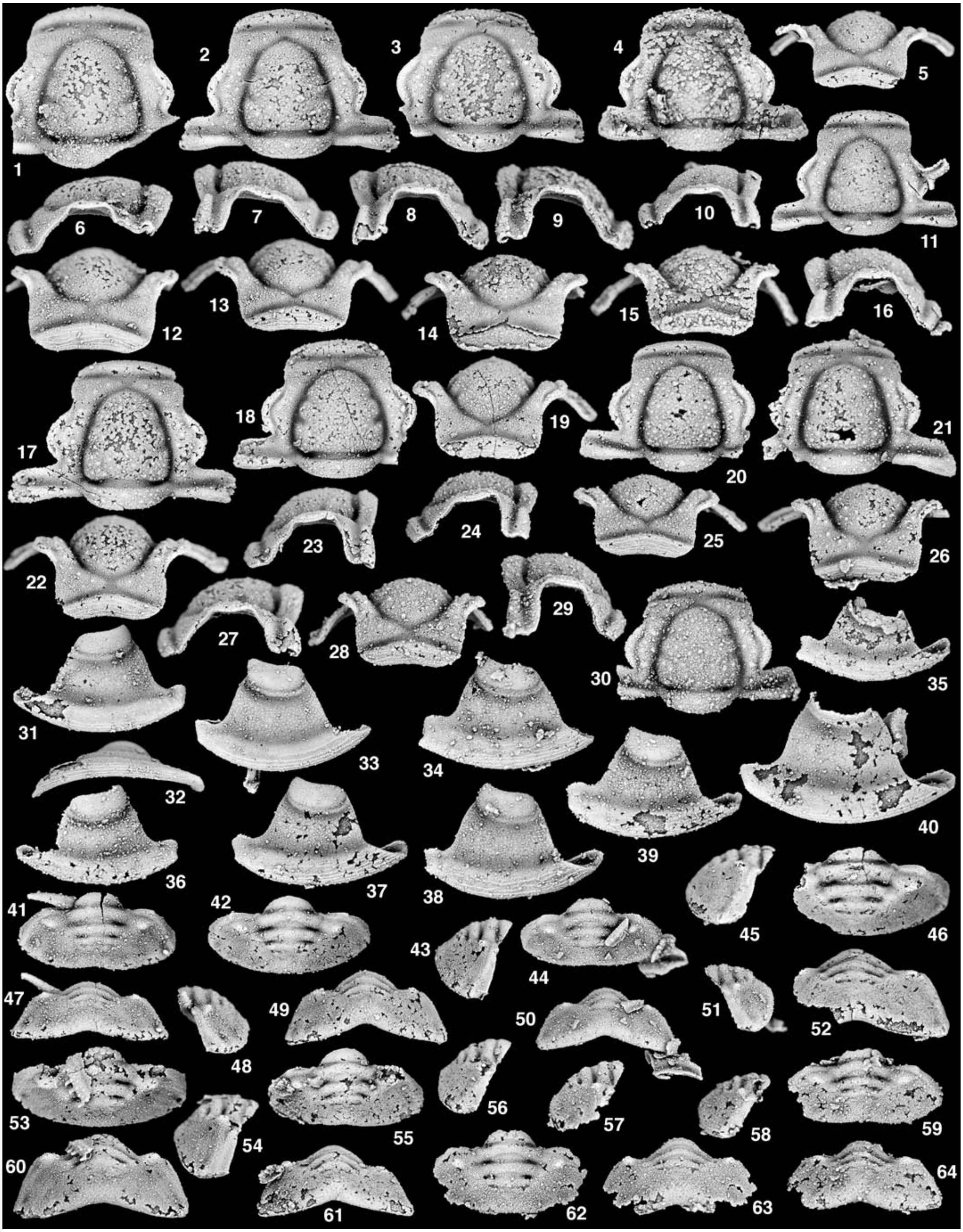

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Fig. 8. *Bearriverops loganensis* n. gen. n. sp., from the lower Fillmore Formation (Stairsian), Section MME 75.5 m, Middle Mountain, Ibex area, Millard County, western Utah. Magnifications are ×7.5, except where noted. (**figs. 8.1, 8.6, 8.12**) Cranidium, SUI 99881, dorsal, left lateral, and anterior views, ×6. (**figs. 8.2, 8.7, 8.13**) Cranidium, SUI 99882, dorsal, right lateral, and anterior views. (**figs. 8.3, 8.8, 8.14**) Cranidium, SUI 99883, dorsal, right lateral, and anterior views. (**figs. 8.4, 8.9, 8.15**) Cranidium, SUI 99884, dorsal, right lateral, and anterior views. (**figs. 8.5, 8.10, 8.11**) Cranidium, SUI 99885, anterior, left lateral, and dorsal views. (**figs.** 8.16, 8.21, 8.26) Cranidium, SUI 99886, right lateral, dorsal, and anterior views, ×10. (**figs. 8.17, 8.22, 8.27**) Cranidium, SUI 99887, dorsal, anterior, and left lateral views. (**figs. 8.18, 8.19, 8.23**) Cranidium, SUI 99888, dorsal, anterior, and left lateral views. (**figs. 8.20, 8.24, 8.25**) Cranidium, SUI 99889, dorsal, left lateral, and anterior views, ×10. (**figs. 8.28–8.30**) Cranidium, SUI 99890, anterior, right lateral, and dorsal views, ×10. (**figs. 8.31, 8.32**) Left librigena, SUI 99891, external and ventrolateral views. (**fig. 8.33**) Right librigena, SUI 99892, external view. (**fig. 8.34**) Right librigena, SUI 99893, external view, ×10. (**fig. 8.35**) Right librigena, SUI 99894, external view, ×10. (**fig. 8.36**) Left librigena, SUI 99895, external view, ×10. (**fig. 8.37**) Right librigena, SUI 99896, external view, ×10. (**fig. 8.38**) Right librigena, SUI 99897, external view, ×10. (**fig. 8.39**) Right librigena, SUI 99898, external view, ×10. (**fig. 40**) Right librigena, SUI 99899, external view. (**figs. 8.41, 8.47, 8.48**) Pygidium, SUI 99900, dorsal, posterior, and left lateral views. (**figs. 8.42, 8.43, 8.49**) Pygidium, SUI 99901, dorsal, right lateral, and posterior views. (**figs. 8.44, 8.50, 8.51**) Pygidium, SUI 99902, dorsal, posterior, and left lateral views. (**figs. 8.45, 8.46, 8.52**) Pygidium, SUI 99903, right lateral, dorsal, and posterior views. (**figs. 8.53, 8.54, 8.60**) Pygidium, SUI 99904, dorsal, right lateral, and posterior views. (**figs. 8.55, 8.56, 8.61**) Pygidium, SUI 99905, dorsal, right lateral, and posterior views. (**figs. 8.57, 8.62, 8.63**) Pygidium, SUI 99906, right lateral, dorsal, and posterior views, ×10. (**figs. 8.58, 8.59, 8.64**) Pygidium, SUI 99907, right lateral, dorsal, and posterior views, ×10.

specimens (Figs. 7.35, 7.38); anterior projection short, terminating in "V"-shaped connective suture; doublure broad and lacking sculpture, with very deep and prominent Panderian notch in front of genal angle.

Rostral plate: Rostral plate transverse and short (Figs. 6.9, 6.11), shaped like laterally stretched hourglass, of similar length sagittally and exsagittally; connective sutures strongly chevron-shaped, receiving "V"-shaped terminus of librigenal anterior projection; rostral plate with sculpture of fine raised lines on anterior part contiguous with those on librigenal lateral border, smooth on posterior doublural sector.

Hypostome: Hypostome (Fig. 6.11) small in relation to cephalon; sagittal length approximately 85% width across anterior wings; width across shoulder 78% of sagittal length; anterior margin with even and moderate anterior curvature; anterior wings large and broad, subtriangular, with ventral pit at terminus marking base of dorsal project for articulation with fossula; lateral and posterior borders formed of prominent, narrow, raised rim with sculpture of closely spaced raised lines; lateral border furrow straight, narrow, and incised, running without interruption into similarly incised posterior border furrow; posterior margin, border, and border furrow with semilunate posterior curvature; middle furrow set about 64% sagittal distance posteriorly from anterior margin, with less posterior curvature than posterior border and margin; anterior part of middle body with greater ventral inflation than crescentic posterior part; middle body lacking sculpture.

Thorax: Thorax of ten segments; axial lobe widest anteriorly, progressively slightly narrower posteriorly; pleural lobes widest at about third segment, slightly narrower anteriorly and progressively considerably narrower posteriorly; axis occupying about 34% thoracic width at segments two to three and about 36% of width across segment ten (based on measurements of holotype); axial ring with very fine granulate sculpture, approximately same length sagittally and exsagittally, bowed forward sagittally and at distal termination so as to describe very shallow "W" shape in dorsal view; ring furrow deep and transverse; articulating half ring large, with prominent dorsal transverse convexity (best seen ventrally, e.g., Figs. 6.9, 6.18); axial furrow relatively shallow, but fully isolating axial ring from pleura; pleural furrow deep and long (exsag.), much shallower and shorter (exsag.) distally behind articulating facet, but extended all the way to distal tip of segment; posterior pleural band about twice length of anterior band, both with moderate dorsal inflation; anterior band lacking sculpture, posterior band with faint transverse row of subdued moderate sized tubercles on anterior segments of large specimens (developed also on posterior segments in smaller specimens, e.g., Fig. 6.10); anterior band with prominent, anteriorly directed, subtriangular articulating process at fulcrum; posterior band with posterior notch to receive process; pleura turned fairly sharply down at fulcrum; anterior band longer distally to form relatively short (exsag.) articulating facet; pleural tips with short posteroventrally directed spine; serial homologues of large subconical spine on first pygidial posterior pleural band set slightly distal to fulcrum on posterior pleural band of segment ten as similarly prominent spine, and in progressively more distal positions on more anterior segments, reduced in size to tubercle from segment nine forward, by segment seven tubercle is set near distal tip above distal spine, so that anterior segments appear to have a double spine.

Pygidium: Pygidial measurements are based on the specimens of Figs. 8.41, 8.42, 8.44, 8.53, and 8.55; pygidium with sagittal length (excluding articulating half ring) 38.9% (38.5%–39.4%) maximum width; axis with maximum with at anterior 37.7% (34.4%–39.8%) that of pygidium; articulating half ring large and crescentic, separated from first axial ring by deep and well incised, transverse to slightly anteriorly arcuate ring furrow, furrow slightly deeper laterally than medially; anterior pygidial margin transversely straight proximal to fulcrum, curving posterolaterally distal to fulcrum; axial furrows very shallow, axis separated from surrounding pleurae mainly by very distinct break in slope, axial furrows almost entirely shallowed posteriorly so that rear of axis more or less grades into post-axial region; three axial rings plainly expressed, faint fourth marked by ring furrow behind third ring and small transverse lateral swellings, nearly obscure on some specimens (e.g., Fig. 8.53); entire dorsal surface of pygidium lacking sculpture; first axial ring slightly shorter


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Fig. 9. *Bearriverops alsacharovi* n. gen. n. sp. **figs. 9.1–9.32, 9.34–9.37** from the lower Fillmore Formation (Stairsian), Section MME 84.0 m, Middle Mountain, Ibex area, Millard County, western Utah. Magnifications are ×10, except where noted. (**figs. 9.1, 9.5, 9.9, 9.14**) Cranidium, holotype, SUI 99908, dorsal, right lateral, anterior, and ventral views. (**figs. 9.2, 9.6, 9.11**) Cranidium, SUI 99909, dorsal, right lateral, and anterior views. (**figs. 9.3, 9.7, 9.8, 9.12**) Cranidium, SUI 99910, dorsal, left lateral, anterior, and ventral views. (**figs. 9.4, 9.9, 9.13**) Cranidium, SUI 99911, dorsal, right lateral, and anterior views, ×7.5. (**figs. 9.15, 9.22, 9.25**) Cranidium, SUI 99912, dorsal, anterior, and right lateral views. (**figs. 9.16–9.18**) Cranidium, SUI 99913, dorsal, anterior, and left lateral views. (**figs. 9.19, 9.20, 9.24**) Cranidium, SUI 99914, right lateral, dorsal, and anterior views. (**figs. 9.21, 9.29, 9.30**) Cranidium, SUI 99915, dorsal, left lateral, and anterior views. (**figs. 9.23, 9.26, 9.31**) Left librigena, SUI 99916, external, ventrolateral, and internal views. (**figs. 9.27, 9.28**) Right librigena, SUI 99917, external and internal views. (**fig. 9.32**) Left librigena, SUI 99918, external view. (**figs. 9.34–9.37**) Pygidium, SUI 99920, dorsal, left lateral, posterior, and ventral views. (**fig. 9.33**) *Bearriverops* sp. cf. *B. ibexe*nsis, left librigena, SUI 99919, external view. (**figs. 9.38–9.46**) *Bearriverops* new species A, from HC6 107.5 m, Garden City Formation (Stairsian, Zone E – Tesselacauda Zone), Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho. Magnifications are ×10. (**figs. 9.38–9.40**) Cranidium, SUI 99921, dorsal, right lateral, and anterior views. (**figs. 9.41, 9.42, 9.44**) Cranidium, SUI 99922, dorsal, left lateral, and anterior views. (**figs. 9.43, 9.45, 9.46**) Cranidium, SUI 99923, left lateral, dorsal, and anterior views.

sagittally than exsagittally, bowed slightly forward medially; second ring furrow deep, transverse, and slot-like laterally, interrupted medially by small, crescentic pseudo-articulating half ring; second ring about 80% width of first ring, almost completely transverse, not bowed forward medially like first ring, of similar length sagittally and exsagittally, otherwise very similar to first ring; third ring furrow very similar in construction to second, with deep lateral slots, medial pseudo-articulating half ring much smaller and shorter; third ring narrow but defined posteriorly in almost all specimens by fourth ring furrow, transverse to very slightly posterior bowed, shorter (sag., exsag.) than first and second rings; fourth ring furrow faint but medially complete in some specimens (e.g., Fig. 8.41), more typically displaying tiny lateral slots similar to but much smaller than those of second and third furrows; fourth ring extremely poorly expressed, but in some specimens (Figs. 8. 41, 8.46) clearly present as a weak transverse band, in others not clearly distinguishable; proximal area of pleura flat and bounded by abrupt change in slope to distal areas, in some specimens (Fig. 8.46) break in slope is almost ridge-like; anterior and posterior bands and pleural furrow of first segment expressed proximally in most specimens, but weakly and with little lateral extent; posterior segments with only a proximal hint expressed of bands and furrow, more typically not discernible; large, conical spine set near fulcrum of posterior pleural band of first segment; distal region smooth, strongly downturned, and featureless, except for articulating facet developed along anterior edge; fairly broad, independently inflated border developed around posterior rim, with sculpture of very fine and somewhat subdued raised lines; pygidium with fairly strong median inflection in posterior view, usually discernible as small indentation in outline of margin in dorsal view; doublure broader laterally than medially, with sculpture of fine raised lines set subparallel to margin.

REMARKS: In phenetic terms (i.e., overall similarity), *Bearriverops loganensis* has its closest comparison in *B. deltaensis*, which is described via differential description below. However, most of the similarity is apparently plesiomorphic, and *B. loganensis* shares several apomorphies with the *B. alsacharovi*–*B. borderinnensis* species pair, including an exsagittally reduced posterior fixigena (Fig. 4.1), a posterior projection that runs nearly transversely instead of distinctly posterolaterally, the retention of a very small spine at the posterolateral corner of the projection (a serial homologue of those on the thoracic pleural tips), and the complete loss of any tubercles on the librigenal field (whereas the external surface of the field of *B. deltaensis* is free of tubercles, their presence is revealed by pits on the internal surface, Fig. 9.28; no such pits are visible in *B. loganensis*, Figs. 6.9, 6.11, 7.34).

Bearriverops deltaensis n. sp.
(Figs. 9.1–9.32, 9.34–9.37, 10)

DERIVATION OF NAME: From the town of Delta, Utah, our base of operations for Ibex fieldwork.

TYPE SPECIMENS: Holotype cranidium SUI 99908 and paratype specimens SUI 99909 – SUI 99918, SUI 99920, SUI 99924 – SUI 99926, all from section MME 84.0 m, Fillmore Formation (Stairsian, Zone E – *Tesselacauda* Zone), Middle Mountain, Ibex area, Millard County, western Utah.

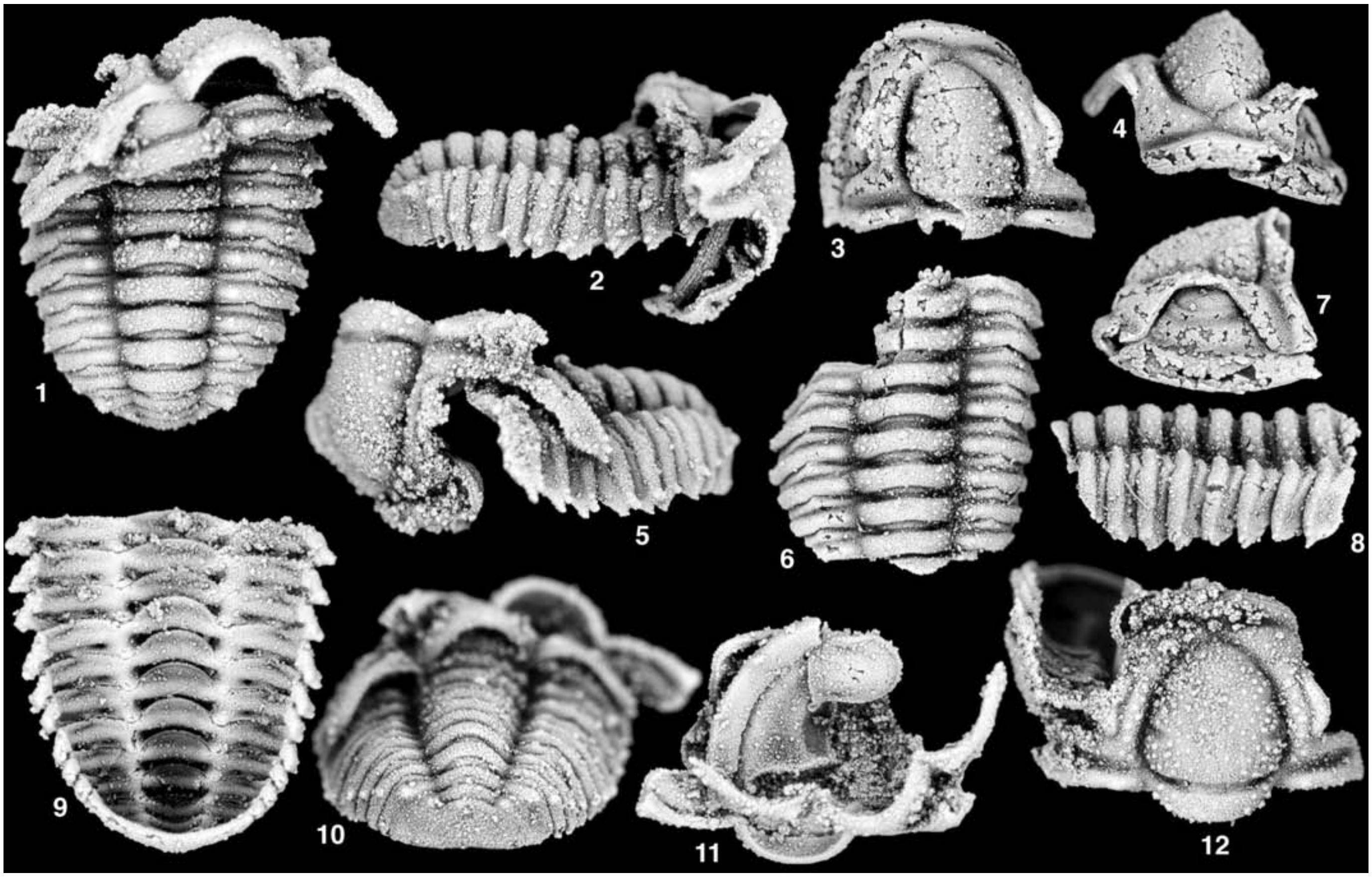
DIAGNOSIS: Genal spine retained as a sharp, subtriangular stub in large specimens; pygidial margin with very weak posteromedian flexure.

DESCRIPTION: *Bearriverops deltaensis* is similar enough to *B. loganensis* that extended written description is considered unnecessary. All points of difference are noted in discussion that follows.

REMARKS: *Bearriverops deltaensis* is clearly a distinct species, but some of the features which differentiate it from the closely similar *B. loganensis* are plesiomorphies shared with *B. ibexensis*. It has few autapomorphies, but these include the genal spine and pygidial features listed in the diagnosis. At first glance *B. deltaensis* is very similar to *B. loganensis*, which occurs 8.5 m beneath it in Section MME. However, close inspection reveals many features of shape, relative dimensions, and sculpture by which the taxa are pervasively differentiated.

Bearriverops deltaensis differs from *B. loganensis* in the possession of a much exsagittally longer posterior fixigena (Fig. 4.1); shorter and slightly narrower palpebral lobes (Fig. 4.2); more directly anteriorly convergent versus slightly laterally bowed anterior sections of the facial suture; posterior cranidial projections that run posterolaterally versus transversely; complete absence of a small spine at the postero-

Fig. 10. *Bearriverops alsacharovi* n. gen. n. sp., from the lower Fillmore Formation (Stairsian), Section MME 84.0 m, Middle Mountain, Ibex area, Millard County, western Utah. (**figs. 10.1, 10.2, 10.5, 10.9–10.12**) Dorsal exoskeleton, SUI 99924, dorsal, right lateral, oblique, ventral thoracic (specimen became separated after dorsal photography), posterior, ventral cephalic, and dorsal cranidial views, ×12. (**figs. 10.3, 10.4, 10.7**) Cranidium and librigena, SUI 99925, dorsal, anterior, and left lateral views, ×10. (**figs. 10.6, 10.8**) Thorax, SUI 99926, dorsal and right lateral views, ×10 (from same sample as and probably from same individual as SUI 99925).



lateral corner of the posterior projection; generally slightly coarser cranidial tuberculate sculpture in similarly sized specimens; a narrower librigenal field that retains traces of tuberculate sculpture; a smaller eye; a larger, subtriangular genal spine that is retained even in the largest specimens; thorax with coarser tuberculate sculpture retained on the abaxial dorsal parts of the axial rings; a longer pygidium; and a pygidial margin that has only a very slight postero-median inflection and is mostly nearly evenly arcuate. The hypostome of *B. deltaensis* (Fig. 10.11) has different morphology than the specimen known for *B. loganensis* (Fig. 6.11), as it is narrower and has a much shallower middle furrow. These contrasts are likely ontogenetic, however, as the *B. loganensis* specimen is about twice the size of the *B. deltaensis* example.

Bearriverops borderinnensis n. sp.
(Fig. 11)

Hystricurus? sp. C; Ross, 1951, p. 54, pl. 10, figs. 17, 21, 22.
Unassigned pygidium, Zone "E," locality 5 (Not described); Ross, 1951, pl. 19, figs. 12, 16.

DERIVATION OF NAME: After the Border Inn, a lonely but fine establishment on the Utah–Nevada border, where we have spent many nights during Ibex fieldwork.

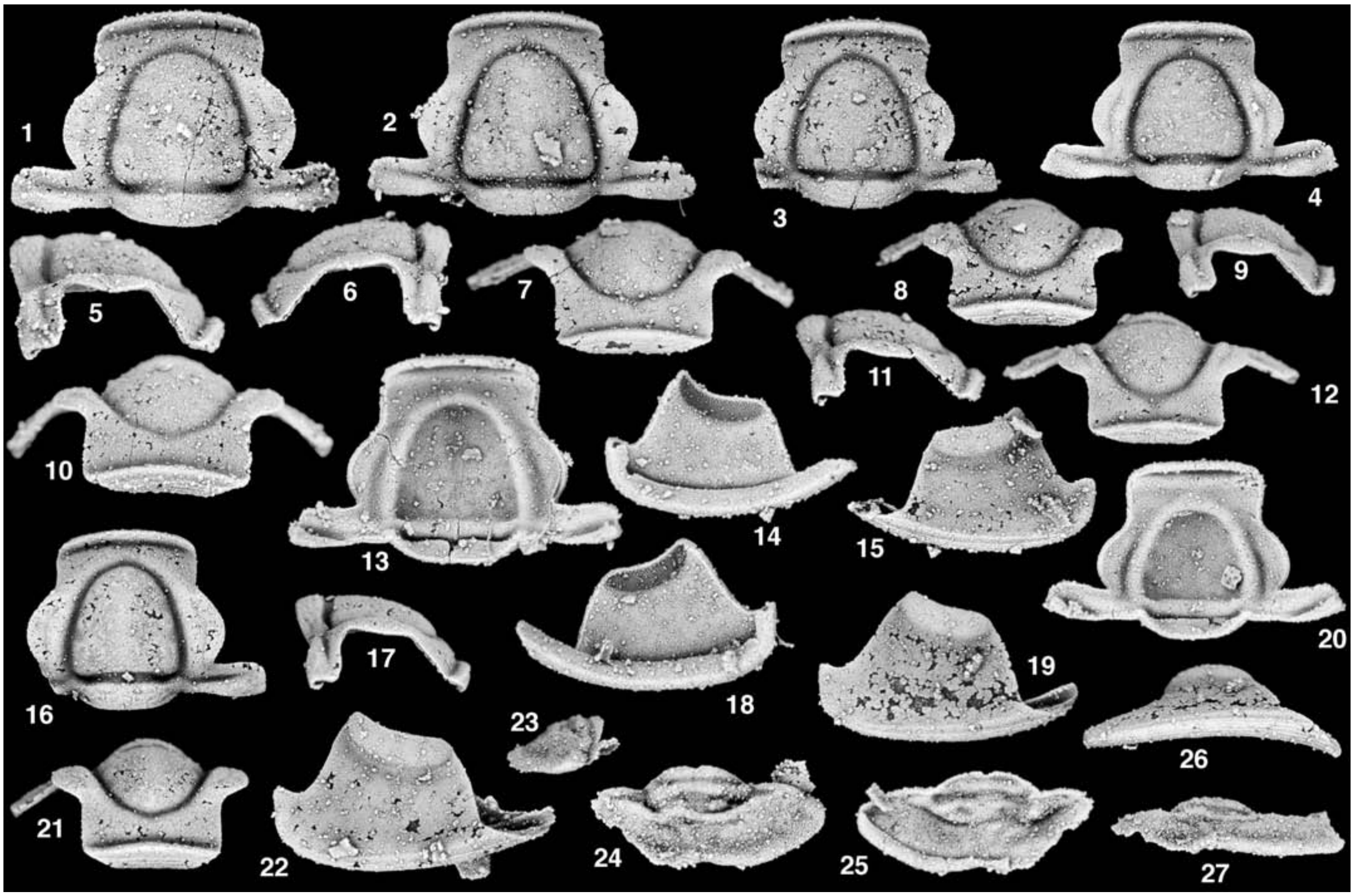
TYPE SPECIMENS: Holotype cranidium SUI 99928 and paratype specimens SUI 99927, SUI 99929 – SUI 99935, all from section MME 75.5 m, Fillmore Formation (Stairsian, Zone E–*Tesselacauda* Zone), Middle Mountain, Ibex area, Millard County, western Utah. Though not sampled in this study, the species definitely also occurs in Zone E of section HC5, Garden City Formation, Franklin Basin, Bear River Range, Franklin County, southeastern Idaho, based on a cranidium and pygidium illustrated by Ross (1951; see synonymy earlier in the text).

DIAGNOSIS: S1 and S2 visible as lateral indentation and very weak, nearly indiscernible furrow adaxially; eye long and narrow; eye socle single band but nearly effaced; librigenal lateral border almost entirely shallowed, so that adaxial part of border is confluent with field, except for faint depression; genal spine completely absent; region around pygidial axis set off from smooth pleural area by raised bounding ridge that runs around rear of axis.

DESCRIPTION:

Cranidium: Cranidial measurements are based on the specimens of Figs. 11.1, 11.2, 11.3, 11.4, and 11.16. Cranidium with sagittal length 91.9% (88.1%–94.9%) width across midlength of palpebral lobes; width across anterior border

Fig. 11. *Bearriverops borderinnensis* n. gen. n. sp., from the lower Fillmore Formation (Stairsian), Section MME 75.5 m, Middle Mountain, Ibex area, Millard County, western Utah. Magnifications are ×10. (**figs. 11.1, 11.5, 11.10**) Cranidium, SUI 99927, dorsal, right lateral, and anterior views. (**figs.** 11.2, 11.6, 11.7, 11.13) Cranidium, holotype, SUI 99928, dorsal, left lateral, anterior, and ventral views. (**figs. 11.3, 11.8, 11.11**) Cranidium, SUI 99929, dorsal, anterior, and right lateral views. (**figs. 11.4, 11.9, 11.12, 11.20**) Cranidium, SUI 99930, dorsal, right lateral, anterior, and ventral views. (**figs. 11.14, 11.15**) Left librigena, SUI 99931, internal and external views. (**figs. 11.16, 11.17, 11.21**) Cranidium, SUI 99932, dorsal, right lateral, and anterior views. (**figs. 11.18, 11.19, 11.26**) Right librigena, SUI 99933, internal, external, and ventrolateral views. (**fig. 11.22**) Right librigena, SUI 99934, external view. (**figs. 11.23–11.27**) Pygidium, SUI 99935, right lateral, dorsal, ventral, and posterior views.



69.5% (66.9%–72.1%) width across midlength of palpebral lobes; glabella with sagittal length (excluding LO and S0) 95.2% (85.3%–101.4%) maximum width; dorsal surfaces of cranidium effaced and lacking in tuberculate or granulose sculpture; glabella with L1 and L2 represented by weak independent inflations, S1 and S2 visible only as subtle indentations in lateral margin of glabella and as very faint, hardly impressed furrows adaxially; S3 not obviously expressed on any specimen, even in ventral view; S0, axial furrows, and preglabellar furrow of similar depth, except S0 deeper in lateral parts behind L1; axial furrows anteriorly convergent, running without obvious break in course into preglabellar furrows, collectively describing inverted “U” shape; S0 slightly longer sagittally than exsagittally, with flattened bottom in sagittal profile, delineated posteriorly by sharper scarped contact with LO than anteriorly, though contact with rear of glabella is nevertheless fairly abrupt; LO longest sagittally and of similar length behind median part of glabella, shorter behind L1, with faint posterior furrow impressed laterally just in front of posterior margin; axial furrow much shallower opposite LO than opposite glabella; preglabellar field quite long and not crossed by median depressed area; anterior border furrow with nearly transverse course, only slight anterior arc, and very faint median posterior deflection, short and well incised, of similar length sagittally and exsagittally; anterior border short, sagittal length 8.5% (7.2%–10.0%) sagittal length of cranidium, nearly flat dorsally and lacking sculpture, forming sharp anterior transverse keel along anterior margin at contact with doublure; doublure set obliquely, facing nearly anteriorly and visible in anterior view, with sculpture of fine subparallel raised lines; frontal area smooth and confluent with preglabellar field and interocular fixigena; anterior sections of facial sutures weakly anteriorly divergent in front of palpebral lobes, reaching maximum divergence about two thirds distance anteriorly, and anteriorly convergent opposite anterior border; interocular fixigena narrow, featureless, tilted slightly toward glabella in transverse profile; palpebral lobes long and relatively narrow, lacking sculpture and horizontal, slightly wider at midlength than posteriorly and anteriorly; palpebral furrow with expression variable from moderately impressed (Fig. 11.4) to almost completely effaced (Figs. 11.1, 11.3), with lateral arc slightly less strong than that of lateral margin of palpebral lobe, bowed posteriorly to run laterally around rear of lobe; posterior fixigena forming laterally extended, smooth strip along anterior part of short but wide posterior projection; posterior border furrow shallow proximally, deep and well incised for most of its course, terminated shy of contact with facial suture, running slightly anterolaterally; posterior border short proximally, much longer and lengthened laterally distal to fulcrum, with very small thorn-like spine posterolaterally; doublure forming unsculptured articulating surface beneath LO, very short articulatory groove beneath narrow proximal part of posterior border, and wide subtriangular section beneath distal part of posterior border.

Librigena: Librigenal measurements are based on the specimens of Figs. 11.15, 11.19, and 11.22. Librigenal field with width at midlength of eye 38.3% (36.0%–41.2%) exsagittal length; eye long and narrow, socle apparently of single continuous band, but expression ranging from very weak (e.g., Fig. 11.22) to nearly indiscernible (e.g., Fig. 11.19); field slightly convex across surface, lacking sculpture; lateral border furrow very shallow and broad, difficult to discern in some specimens; lateral border with width opposite midlength of eye 40.7% (39.4%–42.5%) width of field in same position, adaxial part nearly confluent with field across weak to almost absent lateral border furrow, abaxial part with two prominent raised lines parallel with lateral margin; lateral margin with gentle lateral curvature, ventrolateral aspect with finer and more closely crowded raised lines, ventrolateral margin of border sharp and blade-like in section; genal spine completely absent, genal angle curved evenly but sharply up from lateral margin, forming nearly illaeniform posterior margin; doublure separated from lined ventrolateral part of lateral border by sharp, angular change in slope, with very fine raised lines much more subdued than those on border, prominent Panderian notch beneath genal angle.

Rostral plate, hypostome, and thorax: Rostral plate, hypostome, and thorax not identified.

Pygidium: Pygidial measurements are based on the specimen from the Garden City Formation illustrated by Ross (1951, pl. 19, figs. 12, 16). Pygidium with sagittal length excluding articulating half ring 31% width; axis with maximum anterior width 46% pygidial width; articulating half ring broad but short, longest sagittally, separated from first axial ring by ring furrow that is incised over most of its course but shallowed at abaxial extremes; first axial ring very short, shorter sagittally than exsagittally, lacking sculpture; second ring very weakly developed as two lateral swellings, axis depressed medially; axial furrow distinct opposite first ring; anterior pleural band and pleural furrow of first segment expressed on small pleural region, all remaining area curtailed by raised dorsally inflated, narrow ridge, against which first pleural furrow abuts and terminates and which surrounds abbreviated pleural region and axis; pygidial surface abaxial to ridge smooth and declined; posterior margin with fairly strong posteromedian inflection, distinct but weakly inflated border present around pygidial rim; doublure of similar length over most of course, shorter in sagittal region around posteromedian indentation of margin, lacking sculpture.

REMARKS: *Bearriverops borderinnensis* is a very distinctive species characterized by a high degree of effacement, including nearly illaenimorph librigenae. It share a suite of apomorphies with its sister species, *B. alsacharovi*, including a very shallow palpebral furrow, loss of granulate and tuberculate sculpture on the glabella, the possession of a medially complete preglabellar field, extreme reduction of the eye socle, reduction of the terrace line sculpture on the librigenal lateral border to two prominent lines, reduction to a single well-expressed pygidial axial ring, and modification of the pygidial pleural tubercle to a transverse ridge-like structure. It differs from *B. alsacharovi* in the suites of features listed as autapomorphies in the diagnoses of either species (some of which are variations of their synapomorphies).

In the present study, *Bearriverops borderinnensis* was sampled only at horizon MME 75.5 m in western Utah. However, Ross recorded both a cranidium (1951, pl. 10, figs. 17, 21, 22) and a pygidium (1951, pl. 19, figs. 12, 16) from section HC5 in southeastern Idaho that clearly belong to the species.

Bearriverops alsacharovi n. sp.
(Figs. 12, 13)

Hystricurus sp. C Ross; Hintze, 1953, p. 166, pl. 6, fig. 15 (non pl. 6, fig. 16).

Hystricurus sp. A of Ross, 1951; Terrell, 1973, p. 76, pl. 1, figs. 9, 10, 13.

DERIVATION OF NAME: For Allen Sacharov, consultant, Salt Lake City, Utah.

TYPE AND FIGURED SPECIMENS: Holotype cranidium SUI 99936, from section G 27.0 m, Fillmore Formation (Stairsian, unzoned interval between “Zone E” and “Zone F”), Ibex area, Millard County, western Utah (paratype specimens from G 26.6–27.0 m: SUI 99937 – SUI 99958). Also occurs at section HC6 124.0 m, Garden City Formation (Stairsian, unzoned interval between “Zone E” and “Zone F”), Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho (figured specimens: SUI 99959 – SUI 99969).

DIAGNOSIS: Anterior border long and dorsally flat; palpebral lobes large, palpebral furrow largely or completely effaced; eye ridge discernible dorsally; librigenal field with punctate sculpture; long, thin genal spine present.

DESCRIPTION:

Cranidium: Cranidial measurements are based on the specimens of Figs. 12.1–12.5, 12.16, 12.19, 12.22, 12.41, 13.1, 13.2, 13.4, and 13.15. Cranidium with sagittal length 103.1% (94.0%–113.3%) width across midlength of palpebral lobes; width across anterior border 76.2% (72.3%–83.4%) width across midlength of palpebral lobes; glabella with sagittal length (excluding LO and S0) 96.8% (91.1%–100.6%) maximum width; external surfaces of cranidium entirely lacking granulose or tuberculate sculpture; glabella relatively broad, S1 and S2 variable in expression, ranging from almost indiscernible (Fig. 12.5) to distinct, traceable course but extremely shallow (Figs. 12.49, 13.4), typically visible mainly as lateral impressions on the glabellar outline with faint furrows running adaxially and expressed for only a short distance onto glabella; S1 with contact with axial furrow opposite about 75% distance posteriorly of palpebral lobe; S2 with contact with axial furrow opposite about 25% distance posteriorly of palpebral lobe; S3 not obviously expressed; L1 with very weak independent inflation, so that axial furrow typically bows slightly laterally; L2 generally not independently inflated; overall glabellar sculpture typically smooth, in some specimens very fine and subdued punctate sculpture visible (Figs. 12.19, 12.49, 13.2); S0 sagittally long, of similar length across median third of course, shorter behind L1, flat-bottomed and with abrupt anterior and posterior edges; LO longest sagittally, progressively shorter abaxially, with faint median node set two thirds to three quarters distance anteriorly, sculpture commonly lacking, in some specimens weakly expressed punctate pitting, subdued and faint posterior furrow just in front of posterior margin; axial furrows deep, anteriorly divergent opposite rear of L1, convergent from opposite rear edge of palpebral lobe forward, turning with slight but usually distinct break in course into preglabellar furrow of similar width and depth; preglabellar furrow describing broad and shallow anteriorly directed “U” shape, with subtle median anterior point; preglabellar field relatively long and complete, not traversed by median furrow or depression; anterior sections of facial suture strongly anteriorly divergent in front of palpebral lobe, maximum point of divergence at rear of anterior border furrow, strongly anteriorly convergent opposite anterior border; anterior border furrow very long (sag; exsag.), with steep posterior scarp to preglabellar field and frontal area, but very shallow, gradational contact with rear of border anteriorly, rear part with subtle (Fig. 12.2) to strong (Fig. 12.19) median posterior indentation; anterior border with sagittal length 13.2% (8.6%–16.4%) sagittal length of cranidium, dorsally flat and unsculptured, anterior margin describing even, gentle anterior arc; frontal area and preglabellar field with finely pitted caecal–punctate sculpture; eye ridge present as faint dorsal ridge set obliquely and connecting the anterior edge of the palpebral lobe with a point just in front of the junction of the axial and preglabellar furrow, bicomposite nature of ridge evident ventrally (Fig. 13.3); interocular fixigena weakly inflated and featureless; palpebral lobe long and broad, held in horizontal plane; palpebral furrow at most an extremely faint impression, in most specimens completely effaced so that surface of palpebral lobe grades without interruption into interocular fixigena; interocular fixigena running without interruption into similarly featureless posterior fixigena; posterior projection nearly transverse, relatively narrow (tr.); posterior section of facial suture running posteriorly immediately distal to palpebral lobe, transversely to slightly anteriorly in middle part of course, swept strongly posteriorly around lateral termination of posterior projection; posterior border furrow long (exsag.), flat-bottomed, with sharp anterior and posterior edges, transverse proximal to fulcrum, turned anteriorly and narrower distal to fulcrum; posterior border long and flat-topped proximally, longer and expanded into broad lobe distally, with faint posterior furrow distally and small thorn-like spine at posterolateral point, lacking dorsal sculpture; doublure forming long articulatory surface beneath LO, with sculpture of very subdued, closely spaced, transverse raised lines (Figs. 12.18, 13.3); doublure beneath proximal part of posterior border forming very short, shallow, transverse articulatory groove for leading edge of first thoracic segment; doublure under distalmost part of posterior border slightly longer; doublure beneath anterior border mostly turned forward and external surface not visible in ventral view.

Librigena: Librigenal measurements are based on the specimens of Figs. 12.26, 12.29, 12.30, 12.32, 12.33, 12.39, 13.17, 13.20, 13.24, and 13.27. Librigenal field with width at midlength of eye 30.2% (27.0%–36.0%) exsagittal length; eye very narrow and long; eye socle of single subdued band variable in expression from weak (Figs. 12.32, 13.17, 13.24, 13.27) to fairly strong and complete (Fig. 12.30), separated from visual surface by very narrow furrow and from field by broader depression; field in most specimens with prominent punctate sculpture, not obviously caecal in nature, tubercles completely absent, even ventrally, field broader posteriorly; lateral border furrow narrow and deeply impressed anteriorly, completely shallowed posteriorly in front of genal angle; lateral border with width opposite midlength of eye 71.0% (58.9%–92.7%) width of field in same position, adaxial portion lacking sculpture or with fine punctate sculpture, abaxial portion with two or three very strong raised lines set subparallel with lateral margin, additional finer lines more closely spaced on ventrolateral aspect; anterior projection relatively long; posterior border not developed on librigena; long, narrow genal spine, up to about 60% length of remainder of field minus anterior projection, spine progressively shorter in larger specimens, with faint groove running down dorsal aspect, and fine raised lines from ventrolateral part of border running down ventrolateral aspect; doublure forming sharp, angular contact with border, lacking sculpture, very small and weak Panderian notch developed in front of base of genal spine.

Rostral plate, hypostome, and thorax: Rostral plate, hypostome, and thorax not identified.

Pygidium: Pygidial measurements are based on the specimens of Figs. 12.36, 12.37, and 12.46. Pygidium with sagittal length (excluding articulating half ring) 36.5% (32.1%–40.2%) maximum width; axis with maximum with at anterior 37.4% (34.4%–40.4%) that of pygidium; articulating half ring long (sag.) and large; first ring furrow transverse in strict dorsal view (Fig. 12.36), well incised, of similar length and depth sagittally and exsagittally; first axial ring well expressed, slightly shorter sagittally than exsagittally, lacking dorsal sculpture, with low dorsal inflation in posterior or sagittal view; axial furrow very weak, expressed only opposite first ring; second ring furrow impressed as pair of lateral slots, weak medially around crescentic pseudo-articulating half ring; second ring not clearly expressed, visible ventrally (Fig. 12.42) but scarcely differentiated dorsally from smooth post-axial region; anterior and posterior pleural bands and pleural furrow of only first segment expressed, and only on very narrow proximal region; faint, obliquely set, and tab-shaped raised spine on posterior pleural band of first segment; second spine expressed ventrally (Fig. 12.42), presumably in position of second posterior pleural band, as pair of faint depressions, but not obvious dorsally; axis and narrow proximal pleural


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Fig. 12. *Bearriverops alsacharovi* n. gen. n. sp., from the lower Fillmore Formation (Stairsian). **figs. 12.1–12.48** from Section G, southern Confusion Range, Ibex area, Millard County, western Utah, ×10, except where noted. (**figs. 12.1, 12.6, 12.13, 12.18**) Cranidium, holotype, SUI 99936, dorsal, right lateral, anterior, and ventral views (G 27.0 m). (**figs. 12.2, 12.7, 12.14**) Cranidium, SUI 99937, dorsal, right lateral, and anterior views (G 27.0 m). (**figs. 12.3, 12.8, 12.9, 12.15**) Cranidium, SUI 99938, dorsal, right lateral, anterior, and ventral views, ×7.5 (G 26.6 m). (**figs. 12.4, 12.10, 12.11**) Cranidium, SUI 99939, dorsal, right lateral, and anterior views (G 27.0 m). (**figs. 12.5, 12.12, 12.17**) Cranidium, SUI 99940, dorsal, left lateral, and anterior views (G 27.0 m). (**figs. 12.16, 12.20, 12.21**) Cranidium, SUI 99941, dorsal, right lateral, and anterior views (G 27.0 m). (**figs. 12.19, 12.24, 12.25**) Cranidium, SUI 99942, dorsal, right lateral, and anterior views (G 27.0 m). (**figs. 12.22, 12.27, 12.35**) Cranidium, SUI 99943, dorsal, right lateral, and anterior views (G 27.0 m). (**figs. 12.23**) Left librigena, SUI 99944, external view, ×12 (G 27.0 m). (**fig. 12.26**) Left librigena, SUI 99945, external view (G 26.6 m). (**figs. 12.28, 12.29**) Left librigena, SUI 99946, internal and external views (G 27.0 m). (**fig. 12.30**) Left librigena, SUI 99947, external view (G 27.0 m). (**figs. 12.31, 12.33, 12.34**) Right librigena, SUI 99948, ventrolateral, external, and internal views (G 26.6 m). (**fig. 12.32**) Right librigena, SUI 99949, external view (G 26.6 m). (**figs. 12.36, 12.42–12.44**) Pygidium, SUI 99950, dorsal, ventral, posterior, and left lateral views, ×12 (G 27.0 m). (**figs. 12.37, 12.38, 12.45**) Pygidium, SUI 99951, dorsal, posterior, and left lateral views, ×12 (G 27.0 m). (**fig. 12.39**) Right librigena, SUI 99952, external view (G 27.0 m). (**figs. 12.40, 12.46, 12.47**) Pygidium, SUI 99953, left lateral, dorsal, and posterior views, ×12 (G 27.0 m). (**figs. 12.41, 12.48**) Cranidium, SUI 99954, dorsal and right lateral views (G 27.0 m). **figs. 12.49–12.55** from Section MME 102.2, Middle Mountain, Ibex area, Millard County, western Utah, ×10, except where noted. (**figs. 12.49–12.51**) Cranidium, SUI 99955, dorsal, right lateral, and anterior views. (**fig. 12.52**) Left librigena, SUI 99956, external view, ×12. (**figs. 12.53, 12.54**) Cranidium, SUI 99957, right lateral and dorsal views. (**fig. 12.55**) Cranidium, SUI 99958, dorsal view.

region surrounding by low, nearly ridge-like, sharp break in slope; steeply declined distal pleural region lacking sculpture and featureless, except for flattened articulating facet on anterior edge; pygidial border not independently inflated, weakly differentiated from pleural region; pygidium with moderate median flexure in posterior view, scarcely visible in strict dorsal view, in which posterior margin describes nearly even posterior arc; doublure relatively narrow, shortest sagittally and broadly abaxially.

REMARKS: Hintze (1953, pl. 6, fig. 15) was the first to illustrate a cranidium of this species, but misassociated it with a librigenae belonging to a new genus and species of hystricurid (Adrain and Westrop, unpublished data). Terrell (1973, pl. 76, pl. 1, figs. 9, 10, 13) illustrated two cranidia and a librigena of the species, but did not associate them with Hintze's cranidium. Instead, he misassigned his material to "*Hystricurus* sp. A" of Ross (1951, p. 53, pl. 9, figs. 31, 34, 37). Ross' taxon is a representative of *Hystricurus* s.s. (see Adrain et al. 2003) and does not resemble *Bearriverops*.

Bearriverops alsacharovi was compared with its sister species, *B. borderinnensis* (see earlier in the text). It has considerable biostratigraphic significance, as it occurs in both of the western Utah sections studied, as well as at section HC6 124.0 m in southeastern Idaho. Although there are apparent differences between the Idaho sample (Fig. 13) and material from western Utah (Fig. 12), for example in the average length of the genal spine, these are all size-related, as the Idaho specimens are in general slightly smaller, and no differences are apparent in comparison of similarly sized sclerites (e.g., compare Fig. 12.23 with Fig. 13.27).

Bearriverops ibexensis n. sp.
(Fig. 14)

DERIVATION OF NAME: After the Ibex area, Utah.

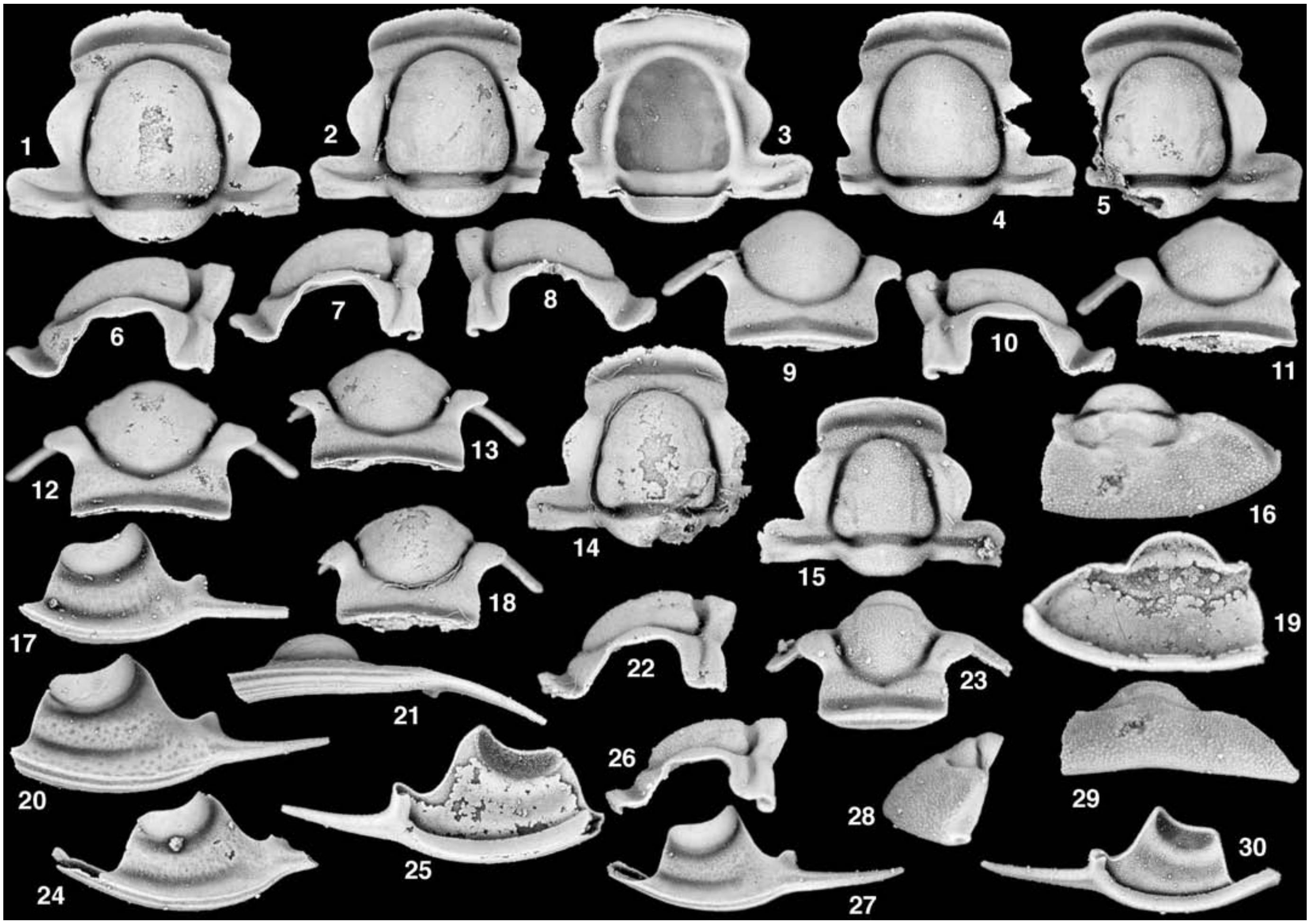
TYPE SPECIMENS: Holotype cranidium SUI 99970 from section G 26.6 m and paratype specimens SUI 99971 – SUI 99981 from G 26.6–27.0 m, Fillmore Formation (Stairsian, unzoned interval between "Zone E" and "Zone F"), Ibex area, Millard County, western Utah.

DIAGNOSIS: Dense tuberculate sculpture on glabella, frontal area, interocular fixigena, librigenal field, thoracic axial rings, and posterior pleural bands; anterior border forming very prominent, prow-like upturned rim, with doublure beneath it almost facing forward; pygidium with two well-expressed axial rings and very weakly expressed third.

DESCRIPTION:

Carnidium: Cranidial measurements are based on the specimens of Figs. 14.1, 14.2, 14.4, and 14.5. Cranidium with sagittal length 90.0% (86.7%–94.4%) width across midlength of palpebral lobes, width across anterior border 77.5% (72.5%–81.9%) width across midlength of palpebral lobes; glabella subelliptical in plan view sagittal length 95.7% (93.0%–98.7%) maximum width, axial furrows laterally curved, arched forward to run without obvious distinction into preglabellar furrow; front of glabellar slightly pointed; glabellar sculpture of densely crowded moderate-sized tubercles; S1 notch-like distally, bent sharply posteromedially and much shallower proximally; S2 also notch-like distally, with very short shallow transverse extent proximally; S3 discernible on some specimens as faint transverse furrow with little extent, obscure on others; LO slightly longer sagittally than exsagittally, with sculpture of crowded tubercles slightly smaller than those on main part of glabella, prominent but subdued median node set slightly anterior to sagittal midlength; S0 deeply impressed, with flat unsculptured bottom, and set off from both glabella and LO by very sharp vertical scarps, longer sagittally than exsagittally; glabella fairly weakly inflated in sagittal profile, deviating only slightly dorsally from arc described by preglabellar field; preglabellar field very short, preglabellar and anterior border furrows close but not in contact; preglabellar field, frontal area, and interocular fixigena with tuberculate sculpture slightly more prominent and dense than that on glabella; anterior border furrow deep and sharply incised, defined posteriorly by sharp scarp, shallower anteriorly and grading into border along course; posterior margin of anterior border faintly posteromedially

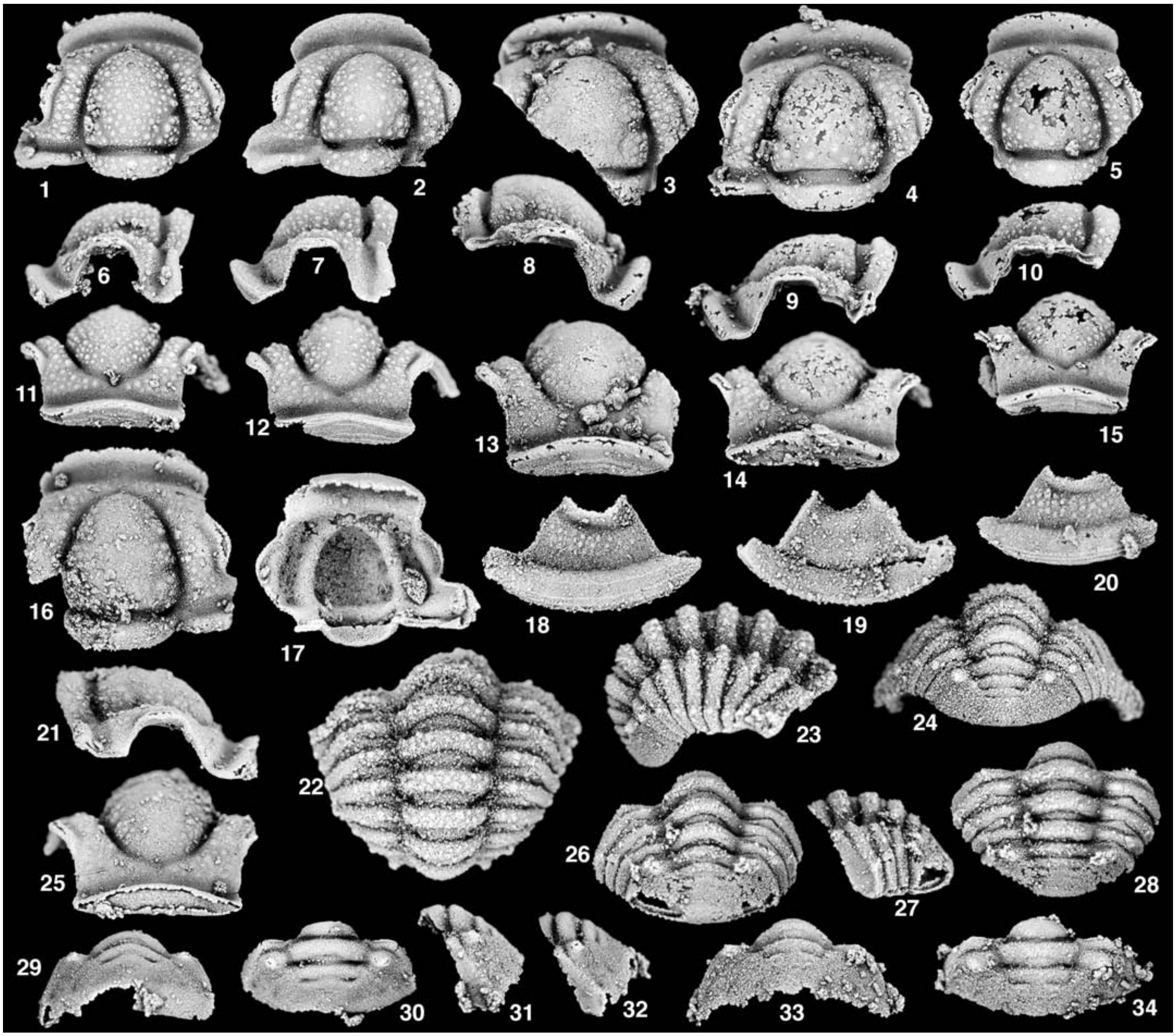
Fig. 13. *Bearriverops alsacharovi* n. gen. n. sp., from Section HC6 124.0 m, Garden City Formation (Stairsian), Bear River Range, Franklin County, southeastern Idaho. Magnifications are ×10, except where noted. (**figs. 13.1, 13.6, 13.12**) Cranidium, SUI 99959, dorsal, left lateral, and anterior views. (**figs. 13.2, 13.3, 13.7, 13.13**) Cranidium, SUI 99960, dorsal, ventral, left lateral, and anterior views. (**figs. 13.4, 13.8, 13.9**) Cranidium, SUI 99961, dorsal, right lateral, and anterior views. (**figs. 13.5, 13.10, 13.11**) Cranidium, SUI 99962, dorsal, right lateral, and anterior views, ×12. (**figs. 13.14, 13.18, 13.22**) Cranidium, SUI 99963, dorsal, anterior, and left lateral views, ×12. (**figs. 13.15, 13.23, 13.26**) Cranidium, SUI 99964, dorsal, anterior, and left lateral views, ×15. (**figs. 13.16, 13.19, 13.28, 13.29**) Pygidium, SUI 99965, dorsal, ventral, right lateral, and posterior views, ×15. (**fig. 13.17**) Left librigena, SUI 99966, external view, ×12. (**figs. 13.20, 13.21, 13.25**) Left librigena, SUI 99967, external, ventrolateral, and internal views. (**fig. 24**) Left librigena, SUI 99968, external view. (**figs. 13.27, 13.30**) Left librigena, SUI 99969, external and internal views, ×12.



indented in some specimens; anterior border long, sagittal length 18.4% (16.8%–19.2%) cranidial sagittal length, upturned along width, with only slight dorsal inflation, forming sharp anterior rim above thick doublure that faces anteroventrally and is visible in direct anterior view; doublure with two or three strong terrace lines subparallel with anterior margin; palpebral lobe long (exsag.) and narrow (tr.), held nearly horizontally, set off from interocular fixigena by deep, incised, laterally bowed palpebral furrow, lacking dorsal sculpture; interocular fixigena relatively broad, with independent but weak dorsal inflation; posterior fixigena with narrow posterior projection, fixigena forming thin subtriangular strip in front of posterior border furrow, on which tuberculate sculpture of interocular fixigena transitions to smooth distal region; posterior border furrow long (exsag.), longer distal to fulcrum than proximally, less deep than S0; posterior border short and enrolled proximally longer and flatter distally, with faint scattered tubercles proximal to fulcrum; posterior projection with broad, lobate lateral terminus; doublure forming articulating surface beneath LO, lacking sculpture; beneath posterior border doublure forms extremely short (exsag.) transverse groove to articulate with leading edge of first thoracic segment, curved forward distally; doublure beneath anterior border facing nearly forward, with prominent raised lines.

Librigena: Librigenal measurements are based on specimens of Figs. 14.18 and 14.20. Field with width at midlength of eye 30.7% (28.9%–32.5%) maximum exsagittal length, with sculpture of small, fairly densely crowded tubercles; visual area and eye socle not well preserved on available specimens, but socle apparently of continuous, narrow, inflated band, set off from field by narrow and sharply incised furrow; lateral border furrow sharply incised, forming steep scarp against lateral border, contact with field more gradational; lateral

Fig. 14. *Bearriverops ibexensis* n. gen. n. sp., from the lower Fillmore Formation (Stairsian), Section G, southern Confusion Range, Ibex area, Millard County, western Utah. (**figs. 14.1, 14.6, 14.11**) Cranidium, **holotype**, SUI 99970, dorsal, left lateral, and anterior views, ×7.5 (G 26.6 m). (**figs. 14.2, 14.7, 14.12, 14.17**) Cranidium, SUI 99971, dorsal, left lateral, anterior, and ventral views, ×10 (G 27.0 m). (**figs. 14.3, 14.8, 14.13**) Cranidium, SUI 99972, dorsal, right lateral, and anterior views, ×7.5 (G 27.0 m). (**figs. 14.4, 14.9, 14.14**) Cranidium, SUI 99973, dorsal, left lateral, and anterior views, ×7.5 (G 27.0 m). (**figs. 14.5, 14.10, 14.15**) Cranidium, SUI 99974, dorsal, left lateral, and anterior views, ×7.5 (G 27.0 m). (**figs. 14.16, 14.21, 14.25**) Cranidium, SUI 99975, dorsal, right lateral, and anterior views, ×7.5 (G 27.0 m). (**figs. 14.18, 14.19**) Right librigena, SUI 99976, external and internal views, ×10 (G 27.0 m). (**fig. 14.20**) Left librigena, SUI 99977, external view, ×10 (G 27.0 m). (**figs. 14.22–14.24**) Partial thorax and pygidium, SUI 99978, dorsal thoracic, right lateral, and dorsal pygidial views, ×10 (G 26.6 m). (**figs. 14.26–14.28**) Partial thorax and pygidium, SUI 99979, dorsal pygidial, left lateral, and dorsal thoracic views, ×12 (G 26.6 m). (**figs. 14.29–14.31**) Pygidium, SUI 99980, posterior, dorsal, and left lateral views, ×10 (G 26.6 m). (**figs. 14.32–14.34**) Pygidium, SUI 99981, left lateral, posterior, and dorsal views, ×10 (G 27.0 m).



border with width 96.2% (94.1%–98.2%) that of field at midlength of eye, slightly narrower anterior and posteriorly than over most of length, entire border laterally bowed, with lateral margin evenly arcuate, background sculpture of very sparse granules surmounted by prominent raised lines running subparallel to lateral margin, more closely spaced near margin; posterior border cut by suture immediately above genal angle, so lateral and posterior borders form subtrapezoidal posterior extension; genal spine marked by small nubbin; doublure lacking sculpture, with distinct Panderian notch in front of genal angle.

Rostral plate and hypostome: Rostral plate and hypostome not identified.

Thorax: Thorax known from posterior eight segments; pleural lobes about 77% width of axial lobe; fulcrum set about half distance distally on pleural lobe; axial ring of similar length sagittally and exsagittally, with sculpture of densely crowded moderate-sized tubercles; articulating half ring large and prominent, set off from axial ring by transverse, strongly incised ring furrow; axial furrow deep, cutting completely across adaxial termination of pleural bands and pleural furrow; pleural lobe with anterior and posterior bands expressed across entire width; anterior band slightly shorter (exsag.) than posterior band, less inflated and set lower than posterior band in lateral view, with granular dorsal sculpture; posterior band with irregular transverse row of tubercles similar in size to those on axial ring; pleural furrow deep, sharply incised and transverse, running slightly posteriorly distal to fulcrum, where anterior band is flattened and expanded into articulating facet and posterior band is somewhat constricted to compensate; pleural furrow becoming fainter and less well incised toward pleural tip; pleural tip rounded, with very small postero-ventrally directed spine on rear half; posterior segments with single prominent tubercle on posterior band, set near fulcrum on last segment, and in an increasingly distal position forward through the thorax, forming longitudinal row in lateral view of articulated thorax; some posterior segments with a prominent swollen tubercle set adaxial to this row, on proximal part of posterior pleural band.

Pygidium: Pygidial measurements are based on specimens of Figs. 14.24, 14.26, and 14.30. Pygidial sagittal length (excluding articulating half ring) 46.1% (42.5%–50.6%) maximum width; axis with maximum anterior width 41.3% (39.7%–42.9%) maximum pygidial width; axis with low inflation from surrounding pleural area in posterior view, with little change in slope from posterior region in sagittal profile; articulating half ring large, subcrescentic, lacking sculpture; ring furrow behind articulating half ring transverse in dorsal view, deeply incised and very short (sag.; exsag.); first axial ring slightly shorter sagittally than exsagittally, slightly bowed anteriorly, with sculpture of fine granules; second axial ring about 80% width of first, relatively shorter (sag.; exsag.) but otherwise of similar shape; second ring furrow deep and prominent, deeper abaxially, shallower adaxially behind very small, pseudo-articulating half ring; third ring furrow much less prominent than second, incised only as abaxial pair of slits, very weak furrow medially; third ring developed only as very faint, transverse abaxial swellings; axial furrow distinct opposite first ring but not impressed posteriorly, second axial ring grades into pleural region with only subtle break in slope; first segment with anterior and posterior pleural bands of approximately equal length (exsag.), very short articulating flange running along anterior edge of anterior band, separated by very fine transverse furrow, posterior band crowded out just distal to fulcrum by expansion of anterior band into teardrop-shaped articulating facet, large peg-like spine with round base set on posterior pleural band at fulcrum; interpleural furrow behind first segment very faint; extremely faint second pleural furrow discernible only proximally; remainder of posterior pleural region merged into smooth surface with very fine granulose sculpture, sloped steeply from axial region; large border rimming pleural region ventrally, set off by very shallow border furrow; posterior margin arcuate, in some specimens with very slight median indentation.

REMARKS: *Bearriverops ibexensis* is interpreted as the most plesiomorphic member of the genus, and its coarsely tuberculate dorsal cephalic and thoracic sculpture is a much closer match for other, mainly undescribed, Skullrockian–Stairsian dimeropygids than that of any other species. It occurs at horizons G 26.6 m and G 27.0 m together with *B. alsacharovi*, but the species have very different morphology, and *B. alsacharovi* is much more abundant, so there is no possibility of confusion of sclerite assignments.

Bearriverops sp. cf. ***B. ibexensis***
(Fig. 9.33)

MATERIAL: Left librigena, ROM 99919, from section MME 84.0 m, Fillmore Formation (Stairsian, Zone E – *Tesselacauda* Zone), Middle Mountain, Ibex area, Millard County, western Utah.

REMARKS: A single cheek from MME 84.0 m differs from those belonging to the commonly occurring *B. alsacharovi* in its narrower, smaller eye and much narrower librigenal field, which bears scattered but subdued tubercles. It certainly belongs to an undescribed species of *Bearriverops*, but no other sclerites that might be associated with it have been recovered. Among the five well known species, a prominently tuberculate librigenal field is seen only in the younger *B. ibexensis*. However, the librigena from MME 84.0 m has a narrower field and apparently a more prominently developed eye socle than those of *B. ibexensis*.

Bearriverops n. sp. A
(Figs. 9.38–9.46)

MATERIAL: Assigned specimens SUI 99921 – SUI 99923, from HC6 107.5 m, Garden City Formation (Stairsian, Zone E – *Tesselacauda* Zone), Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho.

REMARKS: A species occurring at section HC 6 some 18 m above *Bearriverops loganensis* is definitely new, but not enough material is available to adequately describe it and the taxon is reported in open nomenclature. Of the three illustrated cranidia, only one (Fig. 9.41) preserves the dorsal surface; the other two have the finely silicified surface detail mostly exfoliated, and what can be seen is relatively coarse silica filling the thickness of the sclerite between delicate, finely silicified, and difficult to preserve internal and external surfaces. The most distinctive feature of the species is the large, coarse tuberculate sculpture on the interocular fixigena, glabella, and LO. The only other species with coarse tuberculate structure is *B. ibexensis*, but in that taxon, the tubercles are generally smaller, more numerous, and more closely spaced. In general cranidial dimensions, *Bearriverops* n. sp. A is most similar to *B. loganensis*, but it differs from that species in its considerably smaller palpebral lobes, longer and more complete preglabellar field, and narrower glabella. *Bearriverops* n. sp. A appears to have a narrower glabella than any of the other species.

Acknowledgements

Support from National Science Foundation (NSF) grants EAR 9973065 and EAR 0308685 is gratefully acknowledged. We thank T.S. Adrain for curatorial support and assistance with specimen numbers. D. Schultz, B. Beck, and T. Hegna assisted in the field. E. Landing provided lithologic logs for stratigraphic sections in the Bear River Range. Comments by N.C. Hughes, D.-C. Lee, an anonymous reviewer, and Associate Editor B.D.E. Chatterton improved the paper.

References

Adrain, J.M., and Chatterton, B.D.E. 1993. A new rorringtoniid trilobite from the Ludlow of Arctic Canada. Canadian Journal of Earth Sciences, **30**: 1634–1643.

Adrain, J.M., and Fortey, R.A. 1997. Ordovician trilobites from the Tourmakeady Limestone, western Ireland. Bulletin of the Natural History Museum, London, Geology Series, **53**: 79–115.

Adrain, J.M., and Westrop, S.R. 2001. Stratigraphy, phylogeny, and species sampling in time and space. *In* Fossils, phylogeny, and form: an analytical approach. *Edited by* J.M. Adrain, G.D. Edgecombe, and B.S. Lieberman. Kluwer, New York, N.Y., pp. 291–322.

Adrain, J.M., and Westrop, S.R. 2006. New earliest Ordovician trilobite genus *Millardicurus*: The oldest known hystricurid. Journal of Paleontology, **80**: 650–671.

Adrain, J.M., and Westrop, S.R. 2006. New genus of dimeropygid trilobites from the earliest Ordovician of Laurentia. Acta Palaeontologica Polonica, **51**: 541–550.

Adrain, J.M., Westrop, S.R., Landing, E., and Fortey, R.A. 2001. Systematics of the Ordovician trilobites *Ischyrotoma* and *Dimeropygiella*, with species from the type Ibexian area, western U.S.A. Journal of Paleontology, **75**: 947–971.

Adrain, J.M., Lee, D.-C., Westrop, S.R., Chatterton, B.D.E., and Landing, E. 2003. Classification of the trilobite subfamilies Hystricurinae and Hintzecurinae subfam. nov., with new genera from the Lower Ordovician (Ibexian) of Idaho and Utah. Memoirs of the Queensland Museum, **48**: 553–586.

Angelin, N.P. 1854. Palaeontologica Scandinavica. Pars II. Crustacea formationis transitionis. Academiae Regiae Scientarum Suecanae (Holmiae), pp. 25–92.

Barrande, J. 1852. Systême silurien du centre de la Bohême. Ière Partie. Recherches paléontologiques. Prague and Paris.

Barrande, J. 1872. Systême silurien du centre de la Bohême, Ière Partie; Recherches paléontologiques, I. Supplément. Prague and Paris.

Chatterton, B.D.E. 1994. Ordovician proetide trilobite *Dimeropyge*, with a new species from northwestern Canada. Journal of Paleontology, **68**: 541–556.

Chatterton, B.D.E., Edgecombe, G.D., Waisfeld, B.G., and Vaccari, N.E. 1998. Ontogeny and systematics of Toernquistiidae (Trilobita, Proetida) from the Ordovician of the Argentine Precordillera. Journal of Paleontology, **72**: 273–303.

Churkin, M., Jr. 1963. Ordovician trilobites from graptolitic shale in central Idaho. Journal of Paleontology, **37**: 421–428.

Clark, T.H. 1924. The paleontology of the Beekmantown Series at Lévis, Quebec. Bulletins of American Paleontology, 10, pp. 1–134.

Cooper, R.A., and Sadler, P.M. 2004. The Ordovician Period. *In* A Geologic Time Scale 2004. *Edited by* F.M. Gradstein, J.G. Ogg, and A.G. Smith. Cambridge University Press, Cambridge, UK., pp. 165–187.

Dean, W.T. 1971. The trilobites of the Chair of Kildare Limestone (upper Ordovician) of eastern Ireland. Part 1. Monographs of the Palaeontographical Society, 531, pp. 1–60.

Dean, W.T. 1974. The trilobites of the Chair of Kildare Limestone (upper Ordovician) of eastern Ireland. Part 2. Monographs of the Palaeontographical Society, 539, pp. 61–98.

Fortey, R.A., and Owens, R.M. 1975. Proetida — a new order of trilobites. Fossils and Strata, **4**: 227–239.

Hintze, L.F. 1951. Lower Ordovician detailed stratigraphic sections for western Utah. Utah Geological and Mineralogical Survey Bulletin, 39, pp. 1–99.

Hintze, L.F. 1953. Lower Ordovician trilobites from western Utah and eastern Nevada. Utah Geological and Mineralogical Survey Bulletin, 48, pp. 1–249. (for 1952)

Hintze, L.F. 1973. Lower and Middle Ordovician stratigraphic sections in the Ibex area, Millard County, Utah. Brigham Young University Geology Studies, **20**: 3–36.

Horný, R., and Bastl, F. 1970. Type specimens of fossils in the National Museum, Prague. Vol. 1. Trilobita. Museum of Natural History, Prague.

Huelsenbeck, J.P. 1994. Comparing the stratigraphic record to estimates of phylogeny. Paleobiology, **20**: 470–483.

Hupé, P. 1953. Classe des Trilobites. *In* Traité de Paléontologie. Tome 3. Les Formes Ultimes d'Invertébrés. Morphologie et Évolution. Onycophores. Arthropodes. Échinoderms. Stomocordés. *Edited by* J. Piveteau. Masson et Cie, Paris. pp. 44–246.

Imbrie, J. 1956. Biometrical methods in the study of invertebrate fossils. Bulletin of the American Museum of Natural History, **102**: 217–252.

Jaanusson, V. 1956. On the trilobite genus *Celmus* Angelin, 1854. Bulletin of the Geological Institution of Uppsala, **36**: 35–49.

Jell, P.A., and Adrain, J.M. 2003. Available generic names for trilobites. Memoirs of the Queensland Museum, **48**: 331–553.

Kielan, Z. 1960. Upper Ordovician trilobites from Poland and some related forms from Bohemia and Scandinavia. Palaeontologia Polonica, 11, pp. 1–198. (for 1959)

Mergl, M. 1984. Fauna of the Upper Tremadoc of central Bohemia. Sborník Geologických Věd. Paleontologie, **26**: 9–46.

Mergl, M. 1994. Trilobite fauna from the Trenice Formation (Tremadoc) in central Bohemia. Folia Musei Rerum Naturalium Bohemiae Occidentalis. Ser. Geologica, 3, pp. 1–31.

Öpik, A.A. 1937. Trilobiten aus Estland. Tartu Ülikooli Geoloogia-Intituudi Toimetused, 52, pp. 1–163.

Owens, R.M. 2004. Late Ordovician and Early Silurian Proetida (Trilobita) from north-western and central Europe. Palaeontology, **47**: 557–578.

Přibyl, A. 1950. Re-naming some homonymic names of Bohemian and foreign trilobite genera. Sborník Státního Geologického Ústavu Ceskoslovenské Republicky, **17**: 193–200. (In Czech with English summary.)

Qu, X. 1986. Latest Ordovician trilobites from northern Qilian Mountains. Acta Palaeontologica Sinica, **25:** 301–306. (in Chinese with English summary)

Raymond, P.E. 1905. The trilobites of the Chazy Limestone. Annals of the Carnegie Museum, **3**: 328–386.

Raymond, P.E. 1925. Some trilobites of the lower Middle Ordovician of eastern North America. Bulletin of the Museum of Comparative Zoology, Harvard University, 67, pp. 1–180.

Reed, F.R.C. 1896. The fauna of the Keisley Limestone. Part. I. Quarterly Journal of the Geological Society (of London), **52**: 407–437.

Ross, R.J., Jr. 1949. Stratigraphy and trilobite faunal zones of the Garden City Formation, northeastern Utah. American Journal of Science, **247**: 472–491.

Ross, R.J., Jr. 1951. Stratigraphy of the Garden City Formation in northeastern Utah, and its trilobite faunas. Peabody Museum of Natural History, Yale University, Bulletin, 6, pp. 1–161.

Ross, R.J., Jr., Hintze, L.F., Ethington, R.L., Miller, J.F., Taylor, M.E., and Repetski, J.E. 1997. The Ibexian, lowermost series in the North American Ordovician. United States Geological Survey, Professional Paper 1579, pp. 1–50.

Rozova, A.V., Rozov, S.N., and Dubatolova, Y.A. 1985. Stratigrafiya i fauna Ordovika Severo-Zapadnogo Salaira [Stratigraphy and fauna of the Ordovician of northwestern Salair]. Trudy Instituta Geologii i Geofiziki. Sibirskoe Otdelenie, Akademiya Nauk SSSR, 637, pp. 1–176. (In Russian with English abstract and table of contents.)

Růžíčka, R. 1926. Fauna vrstev Eulomovych rudniho loziska u Holoubkova (v Ouzkem). Cast I. Trilobiti. Rozpravy Ceské Akademie Ved a Umeni, tr. 2, 35, pp. 1–26.

Shaw, F.C. 2000. Trilobites of the Králův Dvůr Formation (Ordovician) of the Prague Basin, Czech Republic. Věstník Českého geologického ústavu, **74**: 371–404.

Terrell, F.M. 1973. Silicified trilobite zonation in the Lower Fillmore Formation in western Utah. Brigham Young University Geology Studies, **20**: 67–90.

Ulrich, E.O. 1930. Ordovician trilobites of the family Telephidae and concerned stratigraphic correlations. Proceedings of the United States National Museum, 76, pp. 1–101.

Vaněk, J. 1965. Die Trilobiten des mittelböhmischen Tremadoc. Senckenbergiana lethaea, **46**: 263–308.

Webby, B.D. 1974. Upper Ordovician trilobites from central New South Wales. Palaeontology, **17**: 203–252.

Whittington, H.B. 1963. Middle Ordovician trilobites from Lower Head, western Newfoundland. Bulletin of the Museum of Comparative Zoology, Harvard, 129, pp. 1–118.

Whittington, H.B., and Evitt, W.R. 1954. Silicified Middle Ordovician trilobites. Geological Society of America Memoir, 59, pp. 1–137.